

The physicochemical habitat of *Sclerolinum* sp. at Hook Ridge hydrothermal vent, Bransfield Strait, Antarctica

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Abstract

At Hook Ridge hydrothermal vent, a new species of *Sclerolinum* (Monilifera, Siboglinidae) was found at a water depth of 1,045 m. On the basis of investigations of multicores and gravity cores, the species habitat is characterized. *Sclerolinum* does not occur in sediments that are most strongly influenced by hydrothermal fluids, probably because of high temperature (up to 49°C) and precipitation of siliceous crusts. About 800 individuals m⁻² occur in sediments that are only weakly exposed to hydrothermal flow and have the following characteristics: 20°C (15 cm sediment depth) to -1.5°C (bottom water), 18–40 cm yr⁻¹ advection rates, pH 5.5, <25 μmol L⁻¹ methane, <170 μmol L⁻¹ sulfide, and <0.0054 mol m⁻² yr⁻¹ sulfide flux. Comparison with geochemical data from other reducing sediments indicates that the two groups of Siboglinidae, Monilifera and Frenulata, occur in sediments with low sulfide concentration and flux. In contrast, sulfur-based chemosynthetic organisms that typically occur at hydrothermal vents and cold seeps (e.g., Vestimentifera, vesicomimid clams, and bacterial mats) occur in sediments with higher sulfide availability; threshold values are around 500 μmol L⁻¹ sulfide and 0.1 mol m⁻² yr⁻¹ sulfide fluxes. We did not find typical hydrothermal vent species at Hook Ridge hydrothermal vent, which might be explained by the unfavorable physicochemical habitat: At sites inhabited by *Sclerolinum*, sulfide availability appears to be too low, whereas at sites with higher sulfide availability, the temperatures might be too high, siliceous crust precipitation could preclude their occurrence, or both.

Many marine invertebrate species live in symbiosis with

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chemoautotrophic or methanotrophic bacteria (Fisher 1990). They occur in various areas with sufficient supply of reduced chemical compounds (e.g., at hydrothermal vents, cold seeps, and sediments with high organic matter input). The reduced chemicals that fuel the symbiosis are methane or, more often, sulfide compounds. They are produced in different geological settings by three main geochemical processes: (1) At hydrothermal vents, the fluids are geothermally heated and enriched in reduced compounds during circulation of seawater through the upper ocean crust. (2) At cold seeps, tectonic dewatering causes the slow seepage of methane, other hydrocarbons, or a combination of the two. Sulfide is mainly produced by sulfate reduction coupled to methane oxidation (Boetius et al. 2000). (3) In sediments with organic enrichments, sulfide is produced by anaerobic degradation of organic matter.

Pogonophoran tube worms are present at hydrothermal vents, cold seeps, and sediments with significant organic matter input. The taxonomy of this group has undergone changes during the last few years; we will follow here the taxonomy that is supported by molecular techniques (Halanych et al. 2001; Rouse 2001). The name Siboglinidae is used here in place of the common term pogonophoran tube worms, which strong molecular and morphological evidence

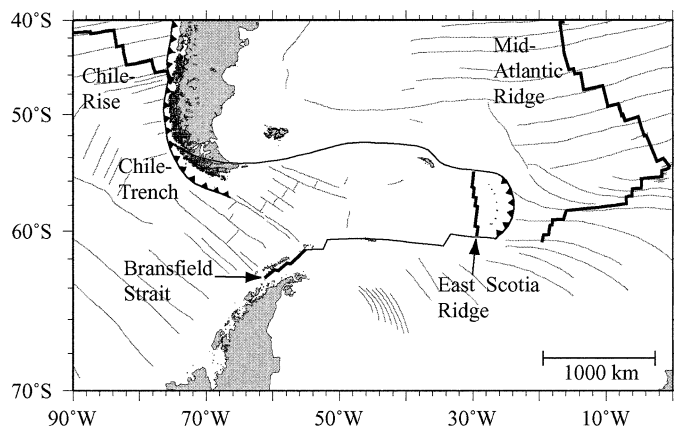


Fig. 1. Tectonic map of the Antarctic Peninsula region. Hook Ridge is a submarine edifice in the Central Bransfield Strait. The Bransfield Strait is isolated from other rift axes (bold) and convergent margins (triangles).

indicates are derived annelids. These comprise three groups: (1) Vestimentifera (=Obturata, =Afenulata), (2) Frenulata (=Perviata, =Anobturata), and (3) Monilifera.

