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Oxygen distribution in *Tentorium semisuberites* and in its habitat in the Arctic deep sea

Friederike Hoffmann^(1*), Eberhard Sauter⁽²⁾, Oliver Sachs⁽²⁾, Hans Røy⁽¹⁾, Michael Klages⁽²⁾

⁽¹⁾ Max Planck Institute for Marine Microbiology, Celsiusstr. 1, 28359 Bremen, Germany. fhoffman@mpi-bremen.de, hroy@mpi-bremen.de

⁽²⁾ Alfred Wegener Institute for Polar and Marine Research, Columbusstraße, 27568 Bremerhaven, Germany. esauter@awi-bremerhaven.de, osachs@awi-bremerhaven.de, mklages@awi-bremerhaven.de

Abstract: The arctic deep-sea morphotype of the hadromerid sponge *Tentorium semisuberites* is common in the Arctic deep sea, where it lives partially buried in soft bottom sediments. To investigate the chemical microenvironment of sponge cells and associated microbes, oxygen gradients in sponge tissue were measured with Clark-type microelectrodes. Profiles with step resolutions between 100 and 500 μm were measured vertically through the sponge body (4 mm). Similar profiles were measured in sediments of the sponge sampling sites. The characteristic shape of the profiles showed that sponges were alive and pumping during profiling. Oxygen concentrations were highest at the sponge surface and decreased towards the centre of the sponge, which vertically coincided with the sediment-water interface. Below, oxygen was found to increase again. The lowest oxygen concentration measured in *T. semisuberites* was 53 μM (15% of surrounding water). Oxygen concentrations from 2 mm above the sediment surface until 2 mm into the sediment ranged from 300 – 270 μM . A part of the water filtered by this species is presumably sediment pore water, which is only slightly lower in oxygen than the overlying bottom water. The sponge tissue thus provides an oxic to hypoxic habitat for the associated Archaea and Bacteria.

Keywords: Arctic deep sea, oxygen microelectrodes, microenvironments, sponge microbes, *Tentorium semisuberites*

Introduction

Sponges amount to a large part of the macrobenthos in the Arctic deep sea. The arctic deep-sea morphotype of *Tentorium semisuberites* (Hadromerida, Demospongiae) is among the most common sponge species of Arctic deep sea soft bottom sediments (Barthel and Tendal 1993). It lives partially buried in the sediment, using tiny stones as substrate (e.g. Fram Strait, west off Spitzbergen), or anchoring with long root-like spicules in the sediment (e.g. central Greenland Sea). The arctic deep-sea morphotype of *T. semisuberites* is cone shaped, 2-5 mm across and 4-5 mm high (Fig. 1A). In shallower waters (ca. 30-600 m) along the Norwegian coast *T. semisuberites* grows on hard substrate and reaches more than twice the size of arctic specimens.

In a recent study combining microbial lipid biomarker analysis and differential fluorescence *in situ* hybridisation (FISH) on sponge sections (Pape *et al.* 2006), we showed that Archaea provide a major and Bacteria a minor part of the microbial endobiont community of *T. semisuberites* – specimens from the “Hausgarten” region. Archaea and Bacteria were evenly distributed throughout the entire sponge body. Indications for Archaea as endobionts have also been reported for several species of the Demospongiae (Preston *et al.* 1996, Webster *et al.* 2001, Margot *et al.* 2002, Lee *et al.* 2003) and, furthermore, for the Hexactinellida (Thiel *et al.* 2002, Pape *et al.* 2004). To investigate the chemical microenvironment of sponge cells and associated microbes,

we measured the oxygen distribution in the tissue of *T. semisuberites* as well as in the sediment and bottom water of its habitat.

Material and Methods

During Expedition AWI-ATL with R/V “L’Atalante” (September 2005), sponges were sampled in the Fram Strait on the continental rise off Svalbard (79°04.34’ N, 4°08.2’ E) at 2440 m depth (Fig. 2). This site is part of the long-term monitoring program “Hausgarten” of the Alfred Wegener Institute Bremerhaven, Germany, and is revisited annually (Soltwedel *et al.* 2005). Samples were taken by Slurp Gun operated by the ROV “Victor 6000” (Fig. 1B). Sponges were kept submersed in ambient bottom water during the rest of the ROV dive. After retrieval of the ROV, sponge specimens were immediately placed in an aquarium filled with bottom water from the sampling site which was kept at *in situ* temperature (0 to -1 °C).

