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Microheterotrophic utilization of mucus released by the Mediterranean coral *Cladocora cespitosa*

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Abstract

The amount of mucus released by the Mediterranean coral *Cladocora cespitosa* (L.) was determined in laboratory experiments and the incorporation of mucus into bacterial biomass was investigated by means of incubation experiments in 1984. Mean mucus release was 8.5 μg (mucus dry wt) polyp^{-1} h^{-1} and amounted to 44% of the respiratory carbon losses of the coral since mean organic carbon content of freshly collected mucus was 102.2 μg C mg (mucus dry wt)$^{-1}$. Due to the abundance of *C. cespitosa* in the shallow littoral of the Bight of Piran, the energy content of mucus released is estimated to correspond to about 20% of the phytoplankton primary production in this area. Furthermore, the carbon conversion efficiency of 20% obtained from the bacterial population during decomposition of mucus indicates the high nutritional value of *C. cespitosa* mucus, although bacterial carbon onto mucus particles contributes less than 0.1% to the total organic carbon pool of the mucus.

Introduction

The role of mucus produced by Anthozoa has been known for many years. Mucus may act as a protective mechanism against sedimentation (Schuhmacher, 1977; Rublee *et al.*, 1980) and as a feeding mechanism (Lewis and Price, 1976; Herndl *et al.*, 1985). Mucus production may confer an ecological advantage to the coral not only in feeding and cleaning processes but also in retarding epiphytic and epizoic growth (Burkholder, 1973) and in removing surface bacterial growth (Ducklow and Mitchell, 1979 b).

Furthermore, mucus aggregates, commonly observed in coral reef waters, are ingested by a variety of coral reef inhabitants, such as fish (Johannes, 1967; Benson and Muscatine, 1974), bivalves (Goreau *et al.*, 1970), crabs (Knudsen, 1967), shrimp (Daumas and Thomassin, 1977), and zooplankton (Richman *et al.*, 1975; Gottfried and Roman, 1983). Quite recently, Coffroth (1984) demonstrated that the amount of allochthonous mucus aggregates ingested by the soft coral *Pseudoplexaura proposa* is sufficient to meet its energy requirements. It is not surprising that mucus aggregates dominate the particulate matter in reef waters (Johannes, 1967; Marshall, 1968; Qasim and Sankaranarayanan, 1970). Coral derived mucus was found to be nutritionally rich, containing wax esters, triglycerides, fatty acids and other energy-rich compounds (Coles and Strathman, 1973; Benson and Muscatine, 1974; Ducklow and Mitchell, 1979 a).

Most of the primary production on coral reefs is linked to the corals via their zooxanthellae (Scott and Jitts, 1977). The photosynthetic products of zooxanthellae are partly incorporated into mucus synthesized by the host (Crossland *et al.*, 1980 a). Crossland *et al.* (1980 b) found that mucus release of *Acropora acuminata* represents a loss of 40% net carbon fixation. This indicates that considerable amounts of energy dissipate through the exudation of mucus. Undoubtedly, coral mucus is a significant source of particulate organic matter for consumers in coral reef areas.

During the last decade a dramatic increase in abundance of the symbiotic coral *Cladocora cespitosa* has been observed in the Northern Adriatic Sea, probably caused by the strong grazing pressure of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* on algae, which usually covers the boulder field of the sublittoral in this area (J. A. Ott, personal communication). Because *C. cespitosa* has some characteristics of a hermatypic coral, it was questioned whether the sudden increase of this organism results in mucus production rates similar to those recorded by other authors from coral reef areas or whether it is a negligible food source for consumers of this ecosystem. The objective of this study was to quantify the mucus release of *C. cespitosa* colonies off Piran (Yugoslavia), to follow the subsequent decomposition, and to estimate the trophic significance of the mucus for this shallow, near-shore body of water.