Vestimentifera include, among others, the well-known genera *Riftia* from hydrothermal vents and *Lamellibrachia* from cold seeps. Frenulata include, for example, the genera *Siboglinum*, *Polybrachia*, and *Spirobrachia* from cold seeps and sediments enriched in organic matter. Monilifera has only one genus, *Sclerolinum*, whose species occur in a wide range of habitats (e.g., at hydrothermal vents at Loihi Seamount, Hawaii; in barite edifices at cold seeps in the Sea of Okhotsk [Sahling et al. 2003]; at Håkon Mosby mud volcano [Smirnov 2000]; or in decaying wood and other organic matter [Southward et al. 1986]).

We have found a new species of *Sclerolinum*, to be described by Eve Southward in a separate paper, in sediments influenced by hydrothermal venting at Hook Ridge, Bransfield Strait, Antarctic Peninsula. It is a tiny, easily overlooked animal, living in 0.2–0.4-mm thin wiry tubes with maximum length of about 15 cm. It houses endosymbionts that are most probably sulfur-oxidizing bacteria (E. Southward and L. Beck pers. comm.).

The finding of *Sclerolinum* sp. and the absence of other vent-typical species at Hook Ridge has puzzled us. Is the lack of vent-typical species caused by the geographic isolation of the Bransfield Strait from other midocean ridges, back-arc spreading centers, and convergent margins at which they potentially occur (Fig. 1)? Did we simply miss finding them despite extensive search with the video sled? Although these two questions are per se not to be answered, we concentrated on a third one: Is the physicochemical environment at which *Sclerolinum* was encountered not favorable for other typical vent-type species?

Because earlier studies have shown that hydrogen sulfide concentrations affect community composition (Barry et al. 1997; Sahling et al. 2002), we took sediment cores with living *Sclerolinum* and analyzed sulfide as well as other chemical compounds to characterize the physicochemical habitat. Calculations based on chloride and silicate concentrations were used to derive in situ fluid advection rates and

temperatures. Comparison of the results with existing environmental data indicates that the *Sclerolinum* habitat is similar to that of other siboglinids that occur in organically enriched sediments, in that it is characterized by low sulfide concentrations and fluxes. We discuss the low sulfide availability at Hook Ridge as a possible factor that might account for the lack of other vent-typical symbiotic species.

Investigation area

Bransfield Strait is located between the South Shetland Islands and the Antarctic Peninsula (Fig. 1). It is considered an extensional marginal basin with intracontinental rifting (Lawver et al. 1995). Hook Ridge is one of several submarine volcanic edifices situated on the central rift axis of the Central Bransfield Basin. It rises about 950 m above the surrounding King George Basin; the summit region is in water depth of ~1,050 m (Fig. 2).

During the expeditions ANT XV/2 (ANT) and NBP 99-04 (NBP), evidence of hydrothermal activity at Hook Ridge was obtained by TV sled tows, water column studies, and recovery of hydrothermal siliceous crusts, as well as warm sediments up to 49°C. (Bohrmann et al. 1999; Klinkhammer et al. 2001). Pore-water studies revealed that subcritical phase separation takes place below Hook Ridge; the liquid phase (brine) diffuses into the adjacent King George Basin, whereas the vapor phase with chloride concentrations of <100 mmol L⁻¹ ascends at Hook Ridge (Dählmann et al. 2001). The fluids vent through a thin sediment layer before they reach the sediment–water interface. During SO 155 (SO) with R/V *Sonne* in 2001, we continued the survey in the Hook Ridge crater area. We found living specimens of *Sclerolinum* sp. in sediments recovered by conventional multicoring.

Methods

Four multicorer (MUC) and two gravity corer (GC) samples were taken within a small area around 62°11.54'S, 57°16.66'W at 1,045 m water depth, close to the southern wall of Hook Ridge crater (Fig. 2). The ship was positioned over this area, and we took one multicore after another (and gravity core), virtually at the same position (within a likely error of around 50 m). The spatial heterogeneity was so high that we recovered living specimens of *Sclerolinum* during two MUC deployments, whereas the other two deployments recovered sediments free of *Sclerolinum* and hydrogen sulfide. The multicorer was equipped with eight tubes 10 cm in diameter. The analysis of methane and other pore-water constituents were conducted on both GC and on two and three cores from the four MUC deployments, respectively. The fauna was carefully removed from the sediments of six selected cores and preserved in 10% buffered formaldehyde.

