

NOTE

Enhancement of pico- and nanoplankton growth by coral exudates

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ABSTRACT: The enhancement of pico- and nanoplankton cell biomass by coral exudates was studied in the laboratory. Two types of mesocosms were used, the first one containing only a carbonate sand layer (control mesocosm) and the second one containing a coral layer over the carbonate sand layer (coral mesocosm). During 10 h incubations, we followed the concentration of bacteria, cyanobacteria, and of auto- and heterotrophic flagellates, as well as the concentrations of inorganic (N and P) and organic (dissolved organic carbon, DOC) nutrients. There were no significant differences in inorganic nutrient concentrations between mesocosms. However, DOC concentrations in coral mesocosms exhibited peaks 5- to 13-fold higher than control mesocosm levels; these peaks took place between 13:00 and 17:00 h and lasted for ca 2 h. As a consequence, microbial growth was significantly enhanced in coral mesocosms. At the end of the incubations, bacterial biomass was 6-fold higher in coral relative to control mesocosms. Autotrophic biomass was 3 to 5 times higher in coral mesocosms. These results indicate that small amounts of coral exudates (0.5 to 10% of maximum DOC concentrations) are enough to greatly stimulate microbial growth.

KEY WORDS: Picoplankton · Nanoplankton · Corals · Organic carbon (DOC) · Mesocosm

Coral reefs are areas of high productivity (Lewis 1977) due to a rapid turnover of organic and inorganic nutrients (Crossland & Barnes 1983). Heterotrophic bacteria have been recognized as one of the most important agents of carbon and nitrogen cycling in coral reefs (Ducklow 1990, Sorokin 1994, Charpy-Roubaud et al. 1996), and bacterial productivity in reef waters is extremely high compared to the open ocean (Moriarty et al. 1985, Linley & Koop 1986, Ducklow 1990). Small

autotrophs (<20 µm), often representing a large fraction of the total phytoplanktonic biomass, also show high production rates in reef waters (Furnas et al. 1990, Charpy et al. 1992, Ferrier-Pagès & Gattuso 1998).

It has therefore been suggested that large amounts of dissolved and particulate organic matter (DOM/POM) are needed to sustain these high production rates (Moriarty 1979). A number of potential sources — such as phytoplanktonic exudates, benthic fluxes, and particle degradation — are at the origin of this organic matter (D'Elia & Wiebe 1990). Corals have been suggested to be an important source of POM and DOM in reef waters (Crossland 1987). Indeed, marked changes in bacterial and POM concentrations have been observed over reef flats (Moriarty 1979), and the highest pico- and nanoplankton production rates have often been measured above corals (Ducklow 1990, Sorokin 1993, 1994). Studies performed at Lizard Island have measured 10-fold increases in bacterial production rates in waters flowing off the back reef compared to those of the reef front (Moriarty et al. 1985).

The contribution of coral mucus (POM) to bacterial production has been assessed in a number of studies (Ducklow & Mitchell 1979, Herndl & Velimirov 1986, Paul et al. 1986, Schiller & Herndl 1989, Coffroth 1990). However, coral mucus can only be used by microbes if it is retained in the reef long enough for decomposition to occur (Capone et al. 1992). Moreover, an important fraction of this mucus may be refractory and thus not consumed during its short transit time across the reef (Hatcher & Sanmarco 1983). Only a few studies have reported DOM fluxes from corals (Means & Sigleo 1986, Crossland 1987, Ferrier-Pagès et al. 1998). Labile DOM like amino acids and sugars are assimilated rapidly by free-living bacteria (Williams 1981) as well as by autotrophic plankton (Palenik & Morel 1990). However, whether DOM fluxes from corals into the overly-

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ing water could sustain large microbial production rates remains to be experimentally tested (Ducklow 1990).

The purpose of this work was to study the capacity of dissolved coral exudates to enhance microbial production. Our main objectives were: (1) to determine the extent of coupling between coral exudation and pico- and nanoplanktonic growth, and (2) to compare biomass production of both auto- and heterotrophic microbes. For this purpose, 2 mesocosms were set up, one containing only a carbonate sand layer and the other one containing a coral layer over the carbonate sand layer. Auto- and heterotrophic populations of pico- and nanoplankton were incubated in dialysis bags, directly over the sediment or the corals, and biomass production rates after 10 h incubations were compared.

Material and methods. Two different sets of experiments were performed. In the first set of experiments (Expt A), a mesocosm was set up successively with and without a coral cover over the sediment (coral and control mesocosm, respectively). In the second set of experiments (Expt B), 2 mesocosms (coral and control mesocosms) were used simultaneously. These 2 approaches were used to eliminate any mesocosm effect.

