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Phytoplankton distribution and grazing near coral reefs

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Abstract

Depletion of phytoplankton cells and pigments over coral reefs was studied in the Gulf of Aqaba, Red Sea, during 1994–1996. Phytoplankton abundance and chlorophyll (Chl) *a* concentrations were 15–65% lower near the reefs than in the adjacent open waters. The decrease in chlorophyll near the reef was typically associated with an increase in the concentration of its degradation products, the pheopigments. The steepest slope of these cross-shore gradients occurred within 1–3 m above bottom. More than 50% of the variation in the extent of the chlorophyll gradients, but not of pheopigments, could be explained by the advection of water during 2 h preceding the transect and by the concentration of Chl *a* in the open water. No cross-shore gradients were observed at a sandy-bottom site without reef. Eukaryotic phytoplankton (<5 μm) contributed >70% of the total depleted carbon near the reef during winter, while the cyanobacterium *Synechococcus* (1 μm) contributed the largest share in summer. The proportions of different taxa in depleted fractions were similar to those in ambient waters, indicating no size selectivity. Direct measurements of phytoplankton removal rates were made in water passing through a unique 5-m-long perforated reef, dominated by herbivorous soft corals. The waters downstream of that reef were strongly depleted of phytoplankton (10 to >36%, or 32 to >100 ng Chl *a* liter^{-1}). When converted to carbon fluxes, these rates greatly exceeded reported values of carbon input to coral reefs via zooplankton predation. Phytoplankton grazing is an important component of benthic–pelagic coupling in coral reefs.

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Benthic grazing on phytoplankton is a principal trophic pathway in shallow, temperate coastal habitats (Asmus and Asmus 1991; Koseff et al. 1993; Yamamuro and Koike 1994). In some bays and estuaries, phytoplankton density in the water column is controlled by benthic grazing (Cloern 1982; Fréchette and Bourget 1987; Cloern and Alpine 1991; Fréchette et al. 1989; Hily 1991). Dominant grazers in such situations appear to be bivalves, ascidians, and polychaetes (Monismith et al. 1990; Riisgård et al. 1996).

Traditionally, studies of benthic–pelagic coupling in tropical coral reefs, unlike those in shallow temperate habitats, have focused on zooplankton rather than phytoplankton as the principal source of prey (Tranter and George 1969; Glynn 1973; Johannes and Gerber 1974; Hamner et al. 1988; Erez 1990). Indeed, numerous coral-reef inhabitants, including the corals themselves, feed on zooplankton (Sebens 1997). The concept that phytoplankton is not a principal food source in coral reefs probably originated from an early comparison between zooplankton and phytoplankton removal rates in a Caribbean coral reef (Glynn 1973), which suggested that zooplankton are by far the most important source of heterotrophic carbon in this ecosystem. Recently, however, Ayukai (1995) observed a substantial retention of picophytoplankton at the Great Barrier Reef, Australia, and Fabricius et al. (1995*a,b*) discovered phytoplankton feeding by some common soft-coral species that had previously been considered exclusive zooplanktivores.

In fact, strong phytoplankton grazing is to be expected at the reef, as numerous members of the coral-reef community are known to feed on particles within the size range of phytoplankton. Such taxa include bivalves (Klumpp et al. 1992; Lesser et al. 1992), gastropods (Lesser et al. 1992), sponges (Reiswig 1971, 1974; Pile et al. 1996, 1997), ascidians (Petersen and Riisgård 1992), crinoids (Rutman and Fishelson 1969), foraminiferans (Cedhagen 1988), polychaetes (Vedel and Riisgård 1993), and soft corals (Fabricius et al. 1995*a,b*). Conceptual considerations also support expectations for intense phytoplanktivory at the reef, as phytoplankton biomass in coral reefs commonly exceeds that of zooplankton by an order of magnitude (Roman et al. 1990; R. Yahel pers. comm.). Furthermore, the bottom topography in coral reefs is typically rough, with numerous living and nonliving objects having a high "slenderness ratio" (height over width), which is an optimal morphology for feeding on small suspended particles (Abelson et al. 1993). Boring mussels (*Lithophaga* spp.), for example, growing in protruding corals, are less likely to experience refiltration of exhaled water than their counterparts in flat soft bottoms (O'Riordan et al. 1995). Direct evidence showing that the above taxa feed on phytoplankton in coral-reef communities are nevertheless scarce (Rutman and Fishelson 1969; Klumpp et al. 1992; Fabricius et al. 1995*a,b*; Pile 1997).

The goals of this study were to characterize the spatial and temporal patterns of phytoplankton distribution near fringing coral reefs and to quantify the rates of phytoplankton removal at a "perforated" reef, where the flow of water through the reef could be measured. Our study focused on small (<8 μm) phytoplankton, termed "ultraphytoplankton" (e.g. Lindell and Post 1995). The trophic contribution of ultraphytoplankton to the reef community, in terms of carbon influx from the ambient waters, is compared with fluxes reported for other heterotrophic pathways.

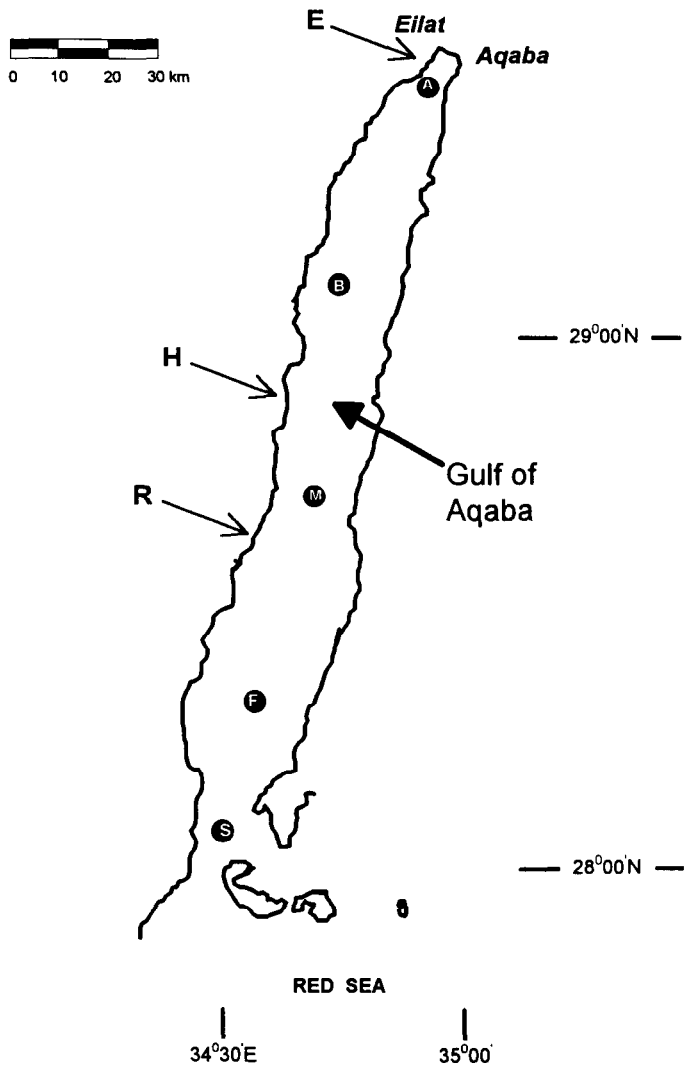

Fig. 1. The study sites in the Gulf of Aqaba (Eilat). Arrows on the left point out coastal sites (E, Eilat; H, Hibik; R, Ras Abu Galum); letters within full circles indicate the locations of the oceanographic stations near the center axis of the gulf (A, B, M, F, and S).