Three TV-guided grab (TVG) deployments at the crater and the crest of Hook Ridge retrieved siliceous crusts but no *Sclerolinum* specimens. The porewater of 10 subcores was investigated; in this study, we selected the profile NBP-TVG 68 from three profiles that are already published (Dähl-

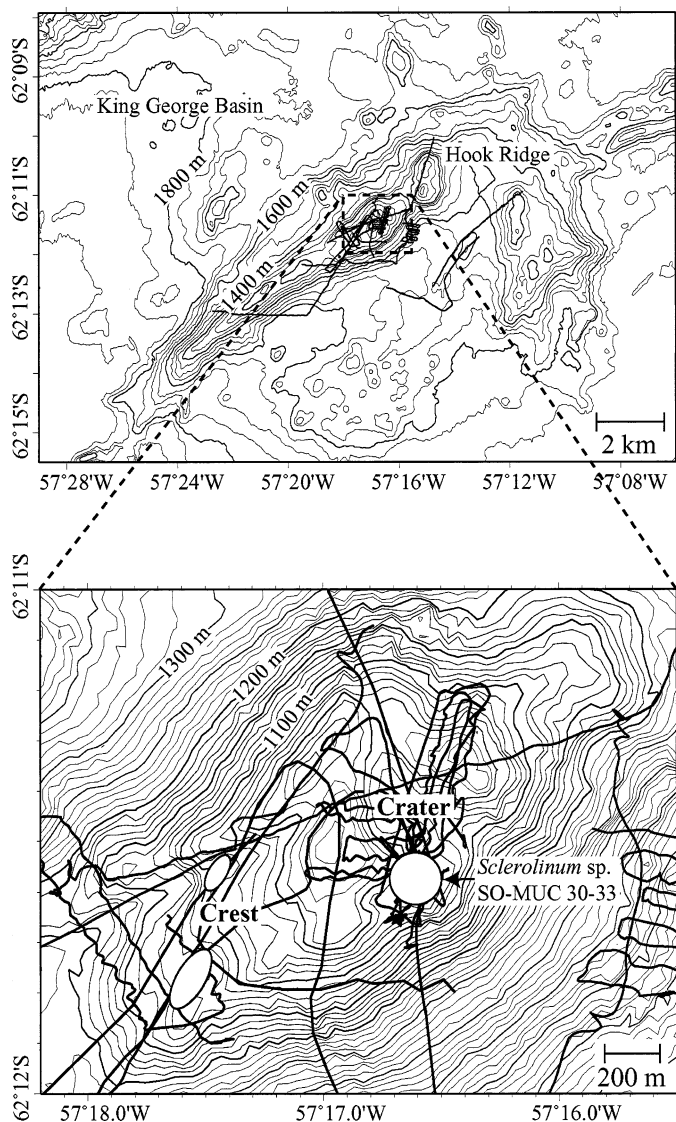


Fig. 2. Bathymetric map of Hook Ridge located in the King George Basin of the Central Bransfield Strait and detailed map of the crest and crater area. Lines show the approximate tracks of all TV sled tows (OFOS) conducted during the ANT, NBP, and SO cruises. The three main venting areas indicated by siliceous crusts (encircled areas) and the sample location of the multicorer with *Sclerolinum* are marked. (Bathymetry courtesy of Carol Chin, Oregon State University.)

mann et al. 2001) to characterize the siliceous crust environment.

Methane was analyzed by the headspace method. Sediment samples (5 ml) were taken in cutoff syringes and injected into 20-ml vials containing 5 ml of supersaturated NaCl solution. After equilibration, aliquots of the headspace were analyzed with a portable gas chromatograph. Methane pore-water concentrations were calculated from the porosity.

Porosity was determined by weighing 5 ml of wet sediment, subsequently drying (24 h, 100°C) and weighing again. It was calculated from the volumes of seawater and dry sediment, assuming a density of 1.025 and 2.6 g ml⁻¹, respectively.

The pH of bulk sediment was measured with a glass electrode, with buffers prepared in artificial seawater. Porewater was separated from the sediment with a pore-water squeezer, with argon gas and 0.45- μ m cellulose acetate filters. Ammonia, hydrogen sulfide, and dissolved silica were analyzed by standard photometric methods (Grasshoff et al. 1983) with some modifications for high sulfide concentrations. Chloride and sulfate were measured by ion chromatography at GEOMAR, Kiel, Germany.

