Mucus trails in the rocky intertidal: a highly active microenvironment

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ABSTRACT: The significance of mucus trails derived from the herbivorous gastropods *Patella caerulea*, *Monodonta turbinata* and *Tegula* sp. in enhancing microbial activity in marine rocky intertidal and sublittoral zones was investigated by means of microcosm and field experiments. A pronounced increase of bacterial abundance concurrently with extracellular glucosidase activity (alpha-D- and beta-D-glucosidase) was observed in mucus-enriched batch cultures within 2 d of incubation; maximum values of exoproteolytic activity (leucine-aminopeptidase) were reached ca 1 d later than the peaks in bacterial abundance and glucosidase activity. In all mucus-enriched treatments the levels of glucosidase activity were significantly correlated with bacterial abundance; a high correlation also existed between alpha-D- and beta-D-glucosidase activity in enriched treatments while exoproteolytic activity was less dependent on bacterial density in the later stage of decomposition; this decoupling might be caused by an enhanced aminopeptidase expression per cell. The activity of total glucosidase in the surrounding water closely followed the disappearance of total carbohydrates from mucous layers. Microalgal biomass on glass fiber filters coated with trail mucus was significantly higher (5.1 µg chl *a* (25 cm)$^{-2}$) after 1 wk of exposure in the field compared to mucus-free control filters (0.9 µg chl *a* (25 cm)$^{-2}$). It is hypothesized that mucus-derived polymers entering the DOM-pool are further hydrolyzed and taken up by the free-living bacterial community. The observed stimulation of microalgal growth supports the idea that the breakdown of mucous material by bacterial enzymes can provide a microenvironment enriched in regenerated inorganic nutrients. The estimated high areal trail mucus production (81 g mucus dry wt m^{-2} yr^{-1} for *P. caerulea*, 544 g mucus dry wt m^{-2} yr^{-1} for *M. turbinata*) suggests that mucus is a significant source for microbial activity in some nearshore waters.

INTRODUCTION

Grazing gastropods are abundant consumers of benthic primary production in many rocky intertidal shores; they can also produce significant amounts of organic detritus either as fecal material or in the form of mucus (Peduzzi & Herndl 1986, Peduzzi 1987). Secretion of mucus by aquatic animals results in a loss of energy from the organisms and provides a medium for microbial growth (Calow 1974, Herndl & Velimirov 1986, Horn 1986). Gastropods produce trails of mucus as they crawl, spending up to 80 % of assimilated energy in this process (Edwards & Welsh 1982, Horn 1986, Davies et al. 1991). Gastropod pedal mucus consists primarily of proteins and polysaccharides with low C:N ratios (Connor 1986). In a previous study (Herndl & Peduzzi 1989) it could be shown that mucous trails produced by marine gastropods are readily degradable and rapidly utilized by microheterotrophs. Rapid structural changes of these mucous layers and loss of total carbohydrates (TCHO) from mucus-coated surfaces (Herndl & Peduzzi 1989, Peduzzi 1990) may suggest a significant transfer of material and energy to the near surrounding water body.

Bacterial extracellular enzymatic activity has long been recognized as an important factor for macromolecular substrate turnover in marine systems (Hoppe 1983, Vives Rego et al. 1985, Hoppe et al. 1988). Bacteria possess a wide range of extracellular enzymes potentially capable of degrading mucoid polymers which cannot be taken up directly by these organisms unless hydrolyzed. Endohydrolases, acting on particulate material such as mucous layers, generate low molecular weight polymers or oligomers which must still be solubilized by exohydrolases (Priest 1984).

The present study attempted to assess the importance of gastropod-derived mucus as a possible source of nutrients for microbes in the water body near mucus trails. It was asked whether extracellular enzymatic activity in free-living bacteria is stimulated due to the

presence of mucus and whether the development of
enzymatic activity in the waters adjacent to mucus is
related to the abundance of suspended bacteria.

In studies by Connor & Quinn (1984) and Connor
(1986), evidence was presented that some herbivorous
gastropods produce mucous trails which can stimulate
benthic microalgal growth. Although it has been shown
that microalgae are able to take up organic nutrients
(Hellebust & Lewin 1977, Myklestad 1978), it is
unlikely that they are able to compete efficiently for
this organic source with the combined free-living and
attached bacterial community. It is more likely that the
rapidly colonizing bacteria (Herndl & Peduzzi 1989,
Peduzzi 1990) in concert with bacterivorous flagellates
provide a microenvironment enriched in inorganic
nutrients. Therefore, it was further asked whether
pedal mucus derived from the gastropod species inves-
tigated here enhances microphytobenthic growth in
natural environments.