Materials and methods

Study sites—The study was carried out in the Gulf of Aqaba (Eilat), Red Sea, between February 1994 and May 1997. The cross-shore distribution of phytoplankton was studied at three sites with fringing reefs and a single control site with a sandy bottom without a reef. The three reef sites (Fig. 1) were at the Coral-Beach Nature Reserve in Eilat (29°30′N, 34°56′E), Ras Abu Galum (28°36′N, 34°33′E), and Hibik (28°52′N, 34°38′E). The sandy site was near Taba (29°28′N, 34°55′E), ~1.5 km south of the nature reserve in Eilat. Measurements of phytoplankton grazing rates were carried out at an artificial reef (hereafter "perforated reef") located at

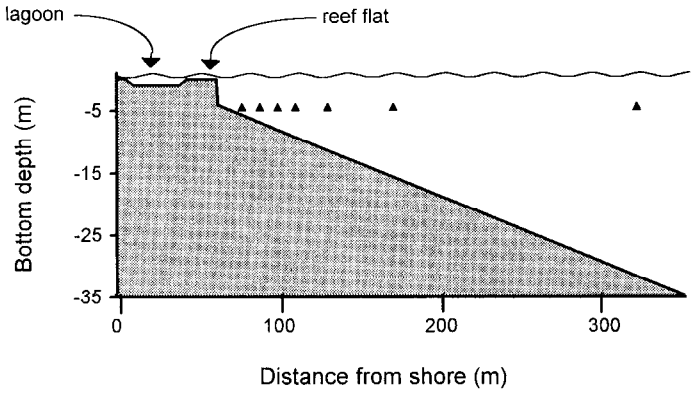

Fig. 2. A schematic plot of the cross-shore topography (dark area) and the sampling points (▲) across the reef in Eilat. Note that the sampling points were all at 5-m depth.

the southern jetty of the Oil Terminal in Eilat, ~1 km north of the nature reserve.

The fringing coral reefs at the three sites were similar with regard to their topography and community structure. They all had a wide (30–50 m) shallow (1–2-m depth) lagoon, located shoreward of a 10–30-m-wide reef flat. The flat ended at its seaward edge at a steep vertical wall (2–5 m in height), seaward from which a rich gradually sloping fore-reef was found, extending some hundreds of meters seaward of the flat (Fig. 2). Our sampling work was carried out over the slope and extended seaward into deeper waters (30 m). The reef community was described by Fishelson (1970) and Benyahu and Loya (1977, and references therein). In short, these reefs were dominated by hermatypic corals, many of them bearing numerous herbivorous endolithic filter-feeders (Hutchings 1983; Loya 1981). Other common taxa included hydrozoan corals (*Millepora dichotoma*), soft corals, anemones, sponges, tunicates, and polychaetes. Soft corals were rare at the fringing reefs.

The perforated reef at the Oil Terminal has grown on the jetty's pilings and their surrounding barbed wire, constructed some 25 years ago. The local community was described by Goren and Benayahu (1992). The section studied (6–15-m depth) was dominated by the herbivorous soft corals *Dendronephthya hemprichi* and *Scleronephthya corymbosa*. A gradual shift of dominance, from *D. hemprichi* to *S. corymbosa*, took place during the course of our study. Other common invertebrates at this reef included a gorgonian coral (*Acabaria* sp.), sponges, ascidians, stony corals, and actinians. Clearly, both the topography and community structure at the perforated reef were different from those at the above-reef slopes. Nevertheless, there are numerous reefs in the Red Sea (and elsewhere) where dominant *Dendronephthya* colonies form similar structures on steeply sloping walls and overhangs (Benayahu 1985). The water in the perforated reef flowed through the benthic community rather than above it (as in the case of the fringing reef). This flow pattern allowed direct measurements of water passage times, which were required to estimate rates of phytoplankton grazing by the benthic community (*see below*).

The slope at the sandy sites was similar to that of the reef slope, except that it had no reef and the bottom was partly covered with sea-grasses (mainly *Halophila stipulacea*). A few coral-bearing boulders were found at the sandy site, but the total abundance of corals and their associated benthic community was several orders of magnitude lower than at the reef slope.

Oceanographic and meteorological conditions in the Gulf of Aqaba were described by Reiss and Hottinger (1984) and Genin et al. (1994, 1995). The currents at our study sites were weak to moderate (<20 cm s^{-1}) and primarily long-shore. Semidiurnal reversals of flow direction occurred during summer–fall, while fluctuations of lower frequencies dominated in winter–spring (Genin et al. 1994; Genin et al. unpubl. data). The cross-shore components, although being much weaker (<10%) than the long-shore components, commonly formed a well-defined coastal circulation consisting of a weak onshore flow in the upper 10–20 m, slow downwelling near the coast, and a return, offshore flow above bottom (Genin et al. unpubl. data). Sea conditions at all sites were relatively calm (wave height $\ll$1 m), except for rare southerly winter storms.

Cross-shore transects—Intense benthic grazing on phytoplankton is expected to produce a prey-depleted layer above the bottom (Cloern 1982; Fréchette et al. 1989), possibly forming a gradient of decreasing phytoplankton concentrations from the open waters toward the reef. If strong grazing is unique to the coral-reef community, such cross-shore gradients are expected to be more pronounced at the reef than at the sandy sites. To test these expectations, water samples were taken at seven points along a cross-shore transect (Fig. 2), starting at a 5-m bottom depth and extending seaward to a bottom depth of 30 m (hereafter "open water"). The sampled water was filtered through a 100-μm mesh to remove large zooplankton and stored in a darkened ice box until processing in the laboratory. All samples were taken at the same depth (5 m); thus, the shorewardmost sample was taken a few centimeters above the bottom, while the seawardmost sample was taken 25 m above bottom (mab), with intermediate samples taken at 1, 2, 3, 5, and 10 mab. Transect lengths varied between 150 to 250 m, depending on the topographic slope. Two such transects, 500–800 m apart (hereafter north and south transects), were sampled at each study site during each visit. Except for a single visit (*see below*), all 57 transects were carried out during the day (Table 1).

The study sites in Eilat were visited 10 times, while the more remote sites along the Gulf of Aqaba were visited once, during a cruise aboard the RV *University I* in August 1996. In order to examine diurnal changes in cross-shore patterns, nocturnal transects preceded the daytime transects at the two reef sites in Eilat in February 1996, while changes between consecutive days were examined through a replication of the complete sampling protocol for 4 and 3 consecutive days in February and June 1994, respectively (Table 1).

Lagrangian sampling—This part of the work was based on consecutive sampling of the same water parcel as it moved above, or through, the reef. Two modes of Lagrangian sampling were used: (1) repetitive sampling of a water

Table 1. Dates and times (hour of day) of the cross-shore transects carried out at the Eilat sites. Two transects >500 m apart were used at each site, one at the northern (N) and the other at the southern (S) section of the reef.

Visit No.	Month	Day	Coral reef		Sandy bottom	
			N	S	N	S
1	Feb 94	2		1200		
		3		1000		
		4		1230		
		6		1000		
		7			1400	
		8			1430	
		9				1000
2	Jun 94	13	1215	1515	1100	1431
		14	1015, 1500	0930, 1515	1200	1120
		15	0940	0900	1140	1100
3	Aug 94	28	0950	1030	1200	1125
4	Dec 94	23	0930	0845	1030	1005
5	Feb 95	18	0815, 1045	0845, 1110	0900	0945
6	Jun 95	23	1525	1610	1345	1430
7	Aug 95	11	1130	1215	1435	1335
8	Dec 95	9	0940, 1030	0850, 1130		
9	Feb 96	16	0540, 0930	0400, 0840		
10	Aug 96	1	1115	1215		
		4				
		6				

Note: Transects were also carried out at Ras Abu Galum on 4 August 1996 (1120 and 1235 h at N and S sections of the reef, respectively) and at Hibik on 6 August 1996 (1215 and 1350 h at N and S sections of the reef).

parcel marked with a drifter drogue as it moved above the reef slope (hereafter "the drogue experiment"), and (2) sampling a water parcel prior to (upstream) and after (downstream) it passed through the perforated reef at the Oil Terminal (hereafter "the perforated-reef experiment"). The goal of the drogue experiment was to test for phytoplankton depletion by grazers dwelling in the water column (e.g. herbivorous zooplankton). The goal of the perforated-reef experiment was to quantify the rates of phytoplankton grazing by the benthic community at that reef.