Oxygen gradients over the surface and into the tissue of *T. semisuberites* were measured with two specimens of *T. semisuberites* using Clark-type oxygen microelectrodes (tip diameters 18-30 μm) as described (Schönberg *et al.* 2004). Adaptation time of sponges in the aquarium prior to lab measurements was 7 hours. All measurements were taken within 40 hours after sampling. Profiles with step-resolutions between 100 and 500 μm were measured vertically through the sponge body (4 mm).

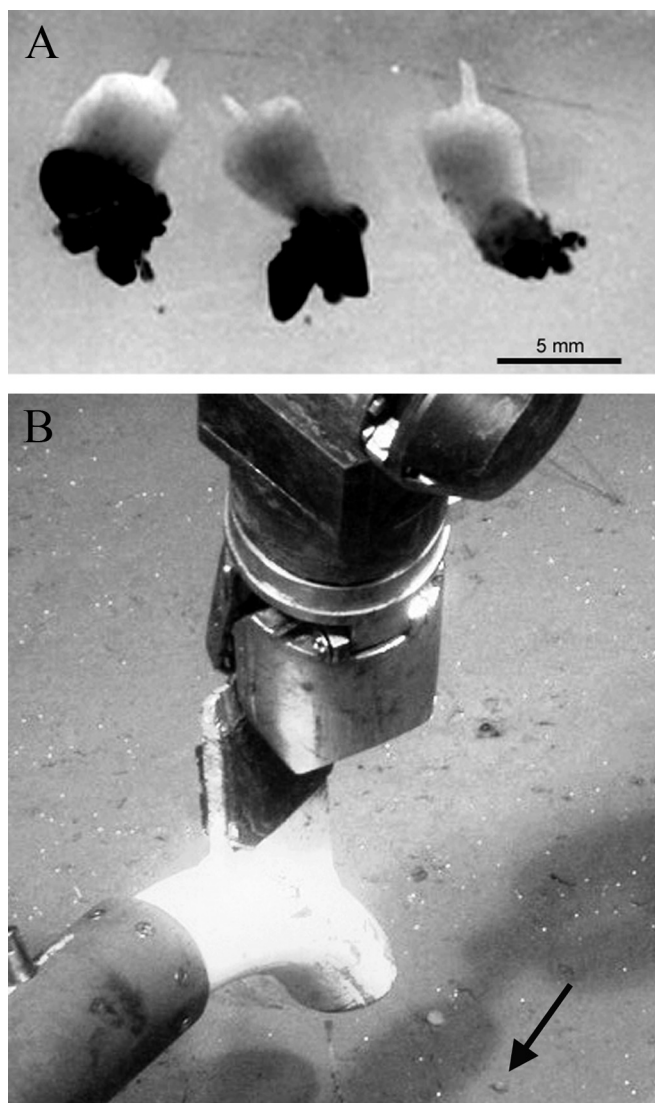


Fig. 1: A. *Tentorium semisuberites* specimens sampled at 2440 m depth. B. Non-intrusive and precise sampling with a slurp gun operated by the ROV “Victor 6000” at 2440 m depth. *Tentorium semisuberites* (arrow) lives partially buried in the sediment and is difficult to detect (Copyright: Ifremer, France).

Oxygen gradients in the sediment were measured *in situ* at 2440 m depth in direct proximity of the sponge sampling sites with the *in situ* microprofiler MIC, operated by the ROV “Victor 6000” (Sauter *et al.* 2004, Soltwedel *et al.* 2005, DeBeer *et al.* 2006).

To measure *in situ* oxygen gradients in sponge tissue was not possible due to optical and mechanical limitations.