Since there is considerable disparity in the limited
information available on the quantity of mucus produc-
tion, the present study also aimed to estimate rates of
pedal mucus secretion. Based on these data together
with the abundance of animals in the field, we tried to
estimate the impact of pedal mucus in sublittoral and
intertidal ecosystems inhabited by grazing gastropods.

MATERIAL AND METHODS

Herbivorous gastropods *Patella caerulea* and *Mono-
donta turbinata* were collected in the intertidal and
shallow sublittoral in the Gulf of Trieste (Northern
Adriatic Sea) off the Laboratorio di Biologia Marine at
Trieste-Aurisina, Italy. *Tegula* sp. specimens were
obtained from the intertidal of 'Pacific Cove', La Jolla,
California, USA. All gastropods were kept in aerated
aquaria at maximum 24 h before being used. Labora-
tory experiments were conducted in the Laboratorio di
Biologia Marina at Trieste-Aurisina and at the Institute
of Marine Resources, Scripps Institution of Oceanogra-
phy, UCSD, La Jolla.

Pedal mucus for incubation experiments was col-
lected by allowing the gastropods to crawl for 20 to 30
min on precombusted (450 °C) Whatman GF/F glass
fiber filters submerged in a sterilized glass tank filled
with 0.2 µm Nuclepore-filtered seawater. Subse-
quently, mucus-coated filters were incubated horizon-
tally with the mucus trail facing upward at in situ
temperatures (Pacific: 18 °C; Mediterranean: 25 °C) in
the dark. To each precombusted (470 °C) glass jar,
250 ml of 0.6 µm (Nuclepore) filtered seawater, col-
lected from the same site as the gastropods, was added
together with 4 to 5 mucus-coated and uncoated (con-
trol jar) GF/F filters.

Parameters were monitored in time series over 70 to
100 h as follows:

(1) Development of bacterial numbers in the incuba-
tion media was measured using the acridine orange
direct counting (AODC) technique (Hobbie et al. 1977).
Water samples were fixed with unbuffered formalin to
a final concentration of 2 % (v/v).

(2) The main purpose of this investigation was to
evaluate a possible stimulation of enzymatic action on
poly- and oligomers of mucous origin in the water
surrounding mucus. In order to estimate bacterial
extracellular enzyme activities fluorogenic model sub-
strates were used. The activity of alpha-D-glucosidase
and beta-D-glucosidase was measured by means of
methylumbelliferyl (MUF) substrates according to
Hoppe (1983) and Somville (1984). For protease activity
L-leucine-methylcoumarinylamid (leu-MCA) was used
(Hoppe 1983, Hoppe et al. 1988). After addition of the
substrates to subsamples (2.5 µM final concentration)
withdrawn from the incubation jars at various time
intervals, fluorescence intensity of these samples was
measured, immediately and usually after 15 to 45 min
of incubation, at 444 nm under 360 nm excitation using
either a Jasco 820-FP or a Farrand MK2 spectro-
fluorometer.

(3) Disappearance of total carbohydrates (TCHO)
from mucus-coated GF/F filters was determined with
the method of Burney & Sieburth (1977) as described in
Herndl & Peduzzi (1989). TCHO-concentration was
selected as a model component for poly- and oligomer
liberation from mucous layers. All TCHO-samples
were stored frozen (−20 °C) until analyzed.

For each gastropod species mucus incubations were
performed in quadruplicate. Two jars were used for
determination of bacterial numbers and enzymatic
activities, 2 chambers for TCHO-measurements; in
each experimental run an additional jar with mucus-
free precombusted glass fiber filters served as a control
for endogenous microbial growth.

To determine the rate of mucus production by gas-
tropods, 48 *Patella caerulea* and 65 *Monodonta turbinata*
of average size were allowed to crawl individually on
single, preweighed sheets of aluminum foil (4 by 4 cm)
which were held in a tank with aerated seawater in a way
that their movement was restricted to the foil. The surface
was roughened by crumpling the foils in order to obtain a
microstructure similar to natural surface conditions. Foil
sheets were replaced every hour over a period of 24 h to
account for possible diurnal variations in movement
activity. The foils with pedal mucus trails were rinsed
briefly with distilled water to remove salts and oven-
dried (60 °C) to constant weight. Care was taken that no
fecal material remained on the sheets.