Experimental setup: The mesocosms were assembled in aquaria (60 × 60 × 60 and 40 × 30 × 30 cm, Expts A and B respectively) following Leclercq et al. (1999) (Fig. 1). A 5 cm carbonate sand layer separated the main seawater reservoir from a small volume of confined seawater. The aquaria were filled with Mediterranean seawater passed through a sand filter and heated to 26°C (controller EliWell PC 902T and Biotherm 2000 Rena, Expts A and B respectively). This temperature was comparable to the temperature of

Mediterranean seawater at the time of the experiment (25 to 26°C, July to September). The water in the mesocosms was continuously aerated (air pump Alizé, Rena) and stirred (powerhead Maxijet 1000 and C20 Rena, experiments A and B respectively). The continuous seawater renewal (5% h⁻¹) was stopped during the experiments. Light was provided by a 400 W metal halide lamp (300 μmol photons m⁻² s⁻¹, Philips HPI-T) with a 12:12 h photoperiod. The reef community was composed of different scleractinian coral colonies collected in the Red Sea and introduced in the mesocosms 3 yr before the present study. The species composition was: Expt A, *Stylophora* sp., *Acropora* sp., *Favia* sp., *Galaxea* sp., and *Euphyllia ancora*; Expt B, *Pectinia paeonia*, *Montipora* sp., *Favia* sp. and *Euphyllia ancora*.

Expt A: A microplanktonic community was obtained from the Mediterranean Sea in the morning at 2 m depth and brought back to the laboratory. This community was immediately size-fractionated by gravity and reverse flow filtration, to avoid cell breakage (Furnas & Mitchell 1986), through nylon screens and Nuclepore™ filters. Three size-classes were obtained in order to remove different predators: <2 μm (bacteria, cyanobacteria and picoflagellates), <5 μm (previous cells and nanoflagellates) and <10 μm (previous cells and small ciliates). Aliquots of each fraction were then carefully transferred into 3 perspex chambers (100 ml) and closed at each end by a dialysis membrane (Furnas et al. 1990, Ferrier-Pagès and Gattuso 1998) of 14 000 to 20 000 Da cut off (Spectra/Por). These membranes allowed the exchange of DOM but prevented grazing of microbes by the corals. Diffusive exchange of a mixture of ¹⁴C-labelled amino acids between chamber and mesocosm water took <30 min to 1 h (unpubl. results). The chambers were incubated for 10 h in the coral mesocosm. The corals were then removed from the mesocosm, the water completely renewed and other chambers incubated the following day for 10 h in the control mesocosm. Samples were taken at the beginning and the end of the incubations to measure pico- and nanoplanktonic, inorganic nutrient, and dissolved organic carbon (DOC) concentrations. These experiments were repeated twice at a 1 wk interval and will be referred as Expts A1 and A2.

Expt B: Seawater was collected at 2 m depth and filtered under reverse flow onto 0.8 μm Millipore™ filters in order to recover the bacterial fraction. Bacteria were transferred into 3 replicate perspex chambers (50 ml) closed by 2 dialysis membranes of 20 000 Da cut off. The chambers were then incubated simultaneously in the coral and control mesocosms for 10 h. Samples were taken at the beginning and the end of the

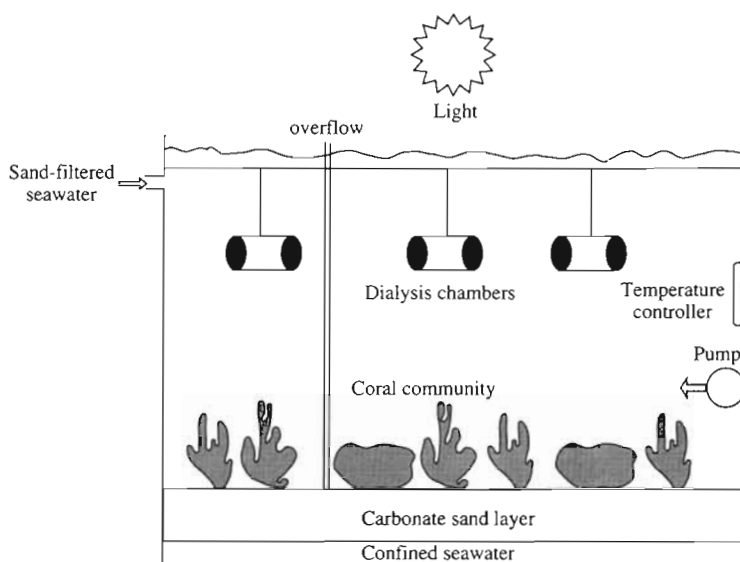


Fig. 1: Design of the experimental setup. Drawing of a mesocosm containing a coral cover

incubations to measure bacterial, inorganic nutrient, and DOC concentrations. This experiment was repeated 3 times at 1 d intervals and will be referred to as Expts B1, B2 and B3.

Analysis and calculations: *Inorganic nutrients and DOC:* Inorganic nitrogen (nitrate, nitrite and ammonium) and phosphate were measured on an Alliance II autoanalyser (Strickland & Parsons 1972), and DOC by high temperature catalytic oxidation (HTCO) (DOC was not measured in Expt A2). Samples for DOC analysis were filtered through acid-washed (10% HCl) 0.2 µm polyethersulphone membrane filters (Gelman). Once placed onto the filtering unit (500°C ignited glasswater), the filters were washed again with 20 ml Milli-Q water prior to sample collection into 20 ml ignited Pyrex tubes. Samples were then acidified to pH ≤ 2 with 2 N HCl and stored at 5°C pending analysis. Samples were sparged with an artificial gas mixture (containing ≤0.1 CO, CO₂ or hydrocarbons) in order to eliminate inorganic carbon and measured on a Shimadzu TOC 5000. DOC concentrations were calculated with a standard calibration curve made with potassium biphthalate. The coefficient of variation of duplicate injections was always <2%.