The drogue experiment was carried out at two sites: Ras Abu Galum and Hibik. A drifter (Davis et al. 1982) was drogued at 5-m depth above a bottom of 6–8-m depth and monitored from a nearby skiff for 30–90 min. Water samples were taken next to the drogue by divers every 5 min.

The perforated-reef experiment protocol was as follows. Prior to sampling, fluorescein dye was released upstream of the reef and the time it took the dyed water to pass through the reef was measured (passage time). Due to mixing and consequent dispersal of the dye during its passage through the reef, the visual estimate of passage time was based on the bulk of the dyed blob, and should therefore be considered an approximate measure. Sampling started 15 min after the fluorescein dye cleared the reef and lasted 30–40 min afterwards. Each sampling set consisted of 8–11 pairs. Within each pair the downstream sample was taken after the upstream sample, delayed by the predetermined passage time. Grazing rates by the perforated-reef community were calculated for each pair as the difference in phytoplankton abundance between the upstream and downstream samples divided by the relevant passage time.

Sample processing—Concentrations of chlorophyll *a* and pheopigments were measured with a fluorometer (Model AU-10, Turner Designs) by using the acidification method (Parsons et al. 1985) after filtering 280 ml of seawater on a Whatman GF/F filter followed by 24 h dark extraction in 90% acetone at 4°C. To allow direct comparisons between the molecular concentrations of the parent chlorophyll and its degradation products, pheopigment concentrations are reported using chlorophyll equivalent units as in Head and Horne (1993). Starting in February 1996, Chl *a* was measured both as indicated above and by the nonacidification method (Welschmeyer 1994) using a Turner Designs TD-700 fluorometer. A reliability test of our chlorophyll measurements indicated a precision of ±5.1% (n = 90) within replicates.

Flow cytometry was used to process a subset of the above samples in order to estimate the concentrations of two dominant autotrophic groups in our waters, *Synechococcus* and pico-eukaryotes. *Prochlorococcus,* the third major autotrophic group in the Red Sea (Lindell and Post 1995), has a very weak chlorophyll fluorescence near the surface, especially in summer. It could not be detected during most of this study with the flow cytometers used, except in February 1996 (*see below*). Taxonomic discrimination was made on the basis of cell-side scatter and forward scatter (a proxy of cell size), orange fluorescence of phycoerythrin, and red fluorescence of chlorophyll (Partensky et al. 1996). Aliquots of 1.5 ml were withdrawn from the same water samples used for pigment analysis and preserved with 0.2% buffered paraformaldehyde (June 1995, February 1996) or with 1% paraformaldehyde and 0.05% glutaraldehyde (August 1996). Samples were frozen in liquid nitrogen and stored at −70°C until processing. Samples of the cross-shore transects and the perforated reef experiment from June 1995 were analyzed on a Coulter EPICS XL flow cytometer equipped with a 488-nm argon laser. Data processing was performed using the EPICS XL workstation (vers. 1.5, 1993, Coulter). The cross-shore transect samples from February and August 1996 were analyzed with a FACSort (Becton-Dickinson) using the standard setup. All cellular parameters were normalized to the values measured for 0.95-μm YG Polysciences beads. Data processing was performed using the Windows software CYTOWIN (Vaulot 1989). Cell numbers were converted to carbon following Campbell et al. (1994).

Size and biomass of phytoplankton in the open waters—Pigment measurements based on water filtered on GF/F filters included a large range of cell sizes (up to 100 μm). The flow cytometer measurements, on the other hand, were confined to ultraphytoplankton cells, i.e. smaller than 8 and 5 μm for the 1995 and 1996 samples, respectively. To evaluate the relative contribution of ultraphytoplankton to total extracted Chl *a,* we used data collected in the Gulf of Aqaba during five oceanographic cruises that partly overlapped the period of our field sampling near the coast (June 1994–August 1995). A total of 24 water samples were collected at 0–20-m depths at five oceanographic stations along the Gulf

of Aqaba (Fig. 1). Each sample (500 ml) was passed through a 100-μm mesh to remove large zooplankton and then split into two equal (250 ml) aliquots. One aliquot was filtered directly on a GF/F filter, while the other was prefiltered through a 8-μm nylon mesh to remove larger cells and then filtered on a GF/F filter.

Abundance of benthic suspension feeders at the reef—The coral-reef community at our study sites in Eilat was surveyed in order to estimate the densities of the main suspension feeders that are either known to feed on phytoplankton or belong to taxonomic groups that include species that feed on phytoplankton in other habitats. The taxa recorded included sponges, bivalves, ascidians, and tunicates but did not include bryozoans and polychaetes. Three benthic transects, one at each of the 4-, 5-, and 6-m isobaths, were made near each of the 0 mab points of the above-described north and south cross-shore transects. Each benthic transect consisted of 11 0.5 × 0.5-m quadrats, positioned 0.5 m apart by scuba divers. A total of 65 quadrats were surveyed. Visual counts of the above taxa were made in each quadrat.

Current measurements—Because currents can affect both the feeding rate of suspension-feeders (Lenihan et al. 1996) and the mixing of depleted and affluent layers, 36 of the 38 cross-shore transects were complemented with current measurements. An electromagnetic current meter (model S4, InterOcean) was deployed on the slope in the vicinity of the transects (<500 m distant). The current meter was attached on a mooring line usually at 12-m depth, except from February and June 1994 visits where the instrument depth was 5 m. The current meter was set to record a 1-min average vector every 10 min for a duration of at least 2 h (but usually several days) prior to sampling. The recorded data were used to calculate the average advection vector for the 1, 2, 4, and 6 h preceding the sampling time of each cross-shore transect. These vectors, together with the magnitude of their cross- and long-shore components, their scalar values, as well as the instantaneous current speed during the transect sampling, were examined for possible correspondence with the strength of the respective cross-shore chlorophyll and pheopigment gradients (*see below*).

Statistical analysis—The significance levels of cross-shore trends were tested using the "Page test" for ordered alternatives (Siegel and Castellan 1988). This nonparametric test is a modified version of the Kruskal–Wallis one-way ANOVA of ranked data. Hence, H_1 for chlorophyll was an occurrence of a gradient of decreasing concentrations from the open water (25 mab) toward the reef (0 mab), whereas H_1 for pheopigment was the occurrence of an opposite gradient.

A multiple linear regression analysis was used to examine the relationships between the various flow parameters (*see above*) and the strength of the cross-shore gradient. This strength was operationally defined as the difference, in percent, between the pigment concentration at the reef (0 mab) and that in the open waters (25 mab). A complete residuals analysis was performed to validate the robustness of the resulting model.

A comparison of the square-root-transformed Chl : pheopigment ratio at the different sampling sites in Eilat was done using a repeated-measures ANOVA. The open-water (25 mab) and shorewardmost (0 mab) values within a transect were considered repeated measures and their statistical effect was crossed with the site effect (coral reef vs. sand site). Because the interaction between site and transects was highly significant (*see results*), a Scheffé post hoc test was used to examine the difference between the reef and the sandy site and between the 0 and 25 mab points within each of the two sites. Homogeneity of variance and normality were verified by Cochran and Kolmogorov–Smirnov tests, respectively.

