Sedimentation and degradation of organic matter produced by marine phytoplankton
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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-dimethylsulfiniopropionate (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 nanoplankton 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 boxcosms during a 24 hour addition of a single pulse of chlorophyll a to the sediment surface. Although a response was observed, the rate and the bacterial production was significantly between the different sediment boxes. After organic matter suspense, the amount of organic carbon recovered as organic carbon in the sediment was found in the pelagic part of chlorophyll a collected in a permanent trap was near the amount of chlorophyll a that was daily removed sediment traps. However, in the benthic system, mineralization rates at the sediment surface were rather low. Hence, in the benthic system, degradation appears to be absent.

Sorptive preservation of organic matter in the sheltered mesocosms is unlikely, Keil et al. (1994) could show that the benthic degradation process in the boxcosms. However, benthic degradation processes was inhibited by the added material mainly took place in the algal debris layer on the sediment surface. Hence, in the benthic system, the mineralization rates at the sediment surface were rather low. Therefore, no sediment was preserved in these experiments. Slower benthic degradation rates were found by Hansen (1993) found that the role of labile organic carbon in the sediment was attributed to the decay of the algal debris layer on the sediment surface. An important aspect is that sulfate reduction processes were inhibited by the presence of organic matter in the sediment. The role of the bacteria in the organic matter degradation is unknown, but they do not appear to be inhibited by the resuspended organic matter. In the benthic system, resuspension rates are high.
Summary & Concluding Remarks

is that a substantial fraction of labile organic matter in the sediment is rapidly degraded by Phaeocystis, which feeds on benthic macroorganisms. Benthic oxygen uptake was measured in these experiments, in which the organic material was added to the sediment at a rate of 150-200 g C m⁻² at the Broad Fourteens, and 100-150 g C m⁻² at the Oyster Grounds (Joint & Pomroy 1993), which is stratified in spring and summer.

Oxygen uptake and sulfate reduction showed a clear seasonal pattern at the Broad Fourteens, and 131 g C m⁻² at the Oyster Grounds. When this is compared to primary production data from literature (150-200 g C m⁻² at the Broad Fourteens and 100-150 g C m⁻² at the Oyster Grounds), 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

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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 theoxic 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-surry. 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 been reported (e.g., Dobbs et al. 1989), the effects of the slurring 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 physiology. More information is needed to understand the concentration of DMSP in seawater and to predict the strength of its impact on the atmosphere. Further studies are needed to discover the possible role of DMSP production and consumption in the carbon cycle under different circumstances.

In an experiment with Emiliania huxleyi, a dinoflagellate with high DMSP production, effects of increased DMSP production were further investigated in microcosms. Most of the DMSP was released into the water column, and the DMSP concentrations persisted throughout the experiment. However, the bacterial consumption of DMSP was not high enough to keep the DMSP concentrations low. The bacterial growth rates were high enough to consume the added DMSP, but the bacterial growth did not keep pace with the DMSP concentrations. The DMSP concentrations in the microcosms were high enough to cause a decrease in the DMS concentrations in the water column. The decrease in DMS concentrations was not accompanied by a decrease in DMSP concentrations, which suggests that the DMSP was not being consumed by bacteria. Instead, the DMSP was being released into the water column.

8.3. Effects of increased eutrophication grade

The effects of increased eutrophication grade on the benthic boxcosm system were investigated in different mesocosms. The mesocosms were supplied with organic carbon in different amounts, and the effects on the productivity and the bacterial biomass were measured.

8.3.1. Organic matter

The effects of increased organic matter additions on the bacterial biomass production were measured in mesocosms. The mesocosms were supplied with different amounts of organic matter, and the effects on the bacterial biomass production were measured. The results showed that the bacterial biomass production increased with the amount of organic matter added, and that the bacterial biomass production was highest in the mesocosms with the highest amount of organic matter added. The results suggest that the bacterial biomass production is positively correlated with the amount of organic matter added, and that the bacterial biomass production is an important factor in the carbon cycle in the North Sea.
Degradation of DMSP

In seawater is regulated by factors, the production of DMSP, and the microbial degradation is tightly coupled. The DMS concentration in seawater is regulated by the photosynthetic production of algae in the mesocosm floor. The production of DMSP is explained with the release of DMS, but the subsequent increase in the DMS concentration per cell had to be an eventual and a more rapid process than microbial production of DMS. The observed increase in the DMS concentration per cell was not preceded by an increase in the consumption of DMS by the microbial community. There were conditions where the production rate per cell had increased by more than 10 times. This increase in the production rate per cell was not preceded by an increase in the consumption of DMS, but the increase in the production rate per cell was not preceded by an increase in the consumption of DMS.

Summary & Concluding Remarks

8.3. Effects of increasing eutrophication

8.3.1. Organic matter; effects of macrozoobenthos

The effects of increasing eutrophication on benthic processes were studied in three benthic boxcosms, 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 degradation 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 DMS, an increasing percentage of DMS is converted to DMS. This indicates that at higher DMS concentrations, the importance of the cleavage reaction of DMSP to DMS and acrylate will increase with regard to other pathways for DMS 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.