Material and methods

Collection and maintenance of colonies

Cladocora cespitosa (L.) colonies were collected off the Marine Research and Training Center at Piran (Yugoslavia) during spring and summer of 1984. Only small colonies (< 10 cm diameter) were collected since epiphytes and cryptofauna are scarce in smaller colonies and epiphyte covery increases with increasing diameter of the colony (Herndl *et al.*, in preparation). The colonies were held in an aquarium under a 14 hL:10 hD photoperiod one week before experimentation. Water temperature varied between 16°–20 °C. Lighting was provided by a white cool fluorescent lamp with a light intensity of 120 μE m^{-2} s^{-1}. Colonies were fed daily with *Artemia sp.*

Measurements of mucus release

Prior to incubation the colony surface was cleaned of inorganic and organic material by a gentle jet of filtered seawater and subsequently placed for 3 h in an aquarium filled with 0.2-μm filtered seawater in order to avoid artificially high mucus production rates through stress situations during incubation. To measure the mucus release, two series of six colonies of *Cladocora cespitosa* were incubated in 1-liter sterilized glass jars containing 0.2-μm filtered seawater for 3 to 4 h. For each colony a single jar was used. After removing the colonies from the jars the water was filtered through a preweighed filter (47-mm diameter, 0.2-μm pore size), rinsed with 5 ml 0.5 N H_2SO_4 to remove free carbonate, and then with 5 ml distilled water. The filter was dried at 70 °C for 24 h and afterwards reweighed. The rate of mucus released per polyp was determined.

Decomposition experiments

Mucus for decomposition experiments was collected by squirting the oral surface with a gentle jet of 0.2-μm filtered seawater. Mucus collected in this way was not visually detectable and precipitation treatments using a magnetic stirrer for 5 min were required before it could be detected. Only stirred mucus was used for experimentation. One hundred ml of this seawater-mucus mixture was used for decomposition experiments. This mixture was incubated in 400 ml seawater which was filtered through a 5-μm filter prior to incubation to remove zooplankton and flagellates. Six decomposition experiments of 32 h each were set up with control runs (5-μm filtered seawater without mucus added). The mucus dry weight in the incubation jars varied between 42 and 66 mg l^{-1}.

All the jars were held in the dark at 20 °C, aerated with 0.2-μm filtered air and sealed. Mucus was held in suspension in the incubation media by means of the turbulence caused by the air stream. Each series was sampled at intervals of 2 to 3 h for 8 h and thereafter at 8 to 16-h intervals. Samples of 2 ml for dissolved organic carbon (DOC) and 5 ml for bacterial density were taken from the incubation media. The samples for the determination of DOC concentrations were filtered through 0.2-μm filters and frozen (–20 °C); samples for bacterial density determinations were fixed with formalin to a final concentration of 4% and stored in the dark until analysis. At the end of each series the incubation media, together with the enclosed mucus particles of each jar, were filtered through preweighed 0.2-μm filters in the way described above. Because only freshly collected mucus was used in all decomposition experiments, the dry weight of the mucus added to each jar was only obtainable after the end of the experiment. Additionally, the development of bacterial density and the carbon content in/onto mucus particles were followed in seven separate experiments over 24 and 72 h, respectively. For this purpose mucus was collected and incubated in the way described above and sampled at intervals of 2 to 3 h at the initial phase and afterwards at 24-h intervals. Mucus particles were removed from the incubation media by means of forceps and Pasteurpipettes, rinsed with 0.5 N H_2SO_4 and distilled H_2O and grinded in a pre-sterilized tissue grinder with 10 ml 0.2 μm filtered distilled water. This 10 ml suspension was divided in 2 ml for total organic carbon (TOC), 3 ml for bacterial density, and 5 ml for dry weight determination.

Carbon analysis

Total organic carbon (TOC) of mucus particles and dissolved organic carbon (DOC) of the incubation media were measured using a Beckman-Tocamaster 915-B. Calibration standards were made from a stock solution (1 000 mg C l^{-1}) of 2.125 g reagent grade anhydrous potassium biphtalate in 1-liter distilled water. Samples were freed of inorganic carbon sources by acidification to about pH 2 with 50 μl HCl (conc. 2%) and application of a stream of synthetic CO_2- free air. At least two replicates were made for each sample.