The occurrence of significant phytoplankton depletion in waters passing through the perforated reef was tested by the Wilcoxon signed-ranks test on pairs of upstream and downstream samples. The overall difference was tested using the mean of the normalized t statistics of the Wilcoxon test (W_{s_t} of Fréchette and Bourget 1985).

Except for the manual calculations of the Page test, statistical analyses were done using STATISTICA for Windows (vers. 5.0, 1995, StatSoft).

Results

Cross-shore patterns—A significant gradient ($P < 0.01$, Page test) of decreasing Chl *a* concentrations from the open waters to the reef was observed during 6 of the 10 visits to the study sites in Eilat, while an opposite gradient, consisting of a reef-ward increase in pheopigment concentrations, was observed during seven visits (Table 2). Opposite gradients (increasing chlorophyll or decreasing pheopigment toward the reef) were not observed. The gradients of chlorophyll and pheopigment at Hibik and Ras Abu Galum were similar to those in the reef of Eilat, but the chlorophyll gradient at the former site was not significant (Fig. 3). The steepest sections of the gradients usually occurred within 10 m from the fore-reef, 1–3 mab. Chl *a* concentrations in this depleted layer were 10–69% (21–115 ng liter^{-1}) lower than those in the offshore waters (25 mab). An average cross-shore transect (Fig. 4), based on all 38 reef transects, exhibited a clear 18.6% (SE 3.1%) decrease in Chl *a* and 73.1% increase (SE 17.0%) in pheopigments from the open water toward the reef. A decrease in the ratio of Chl *a* to pheopigment from the open water toward the reef was observed in all but a single visit (December 1994), with values near the reef being 2–4 times higher than in the offshore region (Table 3).

The repetitive sampling in February 1996 revealed no diel changes in cross-shore patterns of chlorophyll (Fig. 5A), while the daily replications in February and June 1994 exhibited a persistence of the cross-shore patterns over periods of 3–5 d (Fig. 5B,C).

No cross-shore gradients were observed in summers 1994 and 1995, when the ambient concentrations of Chl *a* were low (although a gradient was observed in similar conditions during summer 1996; cf. Figs. 3 and 5C) and in December 1994. The occurrence of significant gradients of chlorophyll did not correspond with the occurrence of significant pheopigment gradients (Table 2). Of all the flow parameters ex-

Table 2. Average (SD) concentrations of chlorophyll *a*, chlorophyll : pheopigment (Chl : Pheo.) ratios, and percentage difference of the concentration of pigments between the open water and the coast at the coral reef and the sand site in Eilat. "Open water" and "coast" indicate the distantmost (25 mab) and the shorewardmost (0 mab) sampling points in each cross-shore transect, respectively. Concentration difference is calculated by subtracting coast values from those in the open water. *P* values are for the Page test (testing for the occurrence of a cross-shore gradient), where H_1 was a shoreward decrease for chlorophyll and an increase for those in the pheopigment. For the sand site, nonsignificant *P* values were also observed for the opposite H_1 (a shoreward increase of chlorophyll) (*N*, number of transects; ns, no significant gradient; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$).

			Chl *a* (μg liter^{-1})		Chl : Pheo. ratio		Chl difference		Pheo. difference	
Site	Month	*n*	Open water	Coast	Open water	Coast	%	*P*	%	*P*
Reef	Feb 94	4	0.212(0.017)	0.165(0.040)	1.90(0.20)	1.42(0.36)	−27(19)	***	8(15)	*
	Jun 94	8	0.148(0.019)	0.147(0.021)	3.24(0.79)	2.06(0.60)	−1(6)	ns	70(76)	***
	Aug 94	2	0.125(0.003)	0.123(0.006)	3.66(0.04)	1.36(0.25)	−2(7)	ns	71(67)	**
	Dec 94	2	0.522(0.019)	0.508(0.000)	2.38(0.29)	2.50(0.65)	−3(4)	ns	−3(33)	ns
	Feb 95	4	0.284(0.017)	0.231(0.032)	1.63(0.28)	1.23(0.27)	−19(12)	***	10(26)	ns
	Jun 95	2	0.208(0.011)	0.134(0.021)	5.38(1.31)	1.04(0.33)	−36(14)	***	235(47)	***
	Aug 95	2	0.087(0.006)	0.092(0.012)	4.34(0.90)	1.68(0.09)	5(7)	ns	170(59)	*
	Dec 95	4	0.295(0.010)	0.199(0.019)	1.99(0.36)	1.21(0.24)	−32(7)	***	14(21)	**
	Feb 96	4	0.206(0.011)	0.171(0.062)	2.77(0.38)	1.84(0.45)	−22(7)	**	7(66)	ns
	Aug 96	2	0.161(0.026)	0.099(0.003)	4.88(1.36)	1.34(0.44)	−47(24)	***	147(147)	**
Sand	Feb 94	3	0.189(0.000)	0.216(0.090)	2.14(0.00)	1.97(0.09)	1(18)	ns	25(28)	ns
	Jun 94	6	0.124(0.036)	0.137(0.045)	3.33(0.42)	3.08(0.35)	10(10)	ns	20(17)	ns
	Aug 94	2	0.170(0.048)	0.227(0.039)	3.86(0.75)	3.51(1.65)	43(63)	ns	57(26)	ns
	Dec 94	2	0.502(0.009)	0.495(0.000)	2.49(0.03)	2.38(0.12)	−1(2)	ns	3(6)	ns
	Feb 95	2	0.293(0.002)	0.334(0.057)	1.78(0.06)	2.08(0.24)	14(19)	ns	−3(1)	ns
	Jun 95	2	0.178(0.000)	0.178(0.000)	3.35(0.00)	3.71(1.63)	0(0)	ns	31(0)	ns
	Aug 95	2	0.058(0.003)	0.082(0.008)	3.49(2.19)	3.87(0.05)	43(21)	ns	22(60)	ns

amined (*see methods*), the net advection of water during the 2 h preceding the transect had the highest (negative) correlation value with the strength of the cross-shore gradients of Chl *a*, but not with the strength of pheopigment gradients ($r_p = -0.456$, $P < 0.05$ for chlorophyll and $r_p = 0.269$, $P > 0.15$ for pheopigment). Temporal variations in the strength of the cross-shore chlorophyll gradients at the reef could be best explained by the above advection term and the concentration of Chl *a* in the ambient (offshore) waters (through multiple linear regression) as follows: Chlorophyll depletion (%) = $0.239 - 2.412A + 0.972C$ (multiple-adjusted $R^2 = 0.502$, $F_{2,28} = 16.106$, $P < 0.0001$) where *A* is the advection distance (m) during the 2 h preceding the transect sampling and *C* is the chlorophyll concentration (μg liter^{-1}) at the 25 mab sampling point of the transect.

No cross-shore gradients were observed at the sandy site ($P > 0.1$, Page test, $n = 19$), where the concentrations of both Chl *a* and pheopigment near the shore were either similar or higher than those found in the open water (Table 2, Fig. 4). Marginally significant higher concentrations of chlorophyll were found at the nearshore sampling points compared with the open water (Fig. 4). The Chl : pheopigment ratios at 0 mab at the sandy site were similar to those found at 25 mab, or 2–4 times higher than the values found at the coral reef on the same sampling dates (Table 3, Fig. 6).

More than 80% of the total Chl *a* measured with GF/F filters in the upper waters (0–20-m depth) in the Gulf of Aqaba was contributed by ultraphytoplankton (cell size <8 μm; Table 4). Direct cell counts with a flow cytometer showed that the observed cross-shore gradients in chlorophyll reflected a decrease in both *Synechococcus* and eukaryotes (Fig. 7). Numerically, *Synechococcus* constituted 77–94% of the removed phytoplankton cells. In winter, however, eukaryotes contributed >71% to the carbon depletion near the reef while in summer their share was <36%. *Prochlorococcus* was present but could not be enumerated with confidence in all but a single transect, where its decreasing trend was similar to that of the other two groups of ultraphytoplankton (data not shown).