A set of experiments was conducted in order to
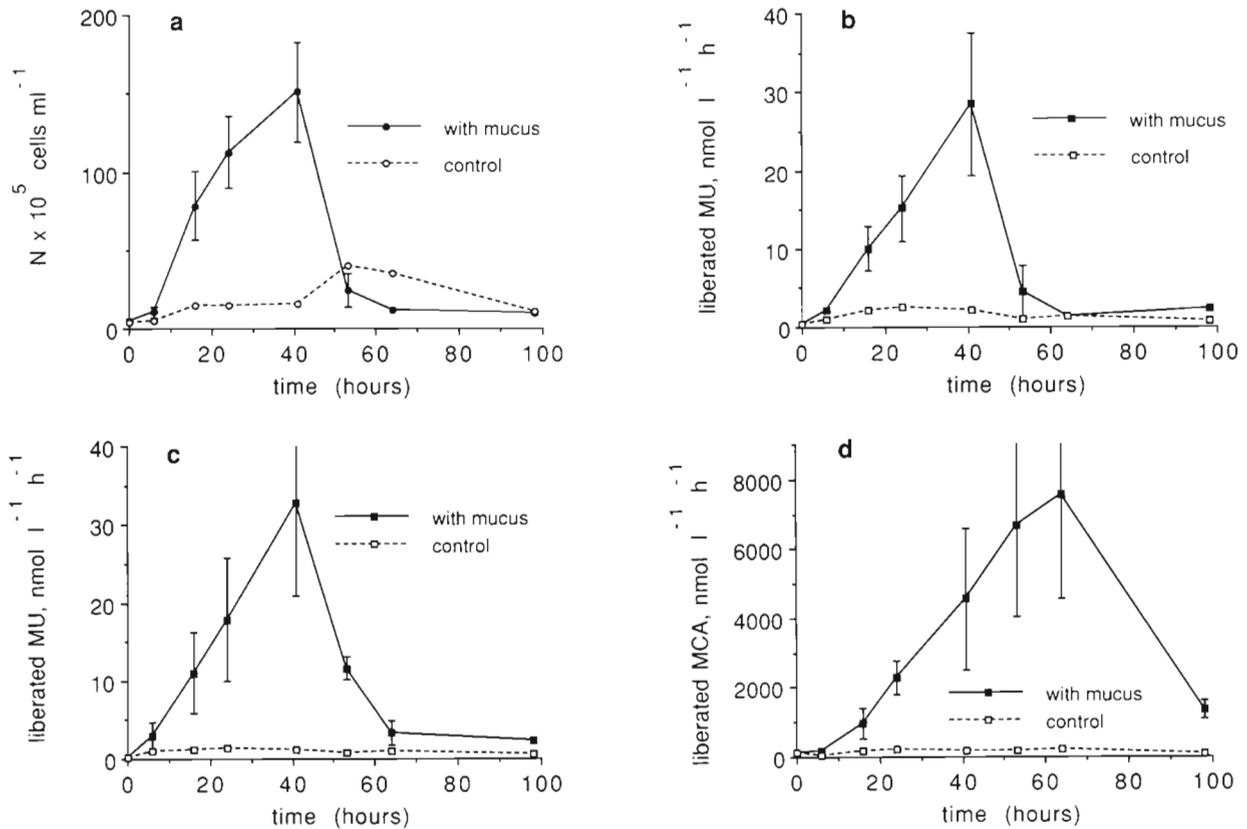determine whether mucus acts as a microalgal growth

Fig. 1. Batch cultures with trail mucus from *Patella caerulea*. Development of (a) free-living bacterial abundance, (b) alpha-D-glucosidase activity, (c) beta-D-glucosidase activity and (d) leucin-aminopeptidase activity in 0.6 μm filtered seawater incubated with pedal mucus and in a mucus-free control. MU: methylumbelliferone, MCA: methyl-coumarinylamid; vertical bars: ± 1 SE of the mean