Advection rates were estimated by fitting a one-dimensional diffusion–advection model described by Aloisi et al. (2004) to the Cl profile. The diffusion coefficient of chloride was corrected for temperature and porosity as outlined by Boudreau (1997). Changes in porosity and temperature with sediment depth were taken into account, and the model was integrated numerically, applying the method-of-lines approach (Luff and Wallmann 2003).

Results and discussion

We found the largest area with the highest densities of siliceous crusts close to the southern wall of the crater at Hook Ridge (Fig. 2). In this area, we deployed a conventional multicorer and recovered living *Sclerolinum* sp. during two out of four deployments (SO-MUC 32 and 33). The fauna of six cores were analyzed. On average, each core contained six or seven specimens of *Sclerolinum*, which is \sim 800 individuals m⁻².

Whereas *Sclerolinum* sp. was generally present in this hydrothermal vent area, it was absent in sediments with siliceous crusts, sampled by the three TVG deployments. These sites showed the most vigorous hydrothermal activity, with temperatures of up to 49°C and strong geochemical fluid signatures (Dahlmann et al. 2001). As a typical example, one profile (NBP-TVG 68) is shown in Fig. 3 (Web Appendix 1, http://www.aslo.org/lo/toc/vol_50/issue_2/0598al.pdf). The fluids are acid, depleted in chloride and sulfate and enriched in silica, ammonia, and hydrogen sulfide. Most probably, the absence of *Sclerolinum* sp. from these sites is a result of hostile chemical and thermal conditions.

The geochemical environment of *Sclerolinum* sp. is only moderately influenced by hydrothermal fluids (SO-MUC 32 and 33, Fig. 3). The profiles from both cores that contained living specimens are comparable, with a hydrothermal signature less distinct than at the hottest site (NBP-TVG 68) but more clearly visible than in a core without *Sclerolinum* sp. (SO-MUC 30). Although the latter core was also slightly influenced by hydrothermal venting, as indicated by the downcore decrease of chloride and sulfate and the increase in silica, the major parameters that characterize this core as a reference site were the absence of hydrogen sulfide (detection limit 1 μ mol L⁻¹) and low ammonia concentrations.

We distinguish three types of geochemical environment—(1) hot fluids with siliceous crusts, (2) *Sclerolinum* habitat, and (3) reference—to characterize the physicochemical habitat (temperature, advection rate, sulfide flux) and to discuss their influence on chemosynthesis-based species.

Because the near-surface pore-water profiles are strongly influenced by the chemical reaction and mixing with bottom

