Sedimentation and degradation of organic matter produced by marine phytoplankton

Osinga, Ronald

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Production of organic matter by photosynthesis and mineralization of this primary production to carbon dioxide and inorganic nutrients are the two major processes in the marine carbon cycle. In sea, most organic matter is produced by phytoplankton. The work presented in this thesis concerned some aspects of the fate of the organic matter produced by marine phytoplankton in general, and the fate of the organosulfur compound β-dimethylsulfoniopropionate (DMSP) in particular. DMSP is biogeochemically important as a precursor for dimethylsulfide (DMS), which plays a role in atmospheric chemistry. The studies in this thesis focused on the situation in the southern North Sea, with emphasis on the colony-forming phytoplankton genus *Phaeocystis*. In the subsequent sections, the most important results will be summarized and discussed.

8.1. Sedimentation and degradation of organic matter

Mineralization of organic matter takes place in pelagic and benthic ecosystems. In most marine systems, the vertical transport of organic matter determines the relative importance of pelagic versus benthic mineralization. Sedimentation of organic particles is the major mechanism for organic matter transport to benthic systems. In a pelagic mesocosm experiment, in which a spring bloom of *Phaeocystis* sp. was simulated, the importance of sedimentation was studied with a simple sediment trap method.

In the sheltered mesocosm systems, sedimentation was quantitatively important: the daily losses of algae to the mesocosm floor were generally equal to the standing stock in the water column. The relative importance of sedimentation did not show considerable changes throughout the bloom and did not increase at the decline of the bloom. At the decline of the bloom, the phytoplankton standing stock decreased even faster than the losses due to sedimentation suggested. The excess loss in standing stock was subscribed to lysis of the *Phaeocystis* cells, which is in agreement with the observations of Brussaard et al. (1995), who found that mass lysis terminated a *Phaeocystis* spring bloom in Dutch coastal waters.

The importance of lysis implies that a substantial part of the organic matter produced by *Phaeocystis* will be degraded by aerobic microorganisms in the water column. This degradation process was studied in oxic batch culture experiments, in which the decay of organic material dominated by *Phaeocystis* sp. was followed. The organic material had been collected in Dutch coastal waters during a *Phaeocystis* spring bloom. To introduce a fresh bacterial and nanozooplankton population, the cultures were inoculated with a seawater sample that had been filtered through a 5 μm mesh. Organic carbon concentrations, bacterial production and bacterial numbers were followed.

A rapidly degradable fraction and a slowly degradable fraction could be distinguished, each comprising about 50 % of the organic carbon present in the material. The labile material in the rapid fraction was degraded within a few days, with a bacterial carbon conversion efficiency (growth efficiency) between 10 and 20 %. During the degradation of the slow fraction, a substantial bacterial production was measured, which did not lead to an equivalent increase in the bacterial standing stock. It was suggested that during the slow, and presumably inefficient degradation of the refractory algal material, a rapid, efficient recycling of bacterial biomass takes place, that keeps the bacterial productivity high.

Phaeocystis apparently produces more refractory compounds during the exponential growth phase: the degradation of the refractory material proceeded slower when the algal material was collected during an earlier phase of the *Phaeocystis* bloom. A higher production of refractory compounds would be in agreement with the yet unexplained observation that *Phaeocystis* colonies in the exponential growth phase are almost entirely free of bacteria (Thingstad & Billen 1994): the bacteria may be unable to degrade the colonial matrix around the algal cells. However, the possibility can not be excluded that species other than *Phaeocystis* produced these refractory compounds.

Benthic degradation of the *Phaeocystis* dominated algal material was studied in experimental benthic systems (boxcosms). Benthic oxygen uptake, sulfate reduction and benthic bacterial production were measured in these

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Sorptive preservation of intrinsically labile organic matter in the sediment, as described by Keil et al. (1994) could be a factor slowing down benthic degradation processes. In the benthic boxcosms, however, bacterial degradation of the added material mainly took place in the algal debris layer laying on the sediment, and only to a lesser extent in the sediment. In the pelagic mesocosms, no sediment was present at all, so that sorptive preservation in sediment can not solely explain the slower benthic degradation. Recently, Kristensen & Hansen (1995) found that anaerobic respiration processes were inhibited by excess concentrations of labile organic carbon. This may have played a role at the floor of the pelagic mesocosms and in the algal debris layer on the sediment surface in the benthic boxcosms. An indication for this inhibitory effect is that sulfate reduction rates in the algal debris layer in the benthic boxcosms were relatively low, when compared to oxygen uptake rates.