stimulant. For these experiments only *Patella caerulea* was used as an example of the 3 species studied. This relatively large gastropod produced the highest quantities of mucus and therefore collection of sufficient pedal mucus was substantially facilitated. Single individuals were allowed to crawl on precombusted GF/F filters (47 mm diameter) for ca 45 min. Between 10 and 15 glass fiber filters coated with mucus were fixed onto PVC-panels and placed in a horizontal position in the shallow sublittoral (depth: 0.5 m) off the laboratory at Aurisina. Equal amounts of uncoated filters were used as a control. To exclude grazing activity and disturbance by animals, cages made of nylon netting (mesh size 3 mm) were placed over the panels. A total of 5 experimental runs were conducted, exposing the filters between 180 and 210 h in the field. The amount of microalgae growing on the filters was measured as chlorophyll *a* as described in Strickland & Parsons (1972). Control experiments were conducted in the laboratory to determine whether these mucous layers act as adhesive traps for suspended microalgae (cf. Connor 1986). To exclude the effect of water circulation, filters were placed in flat tanks covered with seawater from the study site and exposed to the same

light and temperature conditions as in the field experiments. Although the biomass of microalgae measured as chlorophyll *a* exhibited a tendency to be higher in field-exposed GF/F filters, no statistically significant differences could be detected (pooled data: *t*-test, $p > 0.2$, $n = 90$). Therefore microalgal biomass on mucus-coated filters in our field experiments was assumed to be mainly caused by algal growth on the surfaces. However, under bloom conditions, which did not occur during our investigation, the effect of gastropod trail mucus as an adhesive trap for microalgae may be significant.

RESULTS

Development of bacterial numbers and enzymatic activity in surrounding water

Changes in bacterial abundance in the 0.6 μm filtered incubation media with and without the addition of pedal mucus derived from *Patella caerulea* is shown in Fig. 1. In the enriched treatment, average bacterial density increased from 4.8 to 150.8×10^5 cells ml^{-1}
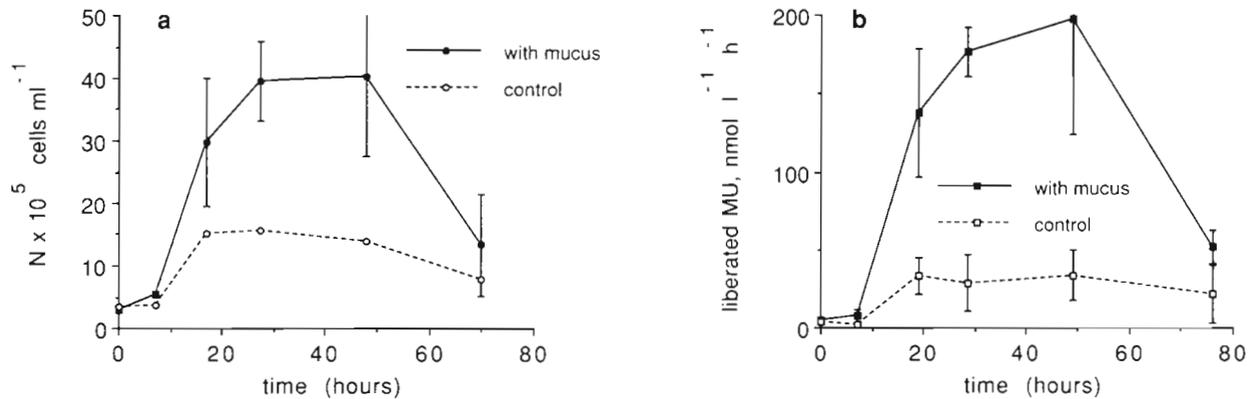
Fig. 2. Batch cultures with trail mucus derived from *Monodonta turbinata*. Time course of (a) free-living bacterial abundance, (b) total (i.e. alpha-D- plus beta-D-) glucosidase activity in 0.6 μm filtered seawater (mucus-enriched and unenriched). Symbols and abbreviations as in Fig. 1
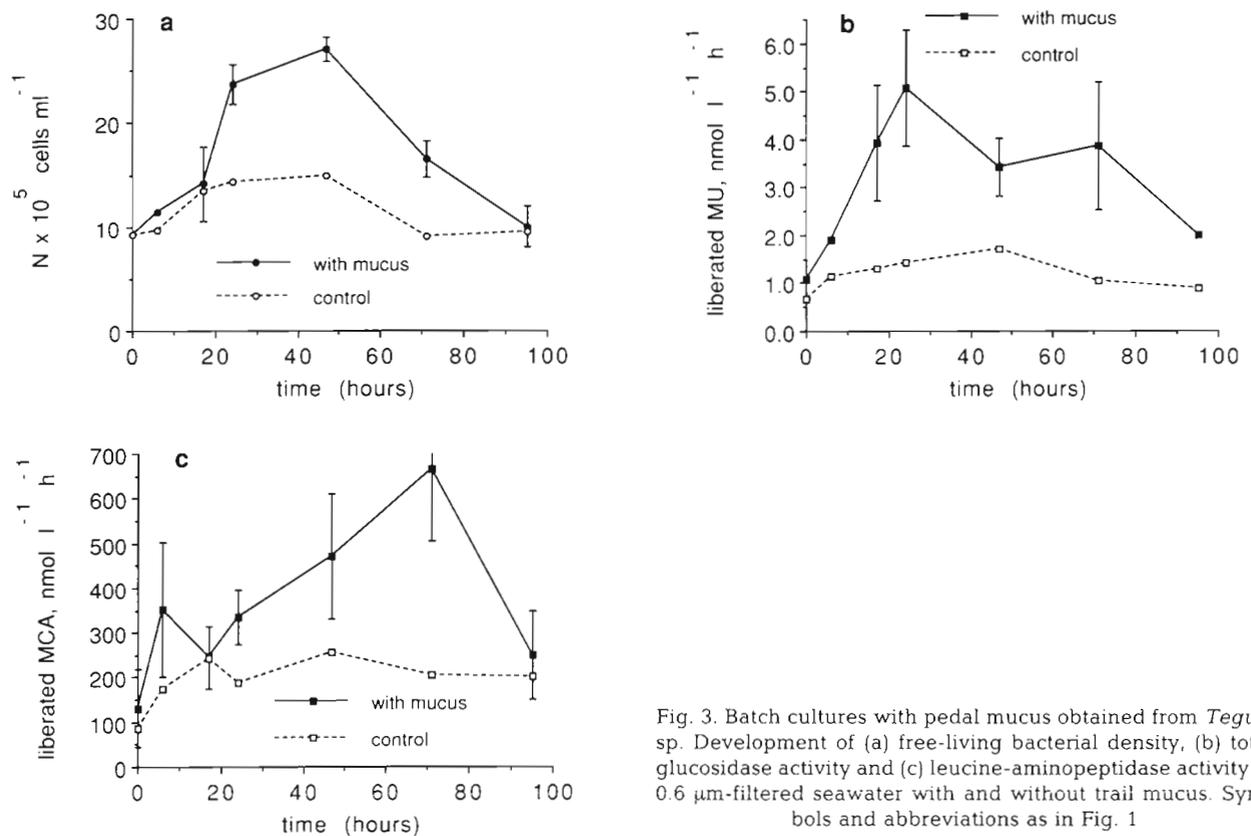