Results

In total, 21 oxygen profiles were measured over the surface and into the tissue of the two sponge specimens, some of them through the entire sponge body from the top to the basis (see Fig. 3). Though the water current created by sponge pumping activity was too low to be visualised with dye, it was obvious

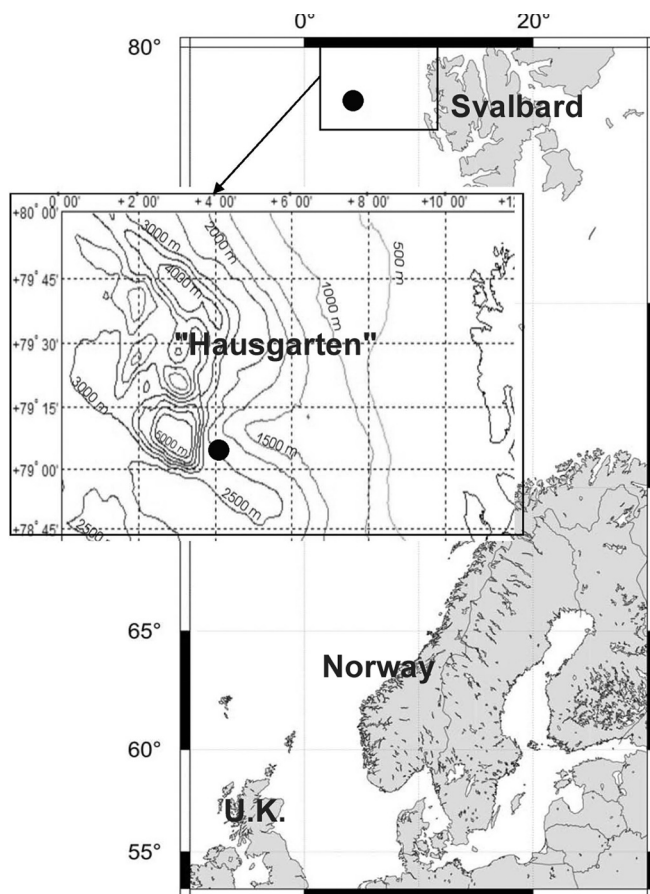


Fig. 2: Sampling site in the Fram Strait on the continental rise off Svalbard, Arctic Sea at 2240 m.

from oxygen profiles that sponges were alive and pumping. Non-pumping sponges show diffusive oxygen profiles, with decreased oxygen concentrations above their surface due to diffusive oxygen fluxes over the boundary layer, and a steep oxygen decrease down to zero in the first millimeter of the tissue (Hoffmann *et al.* 2005a, Hoffmann *et al.* 2005b, Schläppy *et al.* in press). In our investigation, water was oxygen saturated until the sponge surface, and concentrations decreased gradually into the tissue. This is a typical pattern for pumping sponges (Hoffmann *et al.* 2005b, Schläppy *et al.* in press).

Typically, oxygen concentrations decreased towards the centre of the sponge, reaching a minimum 2-3 mm into the sponge tissue. The lowest concentration measured was 53 μM , which is 15% of the oxygen concentration of the surrounding water. This trend was visible in all profiles measured, though the actual oxygen concentrations could vary at the same position when there were several hours between the measurements. Profiles measured in direct sequence, however, were nicely reproducible. Figure 3 shows a series of replicated oxygen profiles measured vertically through the sponge body. Two parallel profiles each were measured at three different positions ranging from close to the outer wall until close to the osculum. Pores for incurrent water were found