Number and biomass of bacteria

Numbers of bacteria were estimated using the acridine orange counting (AODC) technique of Hobbie *et al.* (1977) and Daley (1979). Bacterial cells dimensions were determined from visual estimates during AODC, in which 100 to 150 rods and 60 to 100 cocci were measured and the mean volumes subsequently calculated. The numbers of bacteria and wet biomass were calculated using the conversion factor of Linley *et al.* (1981) and Linley and Field (1982). Conversions to dry biomass and carbon equivalent of the wet biomass were achieved using the coefficient 0.2 (Troitsky and Sorokin, 1967) and 0.1 (Luria, 1960), respectively.

Results

Rates of mucus release

The release of mucus into ambient waters varied between 4.51 and 17.34 μg (mucus dry wt) $polyp^{-1}$ h^{-1} during the

course of incubation experiments. Mean mucus release was 8.54 μg (mucus dry wt) polyp^{-1} h^{-1} (SD = 4.53, n = 12). As already mentioned (see Material and methods), precipitation treatments were required before the rate of mucus release could be measured. This initial, low-viscosity mucus represents an early stage in the polymeric aging process (Ducklow and Mitchell, 1979a) that is able to pass through 0.1-μm Millepore filters (Crossland *et al.*, 1980b). However, after stirring the incubation media, the mucus became a milky colour and was retained by 0.2-μm filters.

Mucus decomposition experiments

The initial bacterial densities in the incubation media varied between 1.5 and 12.1 × 10^5 cells ml^{-1}. The bacteria subsequently increased in numbers to a peak density of 66.2 × 10^5 cells ml^{-1} after 24 h to which 66 mg mucus dry wt l^{-1} had been added. In one out of six incubation experiments the peak density of 49.1 × 10^5 cells ml^{-1} was reached after 32 h. Typical developments of bacterial densities and changes in DOC concentrations in the incubation media during the decomposition of *Cladocora cespitosa* mucus are shown in Fig. 1. While bacteria reached maximum density after 24 and 32 h (Fig. 1a), respectively, DOC concentrations of water enriched with mucus were within the range of the concentration in the control jar (Fig. 1b).

In the jars containing mucus, the mean biovolume of rods increased from 0.46 μm^3 (SD = 0.18, n = 130) up to 1.18 μm^3 (SD = 0.31, n = 140) during the course of incubation; the biovolume of rods in the control jar remained unaffected. The volume of cocci remained constant in both the mucus and in the control jars ($\bar{x}$ = 0.042, SD = 0.013, n = 95).

The development of bacterial density, together with the changes of TOC content of mucus particles during the course of incubation for 24 h, is shown in Fig. 2. In the initial phase, bacterial density in mucus particles increased from 1.45 and 1.87 × 10^6 cells mg (mucus dry wt)$^{-1}$ to 2.31 × 10^6 cells mg (mucus dry wt)$^{-1}$ (Fig. 2a) and 4.53 × 10^6 cells mg (mucus dry wt)$^{-1}$ (Fig. 2b), respectively. During the following hours bacterial density decreased, reaching values below initial bacterial counts 24 h after starting the experiments. Initial TOC values of freshly collected mucus varied between 15.38 and 136.2 μg C mg (mucus dry wt)$^{-1}$ ($\bar{x}$ = 102.2 μg C, SD = 11.87, n = 7). Parallel to the increased bacterial density, TOC concentrations increased slightly during the first 3 h and then declined. After 24 h TOC contents of mucus particles dropped to 40 to 54% of the initial TOC concentrations in all experiments.

The initial exponential growth of bacteria in the incubation media allowed some estimates to be made of the rate of increase of bacterial cells h^{-1} (μ) and the doubling time (g) of the bacteria associated with the initial decomposition of *Cladocora cespitosa* mucus. The increase in bacterial biomass and its carbon equivalent additionally allowed estimations of bacterial carbon production (Table 1).