Pico- and nanoplanktonic concentrations: Cells in each perspex chamber were enumerated in triplicate. Ten ml samples were fixed with borax-buffered formaldehyde (2% v/v final concentration) and stained with DAPI (4'6 diamidino-2-phenylindole, Porter & Feig 1980). Following that, they were filtered onto 0.22 µm black Nuclepore™ filters and stored at -20°C prior to enumeration. Cells were counted under a magnification of ×1000 with a Leica epifluorescence microscope equipped with an HBO-100 epifluorescence illuminator and the excitation/barrier filter sets for UV, blue and green light. Bacteria and heterotrophic flagellates appear blue under UV excitation (Caron 1983). Autotrophic flagellates were distinguished by the auto-fluorescence of the chlorophyll *a* (visualized as red) and chroococcoid cyanobacteria of the phycoerythrin (visualized as yellow, Waterbury et al. 1986). Cell abundances were converted into carbon biomass (B , µg C l⁻¹) according to the following equation:

$$B = N \times V \times C$$

where N is the cell abundance (cell ml⁻¹), V the geometrical cell volume (µm³), and C the conversion factor (125 fg C µm⁻³ for heterotrophic bacteria [Pelegri et al. 1999], 183 fg C µm⁻³ for pico- and nanoflagellates, and 200 fg C µm⁻³ for cyanobacteria [Caron et al. 1995]). Cell volumes were 0.06, 1.77 and 65 µm³ for heterotrophic bacteria, pico- and nanoflagellates respectively.

Statistical analysis of the differences between coral and control mesocosms was performed on StatView by using 1-factor ANOVAs. When a significant effect was

Table 1. Nutrient concentrations (µM) and increases in biomass (µg C l⁻¹) in control and coral mesocosms during the various incubations (mean ± standard error of the mean). Expt A: the means of <2, <5 and <10 µm size fractions are given for bacteria, cyanobacteria and autotrophic pico- and nanoflagellates (APF, ANF); ANOVAs were performed to test the differences between mesocosms. $p < 0.5$ is significant. Nutrient concentrations in Expt B are in the same range as for Expt A

Group	Control mesocosm	Coral mesocosm	ANOVA probability
Expt A1			
Nutrients (µM)			
Nitrite	0.02 ± 0.01	0.02 ± 0.01	p = 0.20
Nitrate	0.20 ± 0.01	0.25 ± 0.01	p = 0.74
Ammonium	0.01 ± 0.01	0.02 ± 0.01	p = 0.10
Phosphate	0.03 ± 0.01	0.03 ± 0.01	p = 0.76
Groups (µg C l⁻¹)			
Bacteria	0.50 ± 0.07	3.27 ± 0.33	p < 0.001
Cyanobacteria	0.25 ± 0.07	0.78 ± 0.05	p < 0.001
APF	0.05 ± 0.01	0.17 ± 0.01	p < 0.001
ANF	2.04 ± 1.06	5.90 ± 1.44	p = 0.040
Expt A2			
Nutrients (µM)			
Nitrite	0.03 ± 0.01	0.02 ± 0.01	p = 0.20
Nitrate	0.24 ± 0.02	0.21 ± 0.04	p = 0.74
Ammonium	0.02 ± 0.01	0.03 ± 0.01	p = 0.10
Phosphate	0.03 ± 0.01	0.04 ± 0.01	p = 0.76
Groups (µg C l⁻¹)			
Bacteria	2.44 ± 0.46	14.39 ± 1.15	p < 0.001
Cyanobacteria	0.24 ± 0.05	2.50 ± 0.25	p = 0.004
APF	0.01 ± 0.01	0.05 ± 0.01	p = 0.010
ANF	0.50 ± 0.13	2.40 ± 0.39	p = 0.19
Expt B1			
Bacteria (µg C l ⁻¹)	2.90 ± 1.1	14.30 ± 0.55	p < 0.001
Expt B2			
Bacteria (µg C l ⁻¹)	4.20 ± 0.40	9.15 ± 0.60	p = 0.002
Expt B3			
Bacteria (µg C l ⁻¹)	3.10 ± 0.90	14.80 ± 0.40	p < 0.0001

found, the means were compared with a Bonferroni/Dunn post-hoc test.