Water parcels—Chl *a* and pheopigment concentrations remained unchanged along the 25–70 min (800–50 m) tracks of the five drifter drogues released in this study, including situations with weak (<1.5 cm s^{-1}) and strong (>20 cm s^{-1}) currents. Pigments concentrations were similar to those found at 1–3 mab in corresponding cross-shore transects.

Conversely, water parcels passing through the perforated reef were significantly depleted of Chl *a* (Wilcoxon sign ranks test, $P < 0.01$), with a mean removal efficiency of 21.5% (SE 3.0%), equivalent to a mean removal of 61 (SE 9) ng Chl *a* per liter of water passing through the 5-m-long section of the reef (Table 5). Considering a cross section of 1 m^2 (5 m^3) and a passage time of 40–80 s, the removal rates ranged from 2.29 to 8.67 μg Chl *a* s^{-1}. Surprisingly, the concentrations of pheopigment did not significantly change during the passage through the perforated reef (Table 5).

Counts of *Synechococcus* and eukaryotes in 10 pairs of samples taken in June 1995 indicated that the removal of these two groups was nonselective and well represented by values of Chl *a* removal (Table 6; Spearman rank correlation between removal of ultraphytoplankton and chlorophyll, $r_s = 0.833$, $n = 8$).

The most abundant suspension-feeders in the coral reef of

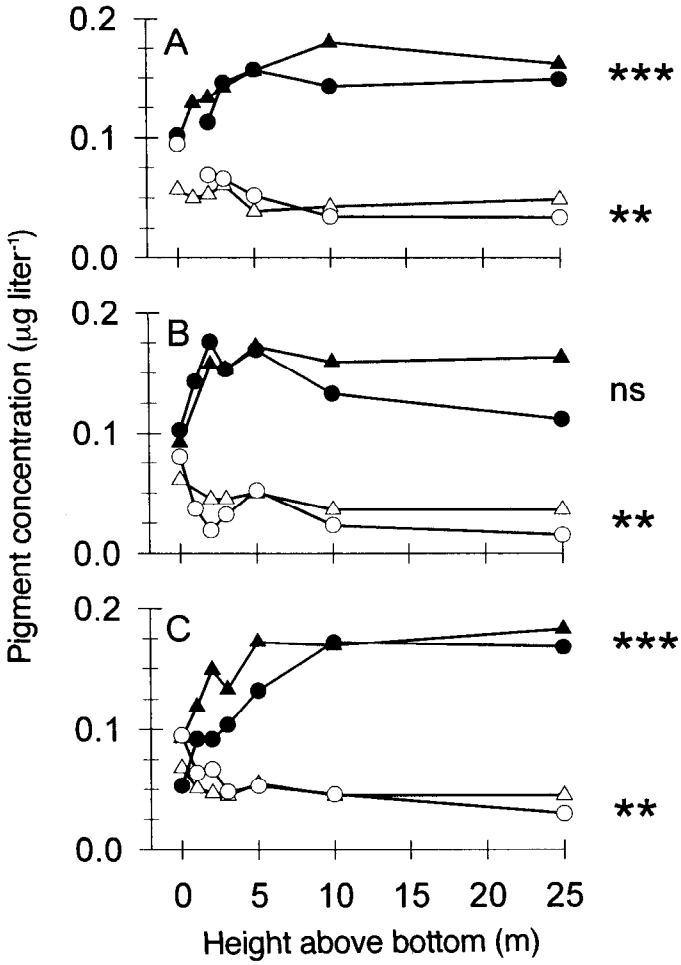

Fig. 3. The cross-shore profiles of chlorophyll *a* (solid symbols) and pheopigments (open symbols) in August 1996 measured in transects across the coral reefs of Eilat (A), Hibik (B), and Ras Abu Galum (C). Triangles are used for northern transects, circles for the southern transect at each site (ns, nonsignificant; **, $P \leq 0.01$; ***, $P \leq 0.001$).

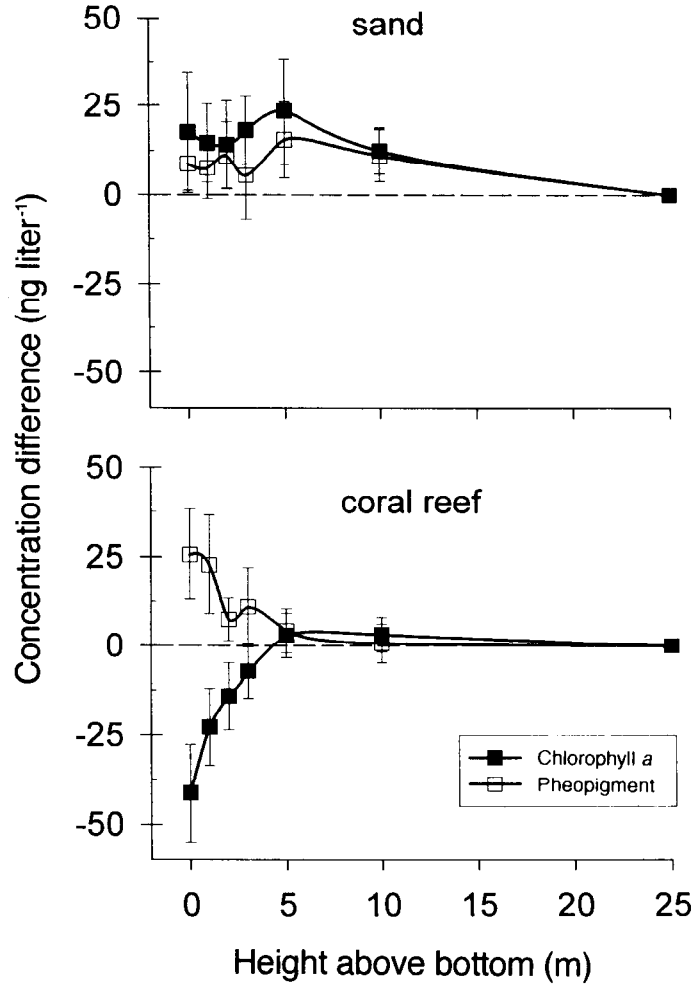

Fig. 4. The average difference in pigment concentration between each sampling point and the open water (25 mab) at the same transect, calculated for all the transects carried out at the sand site (upper panel, $n = 19$) and at three coral reefs (lower panel, $n = 38$). Solid symbols indicate chlorophyll *a*; open symbols indicate pheopigment; error bars indicate 95% confidence interval.

Eilat were the coral-boring mussels (*Lithophaga* spp.), sponges (including members of the genera *Mycale* and *Cliona*), benthic tunicates, and ascidians (Table 7). Octocorals were rare, and none was included in our quadrats. The densities of each of the 15 taxa surveyed did not differ significantly between the north and south sections of the reef in Eilat (Mann–Whitney *U*-test, $n = 32, 33$, $P > 0.1$).

Discussion

Phytoplankton was effectively removed by the benthic community at the coral reefs. A phytoplankton-depleted layer, ~3 m in thickness, was commonly found above the reef slope. At the perforated reef (an arborescent community), ~20% of the phytoplankton was removed during the ~1-min passage of water through a 5-m-long section of the reef. In terms of biomass, the phytoplankton deficiency and removal reported in this study refers mostly to small cells (<8 μm).