Fig. 3. Batch cultures with pedal mucus obtained from *Tegula* sp. Development of (a) free-living bacterial density, (b) total glucosidase activity and (c) leucine-aminopeptidase activity in 0.6 μm-filtered seawater with and without trail mucus. Symbols and abbreviations as in Fig. 1

within 41 h (Fig. 1a). In the mucus-free control chamber bacterial numbers never exceeded 40.3×10^5 ml^{-1}. Concurrently with cell density the activity of extracellular glucosidase (both alpha-D- and beta-D-glucosidase) in the mucus-enriched water increased, reaching peak values also after 41 h of incubation (Fig. 1b, c). The development of exoproteolytic activity exhibited a different pattern (Fig. 1d); maximum values were reached ca 1 d later than the peaks in bacterial abundance and glucosidase activity.

The reaction of the free-living bacterial community and the extracellular enzymatic activity to addition of mucus derived from *Monodonta turbinata* and *Tegula* sp. exhibited a similar pattern to *Patella caerulea* (Figs. 2a, b & 3a, b). Since the activity of beta-D-glucosidase followed the same dynamics as alpha-D-glucosidase during the incubations with mucus in all species studied (as an example see Fig. 1b, c; compare also Table 1), both were summed and presented as 'total glucosidase activity'. In Fig. 3c the exoproteolytic activ-

Table 1. Calculated relationships between various microbial parameters measured during decomposition of gastropod pedal mucus. AGA: alpha-D-glucosidase activity; BD: bacterial density; BGA: beta-D-glucosidase activity; LAPA: leucin-aminopeptidase activity; TCHOdis: % total carbohydrates disappeared from mucous layers; TGA: total glucosidase activity. Units for extracellular enzymatic activity in nmol liberated substrate $l^{-1} h^{-1}$; n = number of pairs, r = correlation coefficient, p = probability