Results. Inorganic nutrients and DOC: No significant differences were observed between initial and final nutrient concentrations (ANOVA, $p > 0.1$) or between coral and control mesocosms (Table 1; ANOVA, $p \geq 0.1$). DOC concentrations remained low in control mesocosms (120 to 163 µM, Table 2), with some occasional small peaks (237 to 385 µM). In coral mesocosms, important DOC peaks (ca 1300 to 1900 µM increase) were observed between 13:00 and 17:00 h and lasted ca 2 h. DOC concentrations during these peaks were significantly higher in coral than in control mesocosms (Table 2; unpaired *t*-test, $p \leq 0.008$)

Pico- and nanoplanktonic concentrations: Initial concentrations of pico- and nanoplanktonic cells were

Table 2. Dissolved organic carbon (DOC) concentrations (μM , mean \pm standard error of the mean) measured during the mesocosm experiments. Unpaired *t*-tests were performed to test the differences in DOC between mesocosms, $p < 0.05$ is significant

Time (h)	Control mesocosm	Coral mesocosm	p
First mesocosm experiment			
Expt A1			
10:00	131 \pm 10	157 \pm 17	0.27
11:00	128 \pm 20	132 \pm 12	0.67
12:00	149 \pm 11	125 \pm 11	0.19
14:00	139 \pm 44	117 \pm 12	0.49
15:30	123 \pm 13	130 \pm 17	0.72
17:00	149 \pm 16	2092 \pm 41	0.001
10:00 (next day)	133 \pm 12	160 \pm 10	0.12
Second mesocosm experiment			
Expt B1			
11:00	145 \pm 19	161 \pm 16	0.07
13:00	133 \pm 21	1546 \pm 298	0.002
14:00	232 \pm 17	265 \pm 35	0.24
15:30	146 \pm 22	145 \pm 12	0.96
17:00	137 \pm 17	153 \pm 27	0.08
18:00	133 \pm 12	161 \pm 12	0.09
Expt B2			
11:00	130 \pm 27	154 \pm 18	0.25
13:00	132 \pm 15	129 \pm 11	0.89
14:00	141 \pm 24	174 \pm 12	0.07
15:30	147 \pm 24	1473 \pm 17	0.003
17:00	237 \pm 19	158 \pm 18	0.04
18:00	163 \pm 12	159 \pm 18	0.75
Expt B3			
11:00	208 \pm 12	207 \pm 38	0.92
13:00	158 \pm 36	217 \pm 25	0.20
14:00	149 \pm 33	170 \pm 39	0.63
15:30	385 \pm 37	1937 \pm 172	0.008
17:00	140 \pm 25	–	–
18:00	133 \pm 12	318 \pm 46	0.03

comparable in both Expts A and B: $6 \pm 1 \times 10^8$ cells l^{-1} for bacteria, $1.5 \pm 0.5 \times 10^7$ cells l^{-1} for cyanobacteria, $10 \pm 2 \times 10^5$ cells l^{-1} for autotrophic picoflagellates, and $7 \pm 1 \times 10^5$ cells l^{-1} for autotrophic nanoflagellates. The concentration of heterotrophic flagellates ($5.5 \pm 0.2 \times 10^5$ and $4.5 \pm 0.1 \times 10^5$ cells l^{-1} , in Expts A1 and A2 respectively) did not change during the incubations (ANOVA, $p < 0.001$) (data not shown). Figs. 2, 3 & 4 show the increases in microbial biomass (number of cells l^{-1} and $\mu\text{g C l}^{-1}$) for Expts A1, A2 and B1 to B3. Biomass increases were different for the various size fractions, the number of predators (and thus grazing) increased with increasing size fractionation. The highest increases in biomass were therefore generally obtained in the smaller fractions, except for autotrophic nanoflagellates, which were mainly present in the $< 5 \mu\text{m}$ size fraction, and except when predators were themselves grazed by the higher level. Pico- and nanoplankton

growth was always greater in coral than in control mesocosms (ANOVA, $p < 0.5$; Table 2). The increase in bacterial biomass was at least 6-fold higher, while the increase in autotrophic cell biomass (cyanobacteria and autotrophic flagellates) was 3- to 5-fold higher in coral relative to control mesocosms.

Discussion. No differences in inorganic nutrient concentrations could be observed between control and coral mesocosms; their concentrations remained low and comparable to those observed *in situ* for reef waters (Smith et al. 1981). However, DOC concentrations varied greatly during these incubations. The small DOC increases (ca 100 μM) observed in control mesocosms could be due to the activity of bacteria and algae in the carbonate sand layer (Sorokin 1993). A much higher production (ca 1200 to 1600 μM , 5- to 13-fold higher than control levels) was measured in coral mesocosms between 13:00 and 17:00 h, and was attributed to corals. Similarly, Means & Sigleo (1986) measured a huge production of DOC during a 5 h incubation of the coral *Acropora palmata* in filtered seawater, and Crossland (1987) observed an *in situ* production of DOC in coral reefs between noon and 16:00 h. According to the values of primary production previously measured in our coral mesocosms (Leclercq et al. 1999), the DOC released by the corals represented between 12 and 16% of the photosynthetically fixed carbon. This is in agreement with the few other previous estimates (8 to 25%, Crossland 1987, Sorokin 1993).