Table 3. The average (SE) contribution (%) of pheopigment to the total pigments (Chl *a* + pheopigment) measured at the open-water and the shorewardmost (coast) points (25 and 0 mab, respectively) for all cross-shore transects made during our study. ANOVA of the square root-transformed pheopigment to chlorophyll ratios showed a highly significant interaction between the two study sites and within the two extreme sampling points of each transect ($F_{1,48} = 12.43$, $P < 0.0001$). *P* values are for a Scheffé post hoc test, which measured the difference between the open water and shoreward samples (in the rows) and between the coral reef and the sandy site (in the columns) (ns, nonsignificant; ***, $P < 0.001$).

	n	Open water, % (SE)	Coast, % (SE)	*P*
Coral reef	34	26.3(1.3)	40.7(1.4)	***
Sand bottom	16	26.1(1.3)	26.7(1.3)	ns
P		ns	***	

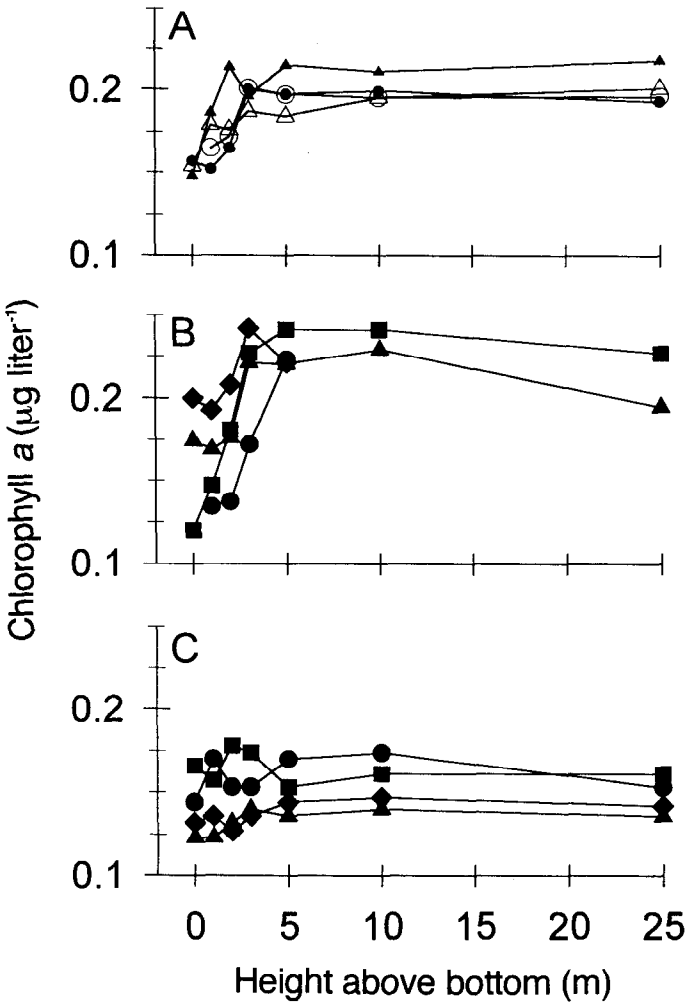

Fig. 5. Short-term variations in the cross-shore distribution of chlorophyll *a* along the coral reef of Eilat. A. Comparison between a nocturnal (filled symbols) and diurnal (open symbols) transects in February 1996. Triangles are used for the northern transects, circles for the southern transect. B. Replications performed daily during 4 consecutive days at the southern transect in February 1994. C. Replications performed daily during 3 consecutive days at the southern transect in June 1994.

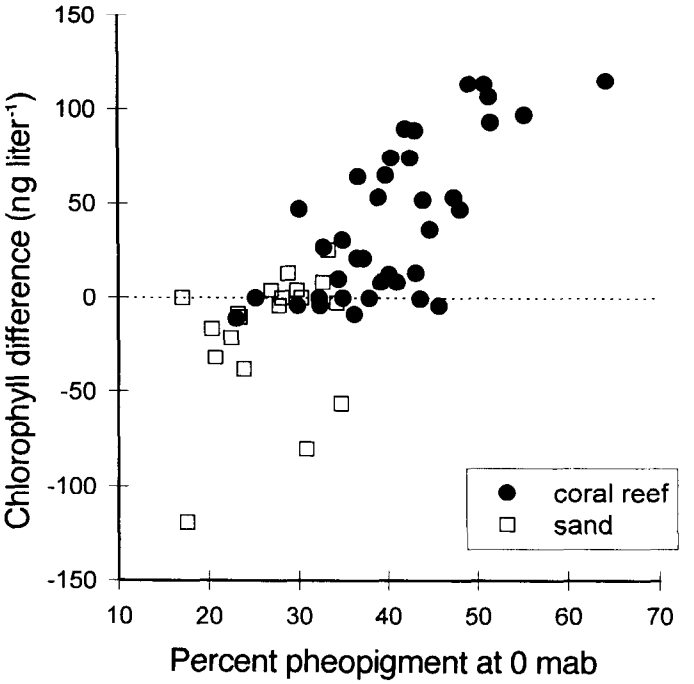

Fig. 6. Differences in the concentration of chlorophyll *a* between the open water (25 mab) and the shorewardmost (0 mab) points vs. percentage of pheopigment at the 0 mab point for all cross-shore transects. The percentage of pheopigment was the concentration of pheopigment divided by the total measured pigments (Chl *a* + pheopigment).

The role of benthic grazing in the observed phytoplankton removal was obvious at the perforated reef. Because this reef was inhabited by massive colonies of soft corals reported as phytoplankton grazers (Fabricius et al. 1995*a,b*, 1998), high rates of phytoplankton removal were expected. However, the occurrence of a well-defined depleted layer over the fringing reef slopes was surprising, as soft corals at those reefs were rare and the local communities were dominated by hermatypic corals, which are not known to be phytoplanktivorous. The confinement of the depleted layer to the nearest 1–3 m above bottom, together with the lack of grazing at the sandy site, indicates that the key grazers responsible for the observed depletion were inherent members of the benthic-reef community. The reason for the slight increase of phytoplankton concentration near the sand bottom is not yet known.

Bottom-associated, yet water-borne grazers (e.g. demersal zooplankton), some of which are phytoplanktivores (Roman et al. 1990), could also contribute to phytoplankton depletion near the reef. However, their contribution was expected to be most conspicuous during night, when the waters overlying coral reefs are replete with demersal plankton (Alldredge and King 1977, 1985; R. Yahel unpubl. obs.). The lack of diel changes in chlorophyll gradients across the reef (Fig. 5A) suggested an insignificant contribution of the grazing by demersal plankton. This conclusion is further corroborated (for daytime) by the absence of phytoplankton depletion in the drogue experiments—the drogue was suspended 1–3 mab so that the water sampled along its path had not been

Table 4. The average (SD) concentration of chlorophyll *a* retained on GF/F filters and the contribution (%) of ultraphytoplankton to those chlorophyll values in seawater collected at 0–20-m depth at the five oceanographic stations in the Gulf of Aqaba (*see Fig. 1*). Ultraphytoplankton is defined as cells passing through a 8-μm mesh (*n*, number of replications).