Relationship	Equation	n	r	p
Patella caerulea				
BD vs AGA	AGA = −0.4049 + 0.1672 BD	16	0.93	< 0.001
BD vs BGA	BGA = 1.0349 + 0.1827 BD	16	0.88	< 0.001
AGA vs BGA	BGA = 1.2395 + 1.1220 AGA	16	0.97	< 0.001
BD vs LAPA	LAPA = 2735.6 + 4.3712 BD	16	0.08	> 0.200
TCHOdis vs TGA	—[a]	−	−	−
Monodonta turbinata				
BD vs AGA	AGA = 5.2296 + 2.2313 BD	12	0.73	< 0.010
BD vs BGA	BGA = −8.4223 + 2.3748 BD	12	0.88	< 0.001
AGA vs BGA	BGA = 12.1910 + 0.5794 AGA	12	0.65	< 0.050
BD vs LAPA	—[a]	−	−	−
TCHOdis vs TGA	TGA = $2.0074 \times 10^{2.2445 e^{-\text{TCHOdis}}}$	10	0.99	< 0.001
Tegula sp.				
BD vs AGA	AGA = −2.0600 + 3.1370 log(BD)	14	0.77	< 0.010
BD vs BGA	BGA = −2.4089 + 3.2603 log(BD)	14	0.77	< 0.010
AGA vs BGA	BGA = −0.1431 + 0.9661 AGA	14	0.94	< 0.001
BD vs LAPA	LAPA ≈ 111.62 + 11.412 BD	10	0.53	> 0.100
TCHOdis vs TGA	TGA = $1.2046 \times 10^{9.0017 e^{-\text{TCHOdis}}}$	8	0.99	< 0.001

[a] No data available

ity is shown for *Tegula* sp.; a maximum was reached 71 h after starting the incubation. Unfortunately, no data are available for *M. turbinata*. In all control treatments (precombusted filters only) the parameters investigated remained at low levels.

Based on our data, regression equations were calculated to determine possible correlations and interdependences (Table 1). Throughout all mucus-enriched treatments the levels of glucosidase activity were significantly correlated with the density of bacterial cells. A high correlation existed also between alpha-D- and beta-D-glucosidase activity in incubations with mucus from all 3 species. No significant correlation was detected between bacterial density and exoproteolytic activity.

Disappearance of total carbohydrates (TCHO) from mucous layers

Approximately 78 % of the TCHO derived from mucous trails produced by *Monodonta turbinata* had disappeared ca 40 to 50 h after starting the incubation (Fig. 4). This 78 % represents the maximum level of mucus TCHO disappearance observed in our experiments. This pattern was followed closely by the activity of total glucosidase in the surrounding water during the first
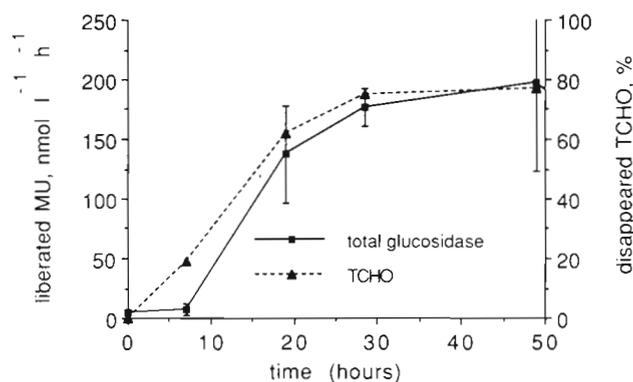

Fig. 4. Incubation with pedal mucus derived from *Monodonta turbinata*. Disappearence of total carbohydrates (TCHO; per cent of initial) from mucous layers and increase in total glucosidase activity during the first 50 h of incubation in 0.6 µm filtered seawater surrounding mucus trails. Symbols and abbreviations as in Fig. 1

50 h as indicated by a highly significant correlation resulting in an exponential regression equation (see Table 1. Using pedal mucus from *Tegula* sp., ca 76 % of TCHO disappeared even after only 24 h of incubation (data not shown). Again, the activity pattern of total glucosidase in the surrounding water was closely related to the amount of surface-disappeared TCHO (see equation and correlation parameters in Table 1).

Growth stimulation of benthic microalgae by pedal mucus

In all experimental runs, the microalgal biomass on GF/F filters coated with trail mucus from *Patella caerulea* and exposed in the field was significantly higher at the end of the incubation period (7.5 to 8.75 d; pooled data: *t*-test, p < 0.001). Normalizing the values to a period of 1 wk field exposure resulted in an average net biomass increase of 5.10 μg chl *a* (SD = 2.41) 25 cm^{-2} mucus-coated filter area wk^{-1} as compared to 0.87 μg chl *a* (SD = 0.32) on an equal area of mucus-free control glass fiber filters. When checking subsamples under the microscope, only diatoms were found which were therefore considered the main microalgal colonizers of the filters.