DOC concentrations in the coral mesocosms decreased ca 2 h after the peak, as has been already observed for *Galaxea fascicularis* (Ferrier-Pagès et al. 1998). In that study, colonies of *G. fascicularis* were incubated in 2 l filtered seawater and the release of DOC monitored each 15 min during 10 h using HTCO and ^{14}C -radiolabelling techniques. Two important releases of DOC took place, one in the morning and another in the afternoon, followed by a 're-uptake' 2 h later. The decrease observed could not be attributed to free-living bacteria, which were present in very low concentrations in the filtered incubation medium. Moreover, when prokaryotic inhibitors were added to the seawater, no 're-uptake' occurred, suggesting that coral-associated bacteria (likely epibiotic bacteria) were responsible for the organic carbon disappearance. High bacterial activity has already been measured in the coral surface mucopolysaccharide layer (Herndl & Velimirov 1986). In our experiments, even assuming that most DOC was rapidly taken up by coral-associated bacteria, enough DOC was still available for planktonic microbial populations. To obtain the total microbial biomass increase measured after 10 h in the coral mesocosm, between 5 and 150 $\mu\text{mol C l}^{-1}$ was needed, if we assume a gross growth efficiency

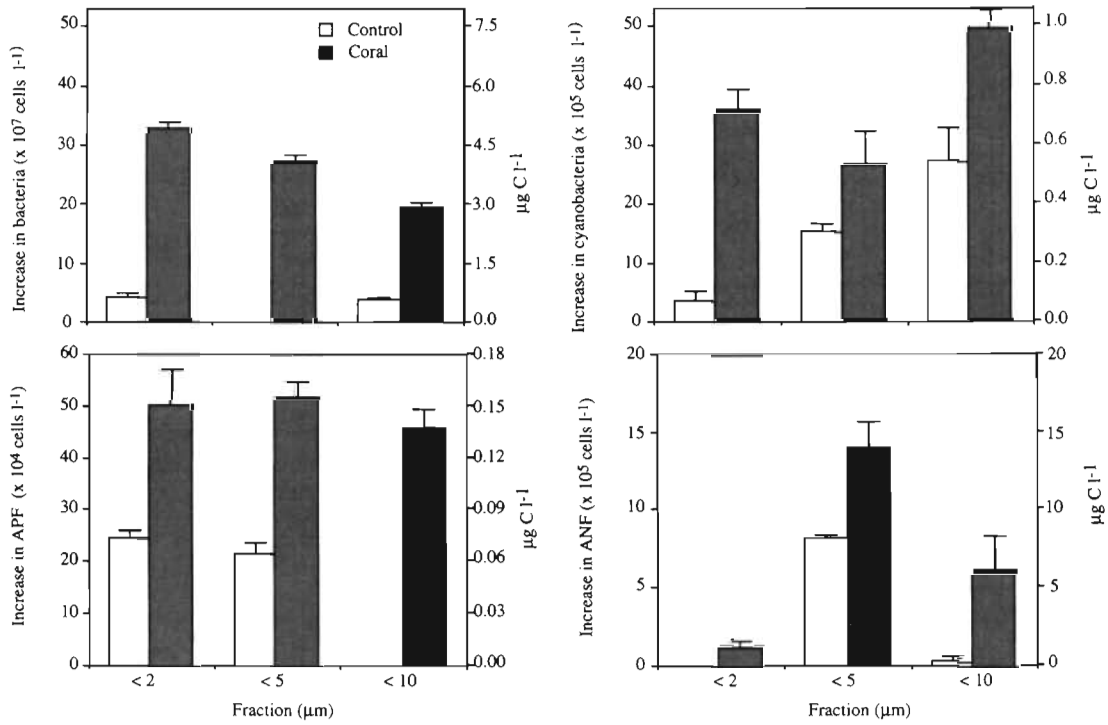


Fig. 2. Expt A1. Increases in cell number (cell ml⁻¹) and carbon biomass (μg C l⁻¹) during 10 h incubations of control (white bars) and coral (grey bars) mesocosms. APF, ANF: autotrophic pico- and nanoflagellates respectively. Pico- and nanoplankton were divided into 3 different size fractions (<2, <5 and <10 μm fractions)