What is the relative importance of pelagic and benthic degradation in the North Sea? How can the carbon flow to the seafloor be quantified? Simple sediment trap techniques as used in the pelagic mesocosm experiment have the major disadvantage that they do not account for resuspension of deposited particles. In turbulent areas, where resuspension rates are high, these techniques will overestimate the vertical transport rates. Multiple-trap techniques in combination with other methods are needed to calculate the impact of resuspension (Blomqvist et al. 1991).

An alternative approach for quantifying the organic carbon flow to the sediment is measuring benthic metabolic activity. Benthic metabolic activity may not always reflect the sedimentation instantaneously, but on an annual basis, most of the deposited organic matter will be mineralized (Hedges 1992). Hence, the annual benthic metabolic activity may give a reasonable estimate for the quantitative importance of benthic degradation. Annual benthic metabolic activity was estimated for two locations in the southern North Sea, that were visited during four cruises held in four different seasons. Benthic oxygen uptake, benthic bacterial production and sulfate reduction were measured at the shallow and turbulent Broad Fourteen area, and at the deeper Oyster Ground area, which is stratified in spring and summer.

Oxygen uptake and sulfate reduction showed a clear seasonal pattern at the Broad Fourteen area, indicating a supply of carbon to the benthic system that is closely related to the standing stock in the water column. This is probably due to the influence of the tide in this part of the North Sea, which causes a permanent mixing of the whole water column. At the Oyster Grounds, a different pattern was observed. Peaks in oxygen uptake and sulfate reduction were found in winter. Irregularly occurring events, such as storms and fishery-activities, are likely to affect benthic mineralization rates in this area to a large extent.

Annual benthic carbon mineralization based on oxygen uptake was 44 gC m^{-2} at the Broad Fourteens, and 131 gC m^{-2} at the Oyster Grounds. When this is compared to primary production data from literature (150-200 gC m^{-2} at the Broad Fourteens and 100-150 gC m^{-2} at the Oyster Grounds)(Joint & Pomroy 1993), it turns out that the relative importance of benthic versus pelagic degradation is much higher in the latter area.

Although the measurements showed that sulfate reduction rates in the southern North Sea are higher than previously reported, aerobic respiration is the most important pathway for benthic carbon mineralization at the stations visited. Sulfate reduction, which is regarded as the most important anaerobic mineralization process, contributed for 26 % (Broad Fourteens) and 28 % (Oyster Grounds) to the annual carbon mineralization.

A discrepancy was found between the benthic bacterial biomass production rates (measured as incorporation of radioactive l-leucine) and the other techniques for studying metabolism. The annual carbon demand of the bacteria in North Sea sediments exceeded the annual primary production rates reported in literature, and the bacterial biomass production was always much higher than the respiration rates suggested by measurements of oxygen uptake and sulfate reduction. Only bacterial growth efficiencies between 70 and 80 % could explain these results. According to literature data (e.g. Ducklow & Carlson 1992), such a high growth efficiency is not very likely for a mixed population of marine bacteria, especially not for sulfate reducers. In addition, it is in contrast with the results obtained from the oxic batch culture experiments. It was therefore suggested that the bacterial production measurements overestimated the real *in situ* rates.

Further support for this idea came from the benthic boxcosm experiments: the calculated carbon budget suggested that only a small fraction of the added organic matter had been degraded after 27 days, which was in agreement with the relatively low carbon losses that could be calculated from the oxygen uptake measurements (10 %). However, the bacterial production rates suggested a bacterial carbon demand of at least 30 % of the added organic carbon.

The most likely explanation for the high bacterial production rates is a stimulation of bacterial activity during sample processing. Leucine incorporation is measured in a sediment-slurry. Substantial increases in bacterial activity as a result of slurry-techniques have been reported previously (Nedwell 1984, Meyer-Reil 1986). Since a decreased bacterial activity in slurry-incubations has also ben reported (e.g. Dobbs et al. 1989), the effects of the slurrying step on leucine incorporation rates should be critically evaluated.

8.2. Sedimentation and degradation of DMSP

The concentration of DMS in seawater is regulated by several factors. Two key factors, the production of DMS from DMSP and the microbial consumption of DMS, are believed to be closely coupled, which keeps the DMS concentration in seawater low. Sudden increases in the production or release of DMSP and subsequent increases in production of DMS may cause a temporal accumulation of DMS. In the pelagic mesocosm experiments with *Phaeocystis* (an important DMSP producer), the hypothesis was tested that after mass sedimentation events, mass release of DMSP, followed by a rapid conversion of DMSP to DMS, would lead to an accumulation of DMS in the water column.