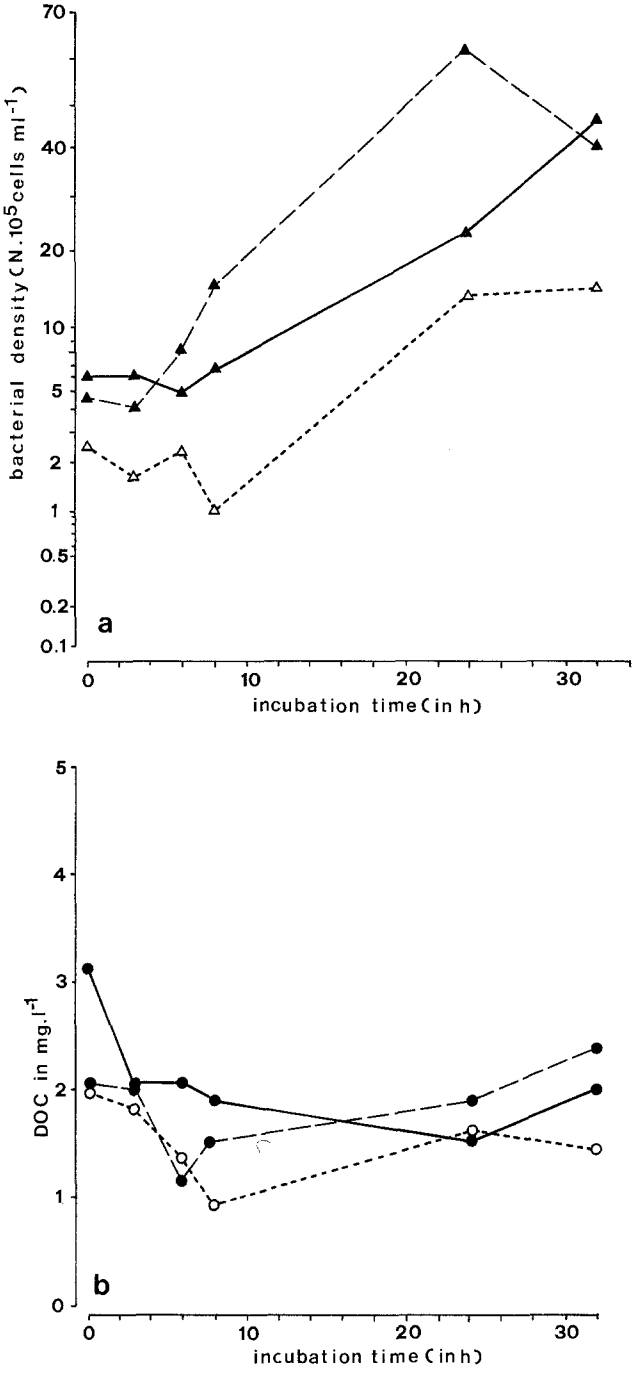

Fig. 1. *Cladocora cespitosa.* Development of (a) bacterial density in N × 10^5 cells ml^{-1} and (b) DOC concentrations in mg C l^{-1} in the incubation media containing 6.2 mg C l^{-1} of *C. cespitosa* derived mucus incubated at 20 °C; 2 representative experiments are shown (full and broken lines). Dotted line indicates control (no mucus added)

Although bacterial carbon production associated with *C. cespitosa* mucus varied considerably ($\bar{x}$ = 11.81, SD = 9.33, n = 6), it was about one order of magnitude higher than in the control jars. Carbon utilization, measured concurrently with increase in bacterial carbon over the initial logarithmic growth phase of bacteria, allowed calculation of the net carbon conversion efficiency (Table 1). The mean car-