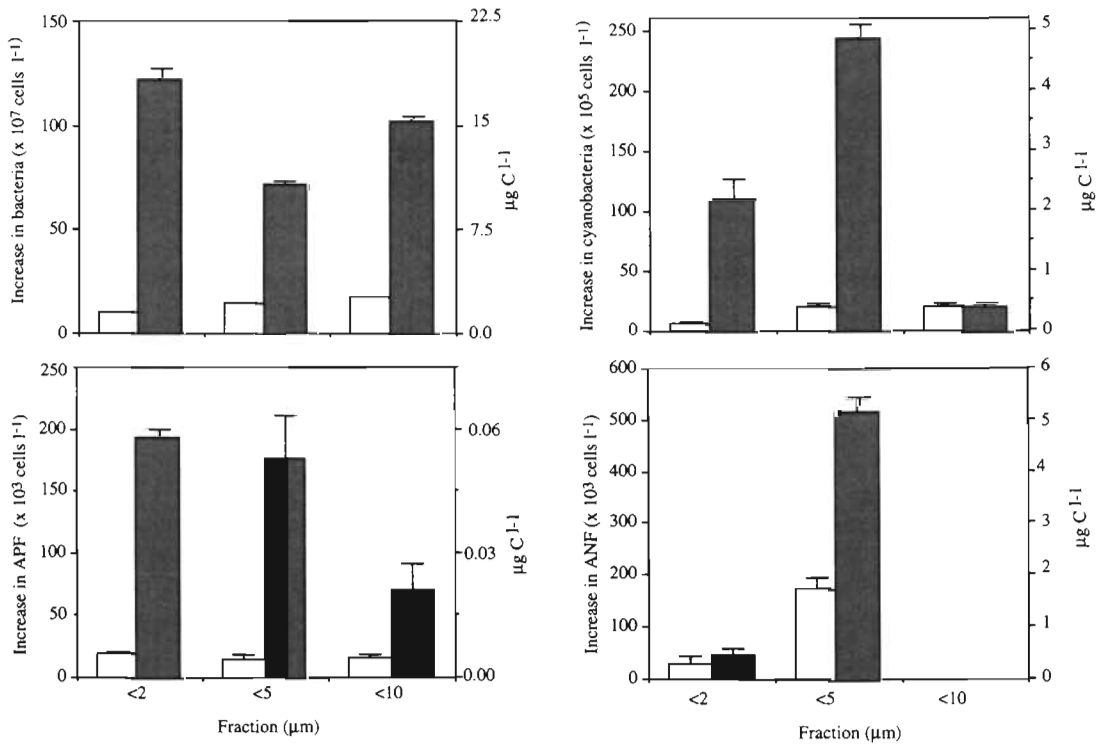


Fig. 3. Expt A2. Increases in cell number (cell ml⁻¹) and carbon biomass (μg C l⁻¹) during 10 h incubations of control (white bars) and coral (grey bars) mesocosms. APF, ANF: autotrophic pico- and nanoflagellates respectively. Pico- and nanoplankton were divided into 3 different size fractions (<2, <5 and <10 μm fractions)

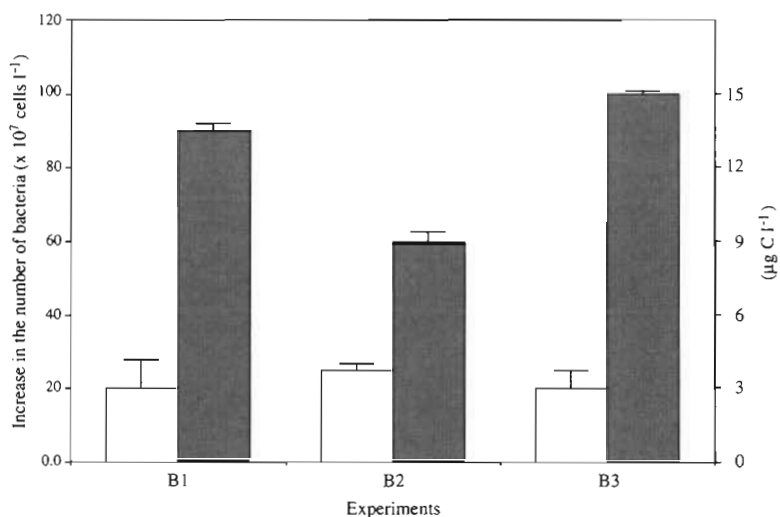


Fig. 4. Expts B1, B2 and B3. Increases in bacterial concentrations (cell ml⁻¹) and carbon biomass (µg C l⁻¹) during a 10 h incubation in the control (white bars) and the coral (grey bars) mesocosms

varying from 2 to 45% (Carlson & Ducklow 1996). This corresponds to 0.3–10% of the maximum DOC concentrations in these mesocosms. Thus, only small amounts of nutrients were needed to sustain high microbial production rates. Indeed, other authors (Carlson & Ducklow 1996, Zweifel et al. 1996) have calculated that free-living bacterioplankton consume 0.04 to 1 µmol C l⁻¹ h⁻¹ DOC. Moreover, DOC excreted by corals is likely a by-product of photosynthesis, and is thus more labile than seawater DOC.

Our findings indicate that the growth of both auto- and heterotrophic microbes was enhanced by coral exudates. Bacteria experienced the highest increase in biomass (at least 6-fold), as would be expected from the addition of organic nutrients. Autotrophic microbial biomass was enhanced by 3- to 5-fold in coral mesocosms relative to control mesocosms. Although autotrophic cells rely principally on dissolved inorganic nutrients, it has been demonstrated that they can also take up DOM such as amino acids (Flynn & Butler 1986, Palenik & Morel 1990). Autotrophic microbial biomass enhancement could have also been caused by an increase in inorganic nutrients, excreted by corals (Szmant et al. 1990, Schlichter & Liebezeit 1991) or recycled by bacteria. A rapid uptake of these nutrients by the phytoplankton could explain the lack of variation in inorganic nutrient concentrations during the incubations.