Production rates of gastropod pedal mucus

Since no consistent diurnal pattern of pedal mucus production was detectable from our hourly measurements the data were pooled to give an estimate of mucus secretion on a daily basis. The dry wt of trail mucus produced by an average sized *Patella caerulea* was 12.27 mg ind.$^{-1}$ d^{-1} (SD = 3.14); *Monodonta turbinata* secreted 5.58 mg dry wt ind.$^{-1}$ d^{-1} (SD = 2.26); this corresponded to 1.35 mg mucus-TCHO ind.$^{-1}$ d^{-1} for *P. caerulea* and 0.55 mg mucus-TCHO ind.$^{-1}$ d^{-1} for *M. turbinata*.

DISCUSSION

Microbial abundance and extracellular activity measured in our incubation experiments with gastropod pedal mucus exhibited a clear tendency. In all incubation chambers containing mucus-coated glass fiber filters growth of bacteria and extracellular enzymatic activity in the surrounding water body was significantly enhanced when compared to unenriched controls. In 0.6 μm filtered seawater (25 °C) enriched with trail mucus derived from *Patella caerulea*, free-living bacteria grew with a turnover time of 4.0 h; in incubations with mucus from *Monodonta turbinata* a generation time of 5.1 h can be calculated during the exponential growth phase. This is in agreement with results obtained in a previous work with mucus produced by *M. turbinata* (Herndl & Peduzzi 1989). Generation times determined for free-living bacteria incubated with mucus from *Tegula* sp. were substantially higher (17.7 h), indicating a less favorable substrate for bacterial growth derived from this type of mucus. However, the lower temperature in incubations with this Pacific species (18 °C) could also have been responsible for the higher generation times. Based on our regres-

sion analyses (Table 1) in water surrounding mucus, glucosidase activity can be considered a function of bacterial abundance and appeared to be most likely associated with the free-living bacteria themselves. This was also pointed out by Somville (1984) and Chrost (1989) studying glucosidase activities in natural waters. Furthermore the highly significant correlation between alpha-D- and beta-D-glucosidase activity in all mucus-enriched incubations indicates a close coupling in hydrolyzation of both alpha- and beta-bound polysaccharides of mucus origin. Beta-/alpha-glucosidase ratios varied among the different types of mucus in a range between 0.6 and 1.1 possibly reflecting different carbohydrate composition of the organic substrate (see also Somville 1984).

The interdependence between bacterial abundance and exoproteolytic activity measured as leucinaminopeptidase activity in mucus-enriched incubations was different to that found for glucosidase activity; rather, bacterial numbers and aminopeptidase activity were not significantly correlated over the entire incubation period (Table 1). Although aminopeptidase activity increased during the first part of the incubation concurrently with bacterial numbers, this increase continued during the following day even after the drop in bacterial abundance (see Figs. 1a, d & 3a, c). There are at least 2 possible explanations for this observation. Although it is strongly suggested that proteolytic activity in natural waters is bound to the envelopes of bacteria (Hollibaugh & Azam 1983, Vives Rego et al. 1985, Rosso & Azam 1987), a varying fraction can be found in the dissolved state (< 0.2 μm) with a considerably increasing percentage in the declining phase of enrichment cultures (Vives Rego et al. 1985). The latter authors argued that no free bacterial proteases are produced, but that in most cases this fraction is due to cell envelope fragments produced upon lysis of cells during the breakdown phase of the population and thus passing 0.2 μm filtration. On the other hand it can be assumed that per cell activity of aminopeptidase was enhanced during the decline of cell density. Based on recent findings that low concentrations of hexoses induce glucosidase activity (Chrost 1989), one can speculate that in the advanced phase of our incubations easily assimilable N-sources (amino acids) fell below a critically low level, due to their rapid uptake by microheterotrophs, thus inducing elevated enzyme expression (see also Albertson et al. 1990). Only when the bacterial abundance in the incubation had declined to the initially low levels (e.g. after 64 h in the incubation with *Patella caerulea* mucus) did the level of aminopeptidase activity also start to drop.