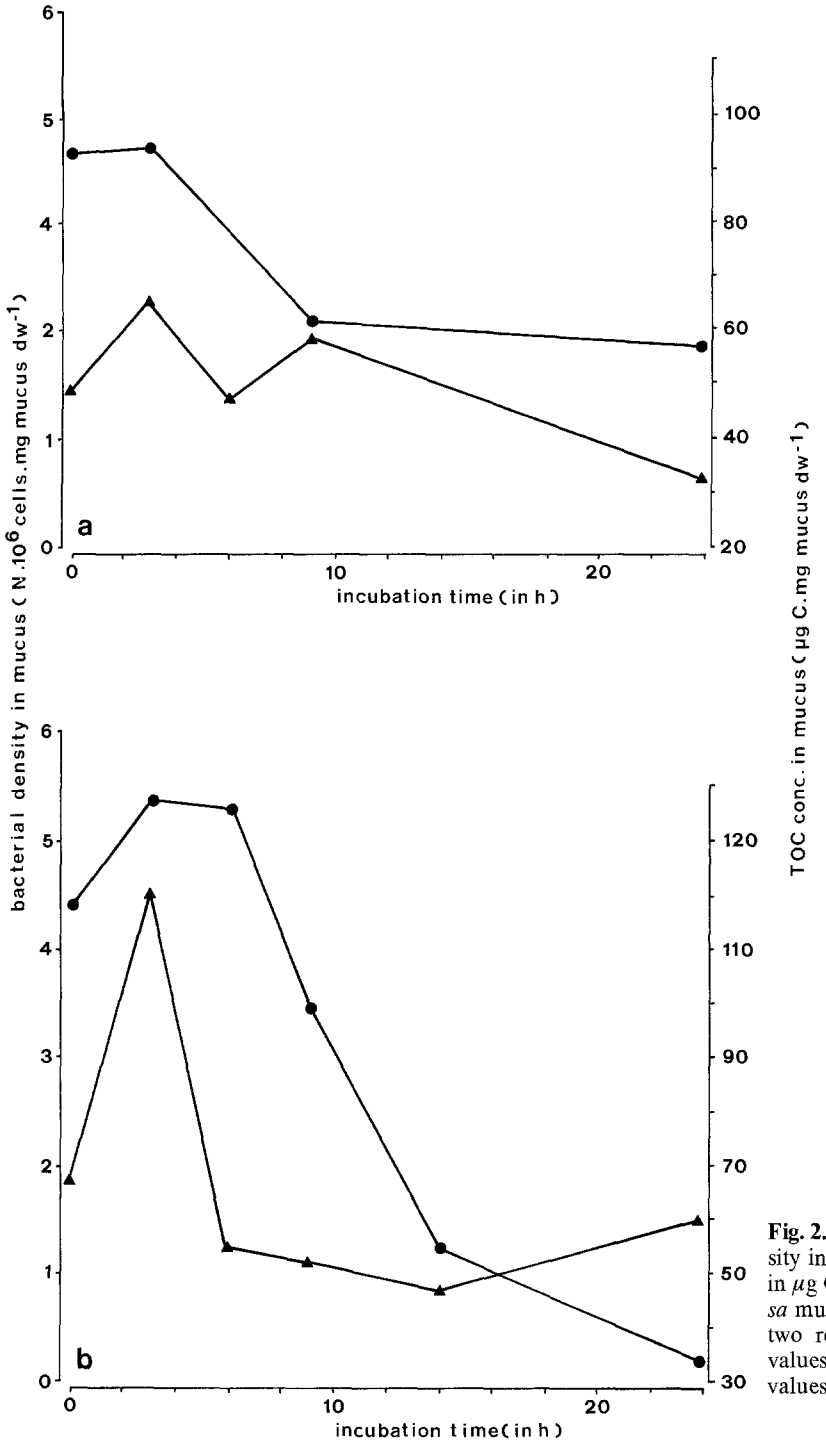

Fig. 2. *Cladocora cespitosa.* Development of bacterial density in $N \times 10^6$ cells mg (mucus dry wt)$^{-1}$ and TOC content in μg C mg (mucus dry wt)$^{-1}$ of freshly collected *C. cespitosa* mucus particles incubated for 24 h at 20 °C shown from two representative experiments (a, b). Triangles indicate values obtained for bacterial densities. Circles represent values of TOC concentrations

bon conversion efficiency during decomposition of *C. cespitosa* mucus was 19.4%, again one order of magnitude higher than the mean carbon conversion efficiency obtained from control media, which lacked mucus particles.