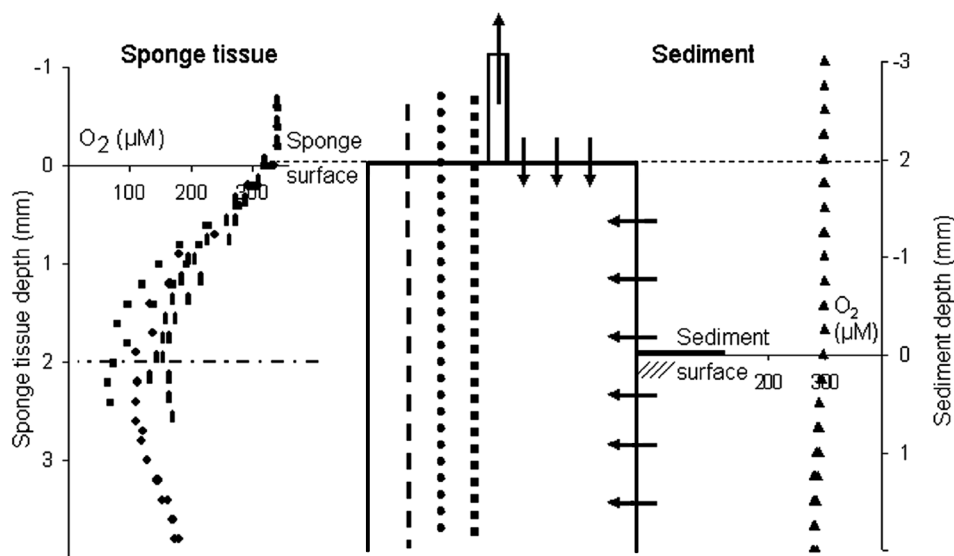


Fig. 3: Left: 3x2 replicated oxygen profiles measured vertically through the entire body of *T. semisuberites* kept in the aquarium under *in situ* conditions. Sketch shows positioning of the profiles. Arrows show direction of water flow through the sponge body. Oxygen concentrations are highest at the sponge surface, where oxygen-rich water enters the sponge from both the top and the side. Oxygen concentration decreases towards the center of the sponge which vertically coincided with the sediment-water interface. Below, oxygen was found to increase again. Right: Three replicated oxygen profiles at the sediment-water interface from 2 mm above the sediment surface until 2 mm into the sediment. Oxygen concentrations ranged from 300 to 270 μM (88-79% oxygen concentration compared to that of bottom water used for the aquarium experiments). Therefore, *in situ* oxygen concentrations in sponge tissue can be expected to be only slightly lower than those measured in aquarium experiments.

both at the porous surface next to the oscule, and to a lower amount also at the side surfaces of the sponge by microscopic investigation. Tissue oxygen concentrations were highest at the sponge surface, where oxygen-rich water entered the sponge from both the top and the side, as indicated by arrows. Oxygen concentration decreased towards the middle section of the sponge, which vertically coincided with the sediment-water interface. Below, oxygen was found to increase again.

In contrast to the gradients measured within the sponge body, the pore water oxygen concentration in the ambient sediment only decreased slightly from 300 μM above the sediment-water interface to 270 μM in 2 mm sediment depth. The oxygen penetration depth in the sediment was not reached by the *in situ* measurements which were performed down to 90 mm sediment depth.

Discussion

The oxygen minimum (53 μM) is most likely due to higher respiration rate or lower pumping activity in the middle section of the sponge, the area where the sponge intersects the sediment-water interface. The higher oxygen concentrations towards the sponge bottom may be explained by the conical shape; when inserted perpendicular to the upper surface, the electrode slightly approaches the side surface, which is reflected by higher oxygen concentrations in the profiles. An alternative explanation is a higher filtration activity in the bottom region of the sponge. *Tentorium semisuberites* usually

lives half buried in the sediment (see Fig. 1B). If it filtrates over its entire surface, as both microscopic investigation and oxygen profiles indicate, or even increases its pumping activity in the lower part, a large part of water filtered by the sponge is actually sediment pore water, which usually is richer in nutrients and organic matter than overlaying bottom water. With a minimum of 270 μM (79% saturation) the oxygen concentration below the sediment-water interface where *T. semisuberites* lives is only slightly lower than the bottom water concentration (300 μM ; 88% saturation - Fig. 3).

Assuming a similar metabolism (similar pumping rates) *in situ* and in the laboratory, the tissue of *T. semisuberites* will then show oxygen concentrations *in situ* only slightly lower than those we measured in the aquarium, where the sponge specimens were entirely surrounded by bottom water with 340 μM oxygen.

From these results, it seems that Bacteria and Archaea associated with *Tentorium semisuberites* usually live in oxic to hypoxic conditions.

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