Two peaks in the DMS concentration were observed during the 35 day incubation period. The first peak occurred immediately after the start of the experiments, and lasted for four days. The second peak occurred during the late exponential growth phase of the *Phaeocystis* bloom and lasted for three days. During these peaks, the DMS concentrations increased up to two orders of magnitude.

As was already mentioned in section 8.2., sedimentation was an important, but rather constant loss factor during the simulated *Phaeocystis* bloom. Mass sedimentation may have caused the early DMS peak: the initial population of DMS consuming bacteria may have been too small to respond instantaneously to an eventual rapid DMS formation on the mesocosm floor. However, the second DMS peak must have had another cause, since it was not preceded by an increased sedimentation rate. There were indications that the DMSP production per cell had increased substantially one day before this DMS peak occurred. A sudden increase in the production of DMSP could very well explain a temporal accumulation of DMS, but the occurrence of this increase in DMSP production in the mesocosm could not be explained with the present theory about the function of DMSP in algal

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physiology. More information on this function is needed to understand the regulation of the concentration of DMS in seawater, and hence, to predict the strength of the DMS flux to the atmosphere. Further research should therefore focus on the possible functions and the regulation of DMSP production in different algal species under different cirumstances.

In an experiment with the algal species *Emiliania huxleyi*, also an important producer of DMSP, effects of sedimentation on DMS formation were further studied. Cultured algae were supplied to anoxic marine sediment microcosms. Most of the algae were deposited onto the sediment within a few hours. One or two days after the addition of the algae, rapid DMS formation was observed. The high DMS concentrations persisted for a few days. Thereafter, DMS decreased gradually. The rapid DMS formation did not occur in a control experiment, in which the algae were kept in suspension. It was concluded that under anoxic conditions, mass sedimentation of algae can lead to mass release of DMSP and accumulation of DMS.

E. huxleyi itself is hardly able to produce DMS from DMSP, in contrast to *Phaeocystis*, which has a very active DMSP-lyase. Hence, the observed effects in the microcosms must be subscribed to bacterial activity. The gradual decrease of DMS in the microcosms shows that under anoxic conditions, microbial production of DMS from DMSP is a more rapid process than microbial consumption of DMS.

8.3. Effects of increasing eutrophication

8.3.1. Organic matter; effects of macrozoobenthos

The effects of increasing eutrophication on benthic mineralization processes were studied in three benthic boxcosm experiments, in which a eutrophication gradient was simulated with three different pulse additions of the algal material dominated by *Phaeocystis*. Oxygen uptake, sulfate reduction, bacterial production and the sediment organic carbon content were monitored. The impact of macrozoobenthos activities on these processes was emphasized in these experiments. Boxcosms from which all benthic macrofauna had been removed were compared to boxcosms in which six sea urchins of the species *Echinocardium cordatum* were present.

The sea urchins augmented benthic oxygen uptake. In the presence of the animals, the oxygen uptake rates increased under increasing organic loadings, while in defaunated boxcosms, the highest oxygen uptake rates were already reached at the intermediate organic loading. Under increasing organic loadings, the sea urchins presumably stimulated both the metabolism of aerobic bacteria and the reoxidation of reduced inorganic compounds.

Overall sulfate reduction rates and bacterial production rates were positively correlated with organic loading, but the overall rates were not enhanced by the sea urchins. However, in the second half of the incubation period, both sulfate reduction rates and bacterial production rates increased in deeper sediment layers of boxcosms with *E. cordatum*. This may be due to an increased, sea urchin-mediated transport of organic matter into the sediment in this phase of the experiments. This idea was supported by an observed increase in the sediment carbon content. Another possibility is that the sea urchins enhanced the degradability of the material: fermentation of large refractory organic molecules may take place in the gut systems of the animals. The products of fermentative processes are good substrates for other anaerobic microorganisms.

8.3.2. DMSP

To study the effects of increasing eutrophication on DMS formation, increasing amounts of *Emiliania huxleyi* cells were supplied to anoxic marine sediment microcosms. It was found that at a higher concentration of DMSP, an increasing percentage of DMSP is converted to DMS. This indicates that at higher DMSP concentrations, the importance of the cleavage reaction of DMSP to DMS and acrylate will increase with regard to other pathways for DMSP degradation, such as demethylation.

In eutrophic areas, sedimentation of DMSP producing algae to anoxic sediments may lead to a rapid formation of DMS. The relative importance of this DMS formation will increase under increasing eutrophic conditions. Hence, eutrophication may not only affect the oxygen dynamics in coastal waters, but may also have effects on the local climate via an increased DMS formation.

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