An additional indication that the free-living bacterial community grows at the expense of pedal mucus is the observed close relationship between disappearance of

total carbohydrates from the mucous trails and increase in total glucosidase activity in the incubation media. There is evidence in the literature that the products of extracellular hydrolyzation of macromolecules are only partly taken up by microheterotrophs cleaving the substrate (Hoppe 1983); endohydrolases may chop the polymers at random, thereby acting in a loose hydrolysis-uptake coupling. We hypothesize that a significant portion of the pedal-mucus-derived material is solubilized and enters the DOM pool by diffusion, thus being accessible to the free-living bacterial population. Dissolved polymers and oligomers may be further hydrolyzed to monomers or small oligomers by the action of exohydrolases. This is supported by several recent studies which conclude that attached bacteria grow too slowly to account for the observed decomposition of organic material (Kirchman & Mitchell 1982, Ducklow et al. 1985, Peduzzi & Herndl 1991). In another study it was found that in the presence of marine snow free-living bacteria responded rapidly with elevated growth, suggesting that marine-snow-derived DOM becomes available to free-living bacteria, while concurrently the monomeric carbohydrate concentrations remained within the range of controls without marine snow (Herndl 1988). Since it is well documented that monomers do not accumulate in the water, a tight hydrolysis-uptake system in the free-living bacterial community can be assumed (Chrost 1989).

A stimulatory effect in the mucus-associated microenvironment is further documented by the increased microalgal biomass on trail mucus exposed for several days. The ability of mucous trails to stimulate microalgal growth as found in our experiments has also been reported for limpets (Connor & Quinn 1984, Connor 1986). These authors speculated whether the degree of stimulation is linked to the amount of energy invested in mucus production and to the ability of the animals to utilize the enhanced microalgal production as food source. Our results support the idea that the breakdown of mucus material by bacterial enzymes can provide a microenvironment enriched in nutrients favorable for microalgal production. The resulting elevated algal biomass might be grazed by herbivorous gastropods, thus returning a part of the energy expended for mucus production to the animal (see also Connor & Quinn 1984, Connor 1986). This stimulation of the growth of the animal's own food source may provide another example of the 'gardening'-concept introduced by Hylleberg (1975). Similar interactions between zoobenthos and microorganisms have been proposed to be highly important in marine benthic environments (Gerlach 1978, Connor et al. 1982, Reise 1983).

Although mucus production rates of neither *Patella caerulea* nor *Monodonta turbinata* varied significantly over a 24 h cycle, a tendency could be observed towards higher secretion during night-time. This might be due to enhanced locomotory activity at night which was also documented in other studies with *M. turbinata* (Wieser & Dalla Via 1982) and *Patella vulgata* (Hawkins & Hartnoll 1983). Based on preliminary estimations concerning the abundance of *P. caerulea* (18 ind. m^{-2}; SE = 11) and *M. turbinata* (267 ind. m^{-2}; SE = 174) in the study area (Gulf of Trieste; unpubl. data), ca 81 g mucus dry wt m^{-2} yr^{-1} may be produced by *P. caerulea* and 544 g mucus dry wt m^{-2} yr^{-1} by *M. turbinata*. Rearranging values reported in the literature, our calculated values appear to be somewhat high. Crude estimates given by Paine (1971) for e.g. *Tegula funebralis* yielded 13.8 g mucus dry wt m^{-2} yr^{-1}; only 2.55 g mucus dry wt m^{-2} yr^{-1} was reported for *P. vulgata* (Wright & Hartnoll 1981). Despite the fact that our provisional annual mucus production values may represent maximum rates since they are based on measurements conducted at summer temperatures, more recent studies indicate that pedal mucus production by gastropods was substantially underestimated in earlier studies. For example, in the above-cited work with *P. vulgata* (Wright & Hartnoll 1981) mucus secretion was estimated at only 4 % of ingested energy; this may be erroneous as demonstrated in a more recent study in which the mucus term in the energy budget for *P. vulgata* was determined at about 40 % of ingestion (Davies et al. 1991). Our pedal mucus production estimates per individual per day are within the same order of magnitude as values in another recent work (Horn 1986) on *Chiton pelliserpentis*.

We have demonstrated that gastropod trail mucus secreted in rocky intertidal and sublittoral shores can provoke significant microbial activity. A distinct temporal distribution of extracellular enzyme activity can be assumed leading to a tight hydrolysis-uptake coupling in the mucus-surrounding microenvironment. It seems evident that mucus release can be of significant importance for microbial (autotrophic and heterotrophic) productivity in nearshore waters with abundant gastropod biomass.

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