Cruise date	Station	*n*	Chlorophyll (μg liter⁻¹)	Ultraphytoplankton, % (SD)
Jun 94	A, B, M, F	7	0.131(0.067)	87.2(27.6)
Mar 95	A	2	0.870(0.052)	83.3(4.7)
May 95	A, B, M	6	0.069(0.036)	91.1(22.9)
Jun 95	A, B, M, F, S	7	0.046(0.015)	85.4(9.1)
Aug 95	A	2	0.055(0.007)	81.7(2.4)
Total		24	0.160(0.239)	86.9(18.5)

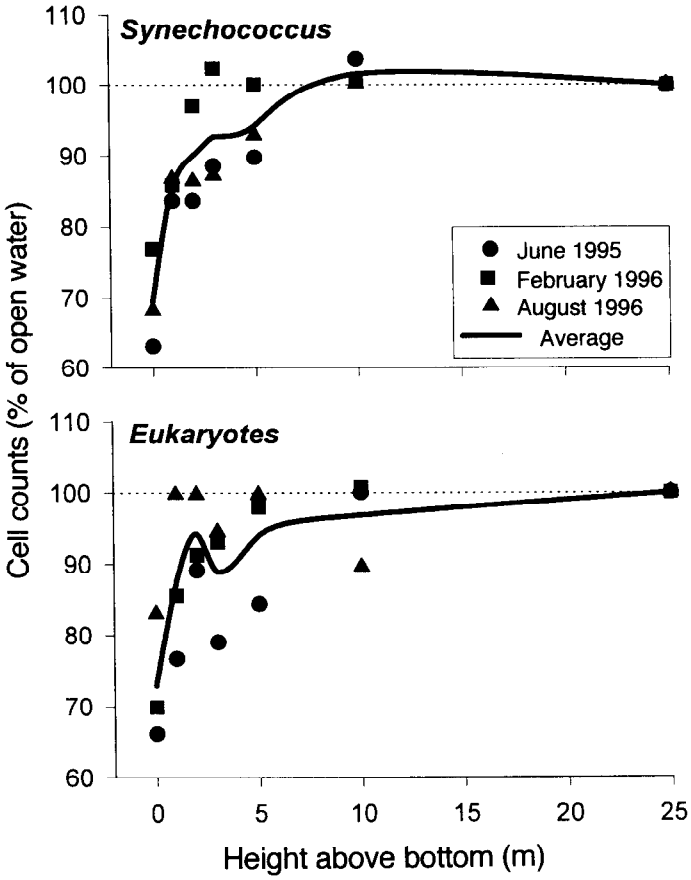

Fig. 7. Cross-shore distribution of ultraphytoplankton based on cell counts in the coral reef of Eilat from three different seasons. Owing to substantial seasonal differences in the absolute densities of these taxa, the data are presented as a percentage relative to the density in an open-water (25 mab) sample in a transect. Absolute densities ranged from 800 to 8,000 cells ml^{-1} for eukaryotic phytoplankton and 8,000 to 30,000 cells ml^{-1} for *Synechococcus*. Each point represents a seasonal average from both northern and southern transects. Full lines indicate averages over all seasons.

in contact with the benthos, except via turbulent mixing (Shashar et al. 1996).

The taxa responsible for the depletion of phytoplankton at the reef were most likely the coral-boring *Lithophaga* spp., sponges, and ascidians. We are currently studying in situ feeding by individual specimens, and find efficient (>60%) grazing rates on eukaryotic phytoplankton, *Prochlorococcus,* and *Synechococcus* by the bivalves *Lithophaga simplex, Lithophaga purpurea,* the sponges *Cliona mussae, Mycale fistulifera, Subarites clavtus,* and the ascidians *Halocynthia gangelion* and *Didemnum candidum* (G. Yahel unpubl. data). Meroz and Ilan (1995) reported densities of the sponge *M. fistulifera* near our site in Eilat similar to those observed in our survey (Table 7). Although the densities reported in Table 7 are high, for some infauna species those values should be regarded as gross underestimates. The cryptic nature of many suspension-feeders, some of which are dwelling within corals and rocks, precluded accurate visual counts of all the specimens present in a quadrat (Hutchings 1983). For example, in the case of the boring mussel *Lithophaga lessepsiana* in branches of the coral *Stylophora pistillata,* visual counts made as above were ~10 times lower than complete counts made after the corals were brought to the laboratory, broken apart, and fully inspected (G. Yahel pers. obs.). Because the information on densities of suspension feeders was not a principal objective of this study, we chose to avoid damaging corals during our survey.

Whereas phytoplankton removal was observed at the perforated reef during all visits, a cross-shore chlorophyll gradient at the slope reef was observed in most, but not all, transects. The variations in the cross-shore gradients can best be explained by the linear regression model (*see results*), suggesting significant contributions by both biology (positive correlation with the ambient concentration of chlorophyll) and physics (negative correlation with water advection). The biological term was related to the fact that three of the four visits with no chlorophyll gradients occurred in summer (Table 2), a season characterized by low Chl *a* concentrations (Genin et al. 1995) and a dominance of small prokaryotic taxa (Lindell and Post 1995). Thus, this parameter in the above model may, in fact, reflect some seasonality, either in phytoplankton, their grazers, or even in some

Table 5. Average (SE) changes in the concentrations of chlorophyll *a* and pheopigments after passing through a 5-m-long section of the perforated reef. Passage time is a bulk measure of the flow speed through that section. Negative and positive values indicate a decrease and increase in the pigment concentrations, respectively. *P* values are for a pairwise Wilcoxon sign rank test of the difference in pigments concentrations between the upstream and downstream samples (ns, no significant difference; *, $P < 0.05$; **, $P < 0.01$; *n*, number of sample pairs).

			Change in Chl *a*			Change in pheopigments		
	Passage time (s)	*n*	%	Absolute (ng $liter^{-1}$)	*P*	%	Absolute (ng $liter^{-1}$)	*P*
Dec 94	60	9	−10.1(8.8)	−65(47)	ns	7.7(14.1)	2(18)	ns
Feb 95	60	11	−15.5(5.0)	−79(26)	**	−5.0(3.3)	−12(7)	ns
Jun 95	80	8	−23.1(7.7)	−48(17)	**	35.9(21.4)	28(18)	ns
Aug 95	70	8	−23.4(16.4)	−32(12)	*	7(7.3)	2(2)	ns
Dec 95	40	11	−21.9(8.1)	−37(13)	**	−20.4(5.0)	−68(17)	*
Nov 96	60	9	−36.3(2.2)	−104(8)	**	−1.3(1.9)	−2(2)	ns
Mean	62	56	−21.5(30)	−61(9)	**	1.2(3.9)	−13(6)	ns

Table 6. Average (SE) densities of *Synechococcus* and eukaryotic phytoplankton and the corresponding concentrations of chlorophyll *a* in the upstream samples (ambient value) and the decrease in those values after the passage of the water through the perforated reef in the June 1995 experiment. Cell numbers, measured with a flow cytometer, were converted to carbon values as in Campbell et al. (1994). A third group of ultraphytoplankton, the *Prochlorococcus*, was abundant at that time but for technical reasons could not be counted. Thus, values of carbon removal do not cover the total contribution of ultrphytoplankton (*n*, number of pairs; *, $P \leq 0.05$; **, $P \leq 0.01$).

	n	Ambient value	Decrease	Fraction removed (%)	Carbon removed (μg liter^{-1})	*P*
Synechococcus (no. ml^{-1})	10	6,533(327)	1,760(596)	27(9)	0.44(0.05)	**
Picoeukaryotes (no. ml^{-1})	10	935(16)	260(28)	28(3)	0.55(0.06)	**
Chlorophyll (μg liter^{-1})	8	0.209(0.006)	0.048(0.017)	23(8)		*

seasonal abiotic factor(s), rather than the chlorophyll concentration as such. Note, however, that a lack of gradient was also observed in December 1994, when the ambient chlorophyll concentration was high (Table 2). This irregular observation could be related to the exceptionally rough conditions caused by a strong southerly storm that occurred a day before our visit. This storm caused massive resuspension of sediment and could have mixed the phytoplankton-depleted waters near the bottom with effluent waters aloft. The physical term in the above model likely reflected a similar effect, namely, an enhanced water mixing and the obstruction of a defined depleted layer. Our model, however, is based on single-point measurements of currents, sometimes made a few hundred meters away from the location of a transect. A much more comprehensive investigation of the current regime should be carried out in order to better explain the effect of water physics on temporal variations in the distribution of phytoplankton near the reef.

The observed phytoplankton depletion encompassed a wide range of cell sizes (0.5–5 μm) with no apparent selectivity either at the fringing reef, where a diverse guild of active suspension-feeders was found, or at the perforated reef, where the benthic community was dominated by passive filter-feeders (soft corals). It is yet unknown whether this nonselectivity, documented here on the community level, reflected a similarly nonselective feeding by individual phytoplanktivores.

