

# BACTERIAL GROWTH IN THE OPEN OCEAN

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The main function of heterotrophic bacterioplankton in marine carbon cycling is the conversion of dissolved organic carbon (DOC, a mixture of uncharacterized organic molecules and characterizable organics released by organisms such as proteins, sugars and lipids) into cellular biomass and carbon dioxide (CO<sub>2</sub>). The relative importance of bacterial biomass production (BP) versus bacterial respiration (BR) is expressed by the bacterial growth efficiency ( $BGE = BP / (BP + BR)$ ). Thus, the bacterial growth efficiency provides information on whether bacteria act more as a 'sink' or a 'link' of organic carbon to higher trophic levels. Bacterial biomass production measurements are frequently performed, but respiration measurements are scarce. Instead, respiration of natural bacterial communities has often been derived from bacterial production measurements alone, assuming constant bacterial growth efficiency, which is usually determined in laboratory experiments. To advance our knowledge on the dynamics of bacterial growth efficiencies in natural systems, an extensive dataset of bacterial production and concomitant bacterial respiration measurements was collected at different trophic sites of the open ocean.

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Bacterioplankton represent the largest living biomass in the world's ocean and they are the only group of organisms able to take up the large pool of DOC in aquatic systems. Their main ecological role is to take up and digest the dissolved organic carbon (DOC) pool in seawater by incorporating a part of it into biomass and respire the remaining major fraction to CO<sub>2</sub>. Depending on the trophic state of the environment, bacterioplankton contribute between 10% and more than 80% to the respiration of the total food web in the open ocean.

While the importance of bacterial respiration in the ocean was recognized already in the 1970s, the research focus to unravel the oceanic carbon cycle until today was on primary production by algae and bacterial secondary production rather than on heterotrophic processes. This bias towards productivity measure-

ments is probably due to the relatively simple and seemingly straightforward methods to measure algal- or bacterial production with radiolabeled substrates. Respiration was mainly modelled from these production measurements, leading to the assumption of a highly efficient conversion of

DOC into cellular mass of bacteria. Consequently, bacteria were mainly seen as a food source to higher trophic levels. Our work in different parts of the open ocean (Fig. 1) using direct measurements of bacterial production and respiration showed, however, that bacteria are all but efficient in producing

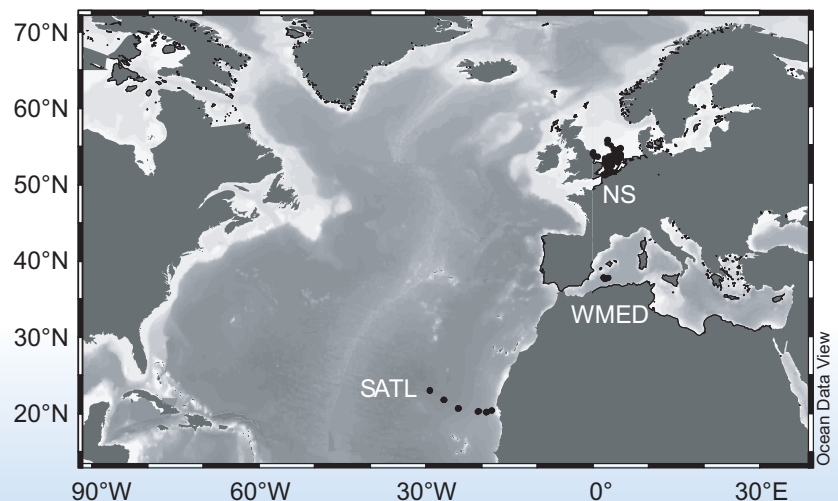


Fig. 1. Map of the study sites in the North Sea (NS), the western Mediterranean Sea (WMED) and the subtropical Atlantic (SATL). Black dots indicate the stations where bacterial production and respiration measurements were performed.