Discussion and conclusions

In the present approach, an attempt was made to minimize stress conditions in order to obtain a mucus release into the water under conditions as natural as possible. By cleaning the coral of sediment and adsorbed POM, interference of foreign organic matter was minimized, and the only exposure to air, lasting at most 20 s, was due to the transfer into the container with 0.2-μm filtered seawater. This short exposure could not be avoided in the experimental approach and may well have an influence on the organisms, resulting at least temporarily in mucus production under stress conditions. For the decomposition experiments, mucus collection had to be achieved by gentle jet squirting of the oral surfaces and stress mucus may have been harvested. However, *in situ,* this stress mucus is perhaps frequently

Table 1. *Cladocora cespitosa.* Rate of increase of bacterial cells μ (= ln 2/g), the doubling time g, the carbon production and utilization from *C. cespitosa* mucus incubated in seawater at 20 °C. The carbon conversion efficiency is also shown. All values calculated over the same period of time up to the peak of bacterial biomass at 21–32 h

Experiment no. and date	Bacteria		Bacterial carbon produced (μg C l^{-1} h^{-1})	Carbon used (μg C l^{-1} h^{-1})	Carbon conversion efficiency % $\frac{\text{Carbon production}}{\text{Carbon used}} \times 100$
	μ (h^{-1})	g (h)			
1 5 Nov	0.066	10.5	17.68	172.08	10.27
2 5 Nov	0.112	6.2	30.14	110.0	27.4
3 31 Oct	0.079	8.7	6.74	79.17	8.51
4 3 Jul	0.056	12.4	4.43	12.17	36.4
5 29 Oct	0.089	7.8	7.12	39.42	18.06
6 29 Oct	0.064	10.9	4.75	30.76	15.44
$\bar{x}\pm$SD	0.077±0.018	9.42±2.07	11.81±9.33	73.93±54.5	19.35± 9.77
Control					
5 Nov	0.059	11.74	1.74	49.06	3.54
31 Oct	0.073	9.52	0.86	46.66	1.84
3 Jul	0.019	35.06	0.61	29.58	2.06
29 Oct	0.0015	468.52	0.147	44.28	0.33
$\bar{x}\pm$SD	0.038±0.029	131.21±195.0	0.84±0.58	42.39±7.59	1.94± 1.14

produced for protection during aeral exposure on the reef flat (Krupp, 1984) and sedimentation (Schuhmacher, 1977).

As mentioned earlier on (see Material and methods), the experiments were performed using 5-μm filtered seawater as incubation media in order to remove heterotrophic flagellates. Despite the possible effects of grazer exclusion (Johannes, 1968; Pomeroy, 1974; Lampert, 1978; Copping and Lorenzen, 1980), this approach was used to measure the increase in biomass of bacteria associated with the degradation of mucus rather than the ^{14}C-method (see also Rodina, 1972; van Es and Meyer-Reil, 1982). The method we used has the advantage that estimates of bacterial production are based on the natural components of dissolved and particulate organic matter (Joint and Morris, 1982; Newell, 1984).

Mean mucus release rate obtained for *Cladocora cespitosa* was 8.54 μg (mucus dry wt) $polyp^{-1}$ h^{-1}. Extrapolating from the mucus release rate obtained in the laboratory to the Bight of Piran, we would expect a mucus production of approximately 320 mg (mucus dry wt) m^{-2} d^{-1}. This value is based on a mean coverage of 2.33% m^{-2} of *C. cespitosa* along transects in front of the Marine Research and Training Center Piran and 6.73 polyps cm^{-2} coral head (SD = 0.49, n = 20) (Herndl *et al.*, in preparation). This estimated production value is relatively close to the 480 mg m^{-2} d^{-1} reported by Johannes (1967) from investigations at Eniwetok and well above the 51 mg m^{-2} d^{-1} recorded by Richman *et al.* (1975) from the nature reserve at Eilat. However, one has to take into account that: (1) we measured the mucus release under laboratory conditions and (2) the occurrence of those dense *C. cespitosa* patches is limited to the Bight of Piran (Tins, 1974). Still our high mucus production value could be explained as an adaptation to the high sedimentation environment of this shallow body of water, since Rublee *et al.* (1980) observed increased mucus production from the soft coral *Briarium asbestinum* with increasing turbidity.