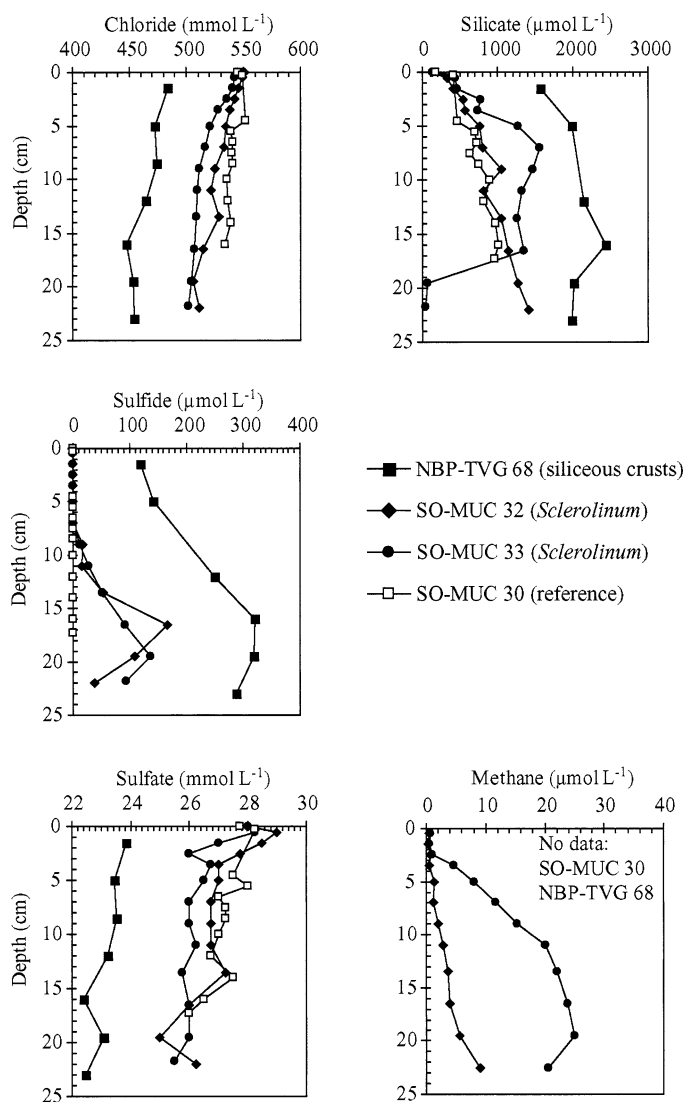


Fig. 3. Concentration of pore-water compounds versus depth in multicorer samples. Three different geochemical environments were sampled: siliceous crusts without macrofauna (NBP-TVG 68), sediments with *Sclerolinum* (SO-MUC 32 and 33), and sediments without hydrogen sulfide (SO-MUC 30).

water, we deployed a gravity corer to sample fluids from deeper sediments. The good overlap of the MUC and GC profiles indicates that we sampled the same geochemical habitat (Fig. 4). On the basis of the least diluted hydrothermal fluid data from the GC, we discuss the prevailing geochemical processes.

Temperature—The sediments with living *Sclerolinum* sp. recovered by the multicorer were still warm (up to 4.5°C) when they came on deck, although they probably cooled down significantly on their way through the 1,000-m cold water column (about -1.5°C). To estimate the in situ temperatures, we used the pore-water silicate concentration and a temperature-dependent solubility equation given by Van Cappellen and Qiu (1997). The assumption of this approach is that the fluids dissolve silicate from the biogenic silica-

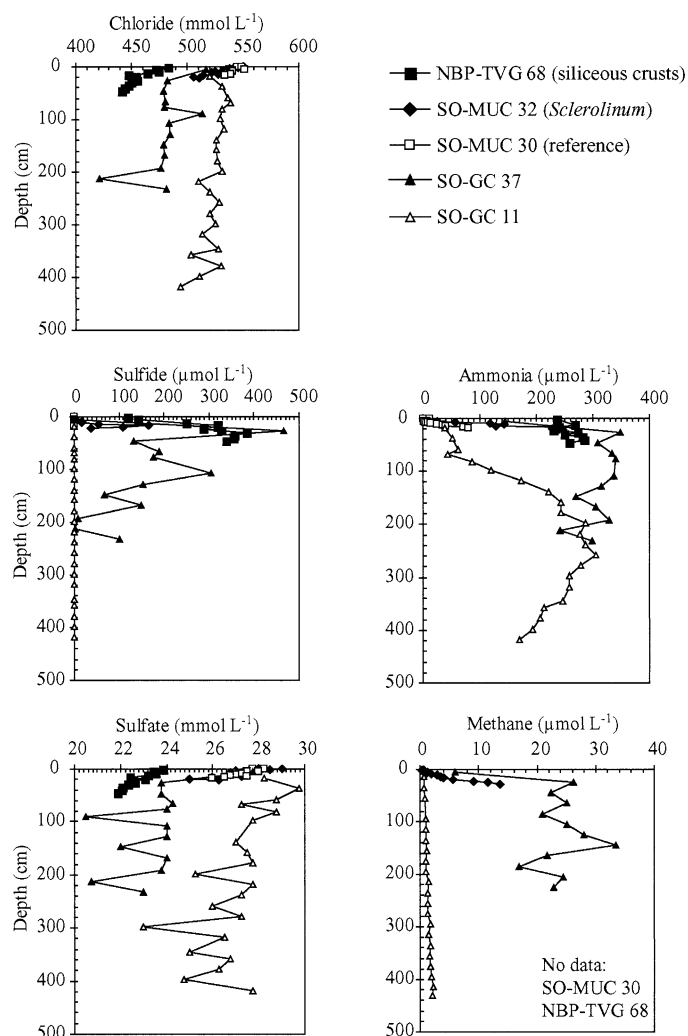


Fig. 4. Concentration of pore-water compounds versus depth in gravity corer samples. For comparison, the data of the multicorer (Fig. 3) are also included. There is good overlap between the SO-MUC 32 and 33 and the SO-GC 37 profiles, indicating that we successfully sampled undisturbed surface sediments with the multicorer and deeper fluids with the gravity corer. SO-GC 11 is less hydrothermally influenced compared with SO-GC 37.