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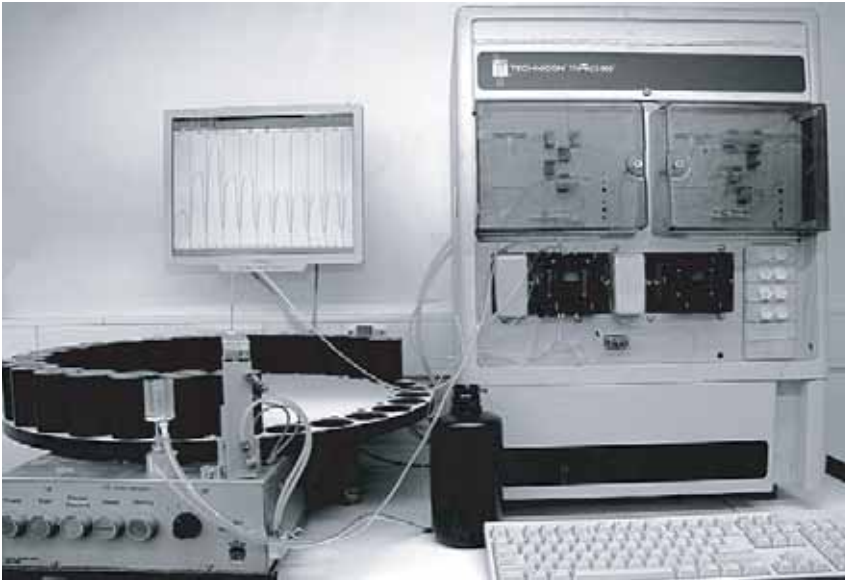


Fig. 2. Continuous-flow analyzer with autosampler to measure oxygen concentrations in seawater.

biomass. To determine bacterial respiration efficiently and accurately, a newly designed semi-automated oxygen determination system, based on the Winkler method was used (Fig. 2).

In eutrophic as well as oligotrophic environments the bacterial growth efficiency was on average 20% (Fig. 3). This means that only 20% of organic carbon is incorporated in the cells and is thus available to higher trophic levels, whereas around 80% of the carbon

taken up by bacteria is respired as  $\text{CO}_2$ . In fact, the oxidation of DOC to  $\text{CO}_2$  mediated by the bacterioplankton in the open ocean is so high, that questions on the supply mechanisms of organic substrates to these remote places arise.

Future research will show whether the horizontal transport of organic carbon from highly productive coastal areas or the local primary production in the ocean is

sufficient to fuel the carbon demand of bacteria in the open ocean. Budget calculations on the organic carbon production and bacterial respiration for the North Atlantic indicate, that the bacterioplankton carbon demand is higher than the surface primary production can provide. Thus, transport from other areas has to fill this gap in the mass balance.

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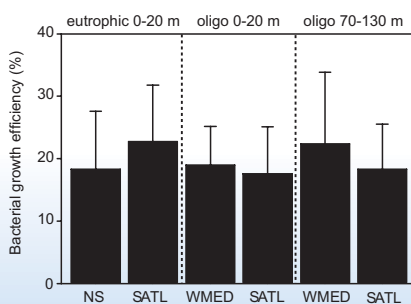


Fig. 3. Bacterial growth efficiency (%) at different trophic sites and depths of the open ocean. For sites sampled and abbreviations see Fig 1.

**Intermezzo:** While the main interest in bacterioplankton respiration is actually  $\text{CO}_2$  evolution, the measurement of concomitant oxygen consumption, is a more reliable and sensitive method for the often minute respiration rates. Oxygen consumption rates are converted to units of carbon with the respiratory quotient ( $\text{RQ} = \text{CO}_2/\text{O}_2$ ). Traditionally, the Winkler titration was the method of choice and it still forms the golden standard for oxygen measurements. However, manual titration is labour intensive and exact measurements demand a high degree of analytical experience. At NIOZ, we have developed an automated spectrophotometric analysis of oxygen concentrations in seawater samples for this purpose, which provides precision and accuracy similar to the Winkler method (Fig. 2).