In terms of carbon the estimated 320 mg (mucus dry wt) m^{-2} d^{-1} released by *Cladocora cespitosa* off Piran would account for about 32 mg C m^{-2} d^{-1}, assuming a mean organic carbon content of freshly collected mucus of 102.2 μg C mg (mucus dry wt)$^{-1}$. As phytoplankton primary production of the Northern Adriatic Sea averaged over an annual cycle is about 171 mg C m^{-2} d^{-1} (Kveder-Revelante, 1970, cited in Stirn, 1971), mucus production in terms of carbon would be equivalent to 19% of phytoplankton primary production.

The mean respiration rate of *C. cespitosa* is 0.29 μl O_2 mg (tissue dry wt)$^{-1}$ h^{-1}, which is equivalent to a respiratory carbon demand of 0.2 μg C mg (tissue dry wt)$^{-1}$ h^{-1} and 1.96 μg C $polyp^{-1}$ h^{-1} (obtained from a mean tissue dry wt of 9.58 mg $polyp^{-1}$) (Herndl *et al.*, in preparation). Mucus release would therefore account for a loss of 0.87 μg C $polyp^{-1}$ h^{-1}, which is about 44% of coral respiration. Johannes (1967) reported values of 40% and Crossland *et al.* (1980 b) estimated that there is a 40% loss of the net carbon fixed, in the form of mucus, in *Acropora acuminata.* Davies (1984) suggested that the loss of 48% of the fixed energy could be attributable to mucus secretion of *Pocillopora eydouxi.*

Bacterial population during mucus decomposition experiments increased in the incubation media up to 24 to 32 h. The rapid decrease observed following peak densities is probably caused by the appearance of heterotrophic flagellates, although the incubation media were filtered through 5-μm filters prior to the start of experimentation. Newell *et al.* (1983) found that bacteria declined 21 h after starting incubation experiments with saltmarsh macrophytes in 5-μm filtered seawater when microflagellates entered logarithmic growth.

Mean bacterial carbon content of mucus particles is 4.3×10^{-2} µg C mg (mucus dry wt)$^{-1}$ (SD = 2.5×10^{-2}, $n = 11$). Compared to the TOC content of mucus particles, bacterial carbon contributes less than 0.1% to the total organic carbon pool of mucus. This indicates that mucus released by corals differs as a food source from most other types of organic aggregates in that colonization of bacteria is not required to increase the nutritional value of mucus, while the availability of macrophyte detritus to consumers needs to be delayed for extensive periods of nutritional enhancement by decomposer processing (Fenchel and Jørgensen, 1977; Velimirov *et al.*, 1981; Mann, 1982), since most detritivores are unable to digest the structural components of the detritus but may utilize the attached microbes as a food source. A series of papers (Coles and Strathman, 1973; Benson and Muscatine, 1974; Ducklow and Mitchell, 1979a) have shown that mucus is nutritionally rich. The high nutritional value of *Cladocora cespitosa* mucus for bacteria is indicated in the present study (Table 1) by the high carbon conversion efficiency. While bacterial carbon production is largely dependent on the concentration and ease of degradation of the detrital source, carbon conversion efficiency is relatively uniform despite wide differences in the concentration and ease of degradation (Newell, 1984). Our mean carbon conversion efficiency is about twice as high as values given by Newell *et al.* (1981, 1983) for diatoms, dinoflagellates, macroalgae and seagrasses, but close to conversion efficiencies obtained for nitrogen rich fecal material of the mussel *Aulacomya ater* (Stuart *et al.*, 1982) and kelp fronds on the strandline (Koop *et al.*, 1982a, b). Where the nitrogen content of the detritus is high, less carbon is required to incorporate the nitrogen necessary for biosynthesis and the carbon conversion efficiency reaches a high value (Newell, 1984).

In summary, our results indicate that *Cladocora cespitosa* derived mucus is nutritionally rich and easily degradable for bacteria, as indicated by the high carbon conversion efficiency. However, the direct utilization of this mucus as a food source for consumers in the Northern Adriatic Sea remains unknown.

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