The depletion of cells in the range of 1 μm in size suggests that heterotrophic bacteria may also be readily eaten at the reef. Because heterotrophic bacteria are extremely abundant in tropical waters, with a carbon pool similar in magnitude to that of phytoplankton (Campbell et al. 1994), their trophic contribution to the coral reef deserves careful attention. Ayukai's (1995) recent observation (*see* Table 8) showed that the depletion of heterotrophic bacteria downstream of his study reefs in Australia were similar to those of phytoplankton. A third group of small cells that may turn out to be an important source of carbon for the reef community, but has so far been overlooked, is *Prochlorococcus*. In the Gulf of Aqaba this is the dominant phytoplanktonic

Table 7. Average (SE) and maximum densities of suspension-feeders that are likely phytoplankton grazers (*see Discussion*) in the coral reef of Eilat (4–6-m depth). Densities are reported per quadrat size (0.25 m^2). Percent occurrence refers to the number of quadrats (of a total of 65) in which at least one specimen was found. For the boring mussel *Lithophaga*, the name of the host coral is given. The bottom three rows list the average (SE) percent cover of living organisms (mostly stony corals), bare rocks (rocky substrate with no visible invertebrates), and sand.

Taxon	Avg density	Max density	% occurrence
	No. 0.25 m^{-2}		
Lithophaga simplex (in *Goniastrea* spp.)	1.06(0.47)	19	15.4
Lithophaga purpurea (in *Montipora erythraea*)	1.23(0.65)	40	13.8
L. purpurea (in *Cyphastrea* spp.)	1.80(0.41)	14	30.8
Lithophaga lessepsiana (in *Stylophora* spp.)	1.00(0.59)	37	10.8
Lithophaga spp. in other corals	0.32(0.20)	11	7.7
Mycale fistulifera (red sponge)	0.12(0.05)	2	9.2
Cliona spp. (boring sponges)	0.38(0.09)	3	24.6
Unrecognized blue sponge	0.94(0.15)	5	50.8
Other sponges	0.31(0.09)	3	18.5
Halocynthia gangelion (solitary ascidian)	0.08(0.03)	1	7.7
Other solitary tunicates	0.46(0.11)	3	26.2
Didemnum candidum (colonial ascidian)	0.12(0.06)	3	9.2
Other colonial tunicates	0.06(0.04)	2	4.6
Tridacna spp. (Giant Clam)	0.03(0.02)	1	3.1
Pedum sp. (medium-size bivalve)	0.25(0.10)	5	12.3
% live cover	40(3)	100	
% bare rock	48(3)	95	
% sand	12(3)	100	

Table 8. Comparison of reported carbon contributions to coral reefs via grazing on different types of planktonic organisms. All values were calculated similarly to ours, based on a comparison of particle concentrations upstream and downstream of a coral reef. Our measurements and the original values of Ayukai (1995) and Hamner et al. (1988) were converted to g C m^{-2} yr^{-1}. A conservative conversion factor of 1 : 30 for the Chl : C ratio was used (Ayukai 1995), although our measurements suggested a factor >60 for our study sites (Yahel unpubl. data).

Organisms	Flux (g C m^{-2} yr^{-1})	Reference
Phytoplankton	4.2–20.2	Ayukai 1995
	413.6 (<100 μm, *D. hemprichi* thicket)	Fabricius et al. 1998
	719.1 (<100 μm, perforated reef)	This study
	3.9 (diatoms >68 μm)	Glynn 1973
Bacteria	9.2–10.2	Ayukai 1995
Protozoa	1.4–6.3	Ayukai 1995
Microzooplankton	0.31–0.52	Ayukai 1991
Zooplankton	116.8 (>330 or 200 μm, night only)	Tranter and George 1969
	61.8 (>68 μm)	Glynn 1973
	197.1 (>60 μm)	Johannes and Gerber 1974
	2.8 (>250 μm, only at day, owing to predation by reef fishes)	Hamner et al. 1988

group during summer–fall (Lindell and Post 1995). Both our single transect that included *Prochlorococcus* (February 1996) and the few transects that included heterotrophic bacteria counts (August 1996) showed that the depletion values for both groups were similar to that of ultraphytoplankton. Pile (1997) and our recent study on individual grazing (G. Yahel unpubl. data) indicated high grazing on heterotrophic bacteria and *Prochlorococcus* by sponges and *Lithophaga* spp.

A significant elevation of pheopigment concentrations was observed at the fringing reefs. In general, phytoplankton grazing increases the concentrations of pheopigments (e.g. Shuman and Lorenzen 1975), and such an increase at the Great Barrier Reef was attributed to grazing by reef-associated zooplankton (Roman et al. 1990). In our study, higher values of chlorophyll depletion near the reef were usually associated with lower values of the Chl : pheopigments ratio at the 0 mab samples (Fig. 6), suggesting that phytoplankton grazing was (at least partly) responsible for the elevated levels of pheopigments at the reef. However, the gradients of pheopigments across the reef did not always coincide with decreasing gradients of chlorophyll. In 5 of our 10 visits to the reef, a significant gradient of chlorophyll co-occurred with a nonsignificant trend of pheopigments or vice versa (Table 2). Note that in all but one visit the Chl : pheopigment ratio was lower near the reef than in the open waters (Table 2). A likely cause for this partial decoupling between phytoplankton chlorophyll and pheopigments is the occurrence of an additional source of pheopigments at the reef, namely, grazing on benthic algae by fish, echinoids, and gastropods. In particular, herbivorous fish, discharging their feces aloft, could have been an additional source for suspended pheopigments in the water column over the reef.

The lack of pheopigment increase downstream of the perforated reef is not well understood. Soft corals may transform the ingested chlorophyll into nonfluorescent compounds or, as with other benthic anthozoans (Sebens and Koehl 1984), they may egest packed material that rapidly sinks to the bottom. A similar lack of pheopigment increase was observed in our past experiments with the soft coral *D. hemprichi* (Fabricius et al. 1998), a dominant taxon at the perforated reef.

Traditionally, investigators of planktivory in coral reefs referred to zooplankton rather than phytoplankton as the principal source of prey (Table 8). Historical perspective, together with the fact that stony corals are exclusively zooplanktivorous, may explain why phytoplankton has been overlooked. Glynn (1973), in a seminal study that for years set the stage for our understanding of planktivory in coral reefs, suggested that the import of carbon to the reef via zooplankton predation surpasses that of phytoplankton removal by more than an order of magnitude. Glynn's estimates of phytoplankton removal by the reef were 3.9 g C m^{-2} yr^{-1}, more than two orders of magnitude lower than those reported here for the perforated reef. An evaluation of such earlier studies, however, should consider the fact that at the time of Glynn's study neither epifluorescence microscopy nor flow cytometers were available for marine ecologists. Not being aware of the great importance of small cells in warm-water oceans (Furnas and Mitchell 1987; Chisholm 1992), Glynn (1973) used a 68-μm mesh net to sample phytoplankton, totally missing ultraphytoplankton.

The occurrence of a concentration boundary layer (Monismith et al. 1990) depleted of phytoplankton is a well-documented characteristic of mussel and polychaete beds in the temperate bays and estuaries (Fréchette and Bourget 1985, 1987; Fréchette et al. 1989; Asmus and Asmus 1991; Riisgård et al. 1996). Our findings, together with Ayukai's (1995) report on the strong depletion of *Synechococcus* hundreds of meters downstream of two Australian reefs, suggest that benthic grazing on ultraphytoplankton may be a ubiquitous characteristic of coral reefs as well. Future studies of carbon and nutrient fluxes in coral-reef communities should consider phytoplanktivory an important allochthonous source of food to the reef community.

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