Planktonic populations, taken from Mediterranean surface waters, could be slightly different from coral reef microbes. However, both ecosystems are oligotrophic and have comparable microbial concentrations (Sherr et al. 1989, Ayukai 1991). Small phytoplankton dominate the autotrophic biomass (Bienfang &

Takahashi 1983, Berman et al. 1984), and the same major microbial lineages are widespread (Sorokin 1981, Waterbury et al. 1986, Cole et al. 1988, Mullin et al. 1995). Moreover, gross growth efficiencies of bacterioplankton growing on natural DOC sources vary from 2 to 45% in marine ecosystems ranging from tropical to polar areas (Carlson & Ducklow 1996).

Grazing of pico- and nanoplankton by higher trophic levels can be roughly estimated in Expt A by calculating the difference in biomass increase between 2 size fractions (Figs. 2 & 3). Our results indicate that at least 25 to 30% of the daily microbial production was consumed by higher trophic levels (mainly heterotrophic nano-flagellates and ciliates). This active protozoan grazing of rapidly growing pico- and nanoplankton led to an efficient transfer of energy from lower to higher trophic levels. This seems to be the case for most

coral reefs characterized by fast and efficient nutrient recycling and low inputs of new nutrients (Crossland & Barnes 1983).

In conclusion, planktonic bacteria seem to take up small amounts of coral exudates. However, these amounts are sufficient to enhance bacterial production by 6-fold and autotrophic production by 3- to 5-fold. Further studies should be directed to determine the lability of DOC compounds excreted by corals.

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LITERATURE CITED

- Ayukai T (1991) Standing stock of microzooplankton on coral reefs: a preliminary study. *J Plankton Res* 13:895–899
- Berman T, Azov Y, Townsend D (1984) Understanding oligotrophic oceans: can eastern Mediterranean be a useful model? In: Holm-Hansen O, Bolis L, Gilles R (eds) *Marine phytoplankton and productivity: lecture notes on coastal and estuarine studies*, Vol 8. Springer-Verlag, Berlin, p 101–112
- Bienfang PK, Takahashi M (1983) Ultraplankton growth rates in a subtropical ecosystem. *Mar Biol* 76:203–211
- Capone DG, Dunham SE, Horrigan SG, Duguay LE (1992) Microbial nitrogen transformations in unconsolidated coral reef sediments. *Mar Ecol Prog Ser* 80:75–88
- Carlson CA, Ducklow HW (1996) Growth of bacterioplankton and consumption of dissolved organic carbon in the Sargasso Sea. *Aquat Microb Ecol* 10:69–85
- Caron DA (1983) Technique for enumeration of heterotrophic

- and phototrophic nanoplankton, using epifluorescence microscopy and comparison with other procedures. *Appl Environ Microbiol* 42(2):491–498
- Caron DA, Dam HG, Kremer P, Lessard EJ, Madin LP, Malone TC, Napp QJM, Peele ER, Roman MR, Youngbluth MJ (1995) The contribution of microorganisms to particulate carbon and nitrogen in surface waters of the Sargasso Sea near Bermuda. *Deep-Sea Res* 42:943–972
- Charpy L, Blanchot J, Lo L (1992) Cyanobacteria *Synechococcus* spp. contribution to primary production in a closed atoll lagoon (Takapoto, Tuamotu, French Polynesia). *CR Acad Sci Paris* 314:395–401
- Charpy-Roubaud C, Charpy L, Sarazin G (1996) Diffusional nutrient fluxes at the sediment-water interface and organic matter mineralization in an atoll lagoon (Tikehau, Tuamotu Archipelago, French Polynesia). *Mar Ecol Prog Ser* 132:181–190
- Coffroth MA (1990) Mucous sheet formation on poritid corals: an evaluation of coral mucus as a nutrient source on reefs. *Mar Biol* 105:39–49
- Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Mar Ecol Prog Ser* 43:1–10
- Crossland CJ (1987) In situ release of mucus and DOC-lipid from the coral *Acropora variabilis* and *Stylophora pistillata*. *Coral Reefs* 6:35–42
- Crossland CJ, Barnes DJ (1983) Dissolved nutrients and organic particulates in water flowing over coral reefs at Lizard Island. *Aust J Mar Freshw Res* 34:835–844
- D'Elia CF, Wiebe WJ (1990) Biogeochemical nutrient cycles in coral reef ecosystems. In: Dubinsky Z (ed) *Coral reefs, ecosystems of the world*, Vol 25. Elsevier, Amsterdam, p 49–74
- Ducklow HW (1990) The biomass, production and fate of bacteria in coral reefs. In Dubinsky Z (ed) *Coral reefs, ecosystems of the world*, Vol 25. Elsevier, Amsterdam, p 265–289
- Ducklow HW, Mitchell R (1979) Bacterial populations and adaptations in the mucus layers on living corals. *Limnol Oceanogr* 24:715–725
- Ferrier-Pagès C, Gattuso JP (1998) Biomass, production and grazing rates of pico- and nanoplankton in coral reef waters (Miyako Island, Japan). *Microb Ecol* 35:46–57
- Ferrier-Pagès C, Gattuso JP, Cauwet G, Jaubert J, Allemand D (1998) Release of dissolved organic carbon and nitrogen by the zooxanthellate coral *Galaxea fascicularis*. *Mar Ecol Prog Ser* 172:265–274
- Flynn KJ, Butler I (1986) Nitrogen sources for the growth of microalgae: role of dissolved free amino acids. *Mar Ecol Prog Ser* 34:281–304
- Furnas MJ, Mitchell AW (1986) Phytoplankton dynamics in the Central Great Barrier Reef. 1. Seasonal changes in biomass and community structure and their relation to intensive activity. 2. Primary production. *Cont Shelf Res* 6:363–384
- Furnas MJ, Mitchell AW, Gilmartin M, Revelante N (1990) Phytoplankton biomass and primary production in semi-enclosed reef lagoons of the Central Great Barrier Reef, Australia. *Coral Reefs* 9:1–10
- Hatcher BG, Sanmarco PW (1983) The role of detritus in the metabolism and secondary production of coral reef ecosystems. In: Baker JT, Carter RM, Stark KP (eds) *Proceedings Inaugural Great Barrier Reef conference*. James Cook University, Townsville, p 317–326
- Herndl GJ, Velimirov B (1986) Microheterotrophic utilization of mucus released by the Mediterranean coral *Cladocora cespitosa*. *Mar Biol* 90:363–369
- Leclercq N, Gattuso JP, Jaubert J (1999) Measurements of oxygen metabolism in open-top aquatic mesocosms: application to coral reef community. *Mar Ecol Prog Ser* 177:299–304
- Lewis JB (1977) Processes of organic production on coral reefs. *Biol Rev* 52:305–347
- Linley EAS, Koop K (1986) Significance of pelagic bacteria as a trophic resource in a coral reef lagoon, One Tree Island, Great Barrier Reef. *Mar Biol* 92:457–464
- Means JC, Sigleo AC (1986) Contribution of coral reef mucus to the colloidal pool in the vicinity of Discovery Bay, Jamaica. *W I Bull Mar Sci* 39:110–118
- Moriarty DJW (1979) Biomass of suspended bacteria over coral reefs. *Mar Biol* 53:193–200
- Moriarty DJW, Pollard PC, Hunt WG (1985) Temporal and spatial variation in bacterial production in the water column over a coral reef. *Mar Biol* 85:285–292
- Mullin TD, Britschgi TB, Krest RL, Giovannoni SJ (1995) Genetic comparisons reveal the same unknown bacterial lineages in Atlantic and Pacific bacterioplankton communities. *Limnol Oceanogr* 40(1):148–158
- Palenik B, Morel FMM (1990) Amino acid utilization by marine phytoplankton: a novel mechanism. *Limnol Oceanogr* 35:260–269
- Paul JH, DeFlaun F, Jeffrey WH (1986) Elevated levels of microbial activity in the coral surface microlayer. *Mar Ecol Prog Ser* 33:29–40
- Pelegri SP, Dolan J, Rassoulzadegan F (1999) Use of high temperature catalytic oxidation (HTCO) to measure carbon content of microorganisms. *Aquat Microb Ecol* 16:273–280
- Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. *Limnol Oceanogr* 25:943–948
- Schiller C, Herndl GJ (1989) Evidence of enhanced microbial activity in the interstitial space of branched corals: possible implications for coral metabolism. *Coral Reefs* 7:179–184
- Schlichter D, Liebezeit G (1991) The natural release of amino acids from the symbiotic coral *Heteroxenia fuscescens* (Ehrb.) as a function of photosynthesis. *J Exp Mar Biol Ecol* 150:83–90
- Sherr EB, Rassoulzadegan F, Sherr BF (1989) Bacterivory by pelagic ciliates in coastal waters of the NW Mediterranean Sea. *Mar Ecol Prog Ser* 55:235–240
- Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment. Perspectives on ecosystem responses to nutritional perturbation. *Pac Sci* 35:279–396
- Sorokin YI (1981) Microheterotrophic organisms in marine ecosystems. In: Longhurst AT (ed) *Analysis of marine ecosystems*. Academic Press, New York, p 293–382
- Sorokin YI (1993) Coral reef ecology. *Ecol Stud* 102
- Sorokin YI (1994) Role of plankton in the turnover of organic matter on the Great Barrier Reef, Australia. *Hydrobiologia* 308:35–44
- Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis, 2nd edn. *Bull Fish Res Bd Can* 167
- Szmant AM, Ferrer LM, FlitzGerald LM (1990) Nitrogen excretion and O:N ratios in reef corals: evidence for conservation of nitrogen. *Mar Biol* 104:119–127
- Waterbury JB, Watson SW, Valois FW, Franks DG (1986) Biological and ecological characterization of the marine unicellular Cyanobacterium *Synechococcus*. *Can Bull Fish Aquat Sci* 214:71–120
- Williams PJeB (1981) Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kiel Meeresforsch* 5:1–28
- Zweifel UL, Blackburn N, Hagström Å (1996) Cycling of marine dissolved organic matter. I. An experimental system. *Aquat Microb Ecol* 11:65–77