rich sediments during hydrothermal circulation. The silica solubility is then mainly a function of temperature and pH. Dählmann et al. (2001) showed (on profile NBP-TVG 69) that this is a reliable method by comparing calculated in situ temperatures on the basis of this approach ($\sim 42^{\circ}\text{C}$) with $\delta^{18}\text{O}$ -derived values obtained from the siliceous crusts ($\sim 38^{\circ}\text{C}$) and temperatures measured ex situ with a temperature probe in the sediments of the voluminous ($\sim 1 \text{ m}^3$) TVG sediment block ($\sim 42^{\circ}\text{C}$).

The silicate concentrations at the maximum depth where *Sclerolinum* is found (15 cm) were $1,100\text{--}1,300 \mu\text{mol L}^{-1}$, which corresponds to in situ temperatures of about $11\text{--}18^{\circ}\text{C}$. This is a minimum estimate because, first, the low pH value of the hydrothermal fluids (~ 5.5) compared with seawater (~ 8) increases the silicate solubility. Roughly, this effect adds 5°C to the calculated values (by adding $\sim 150 \mu\text{mol}$

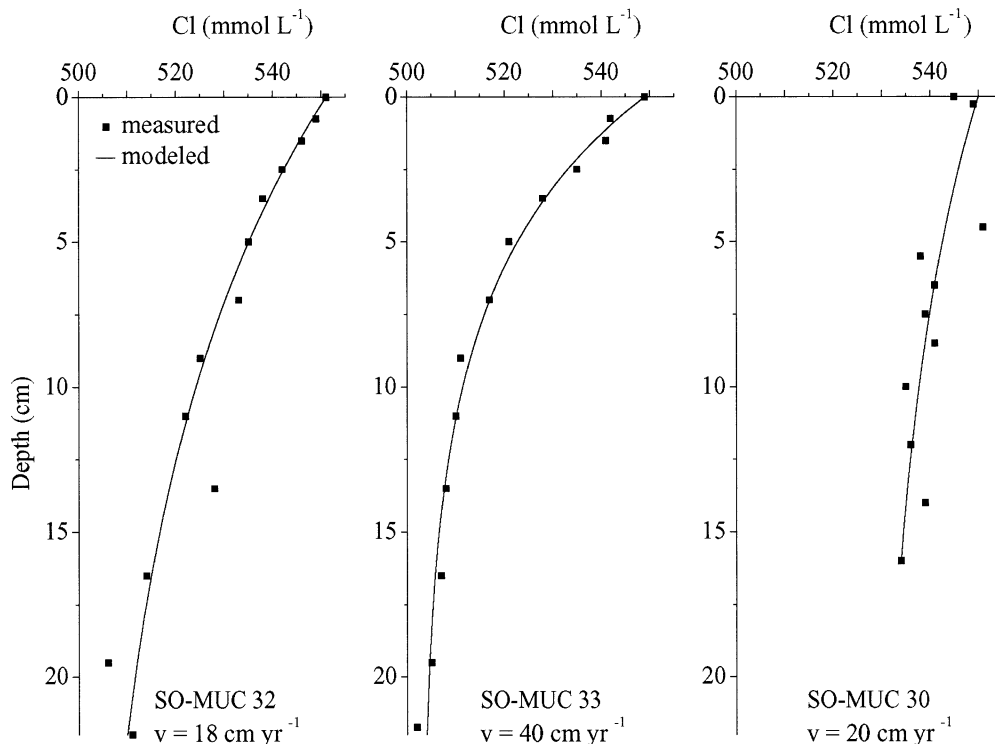


Fig. 5. Measured and modeled pore-water chloride profiles of sediments with *Sclerolinum* (SO-MUC 32 and 33) and without (SO-MUC 30). The chloride profiles were modeled with a one-dimensional transport-reaction model. Best fit curves were obtained by applying the flow velocities shown.

L^{-1} silicate, as read from the graph in Van Cappellen and Qiu 1997). Second, silicate can precipitate during heaving, sampling, and the analytical procedure. Thus, we assume that *Sclerolinum* individuals are exposed to temperatures of $\sim 20^{\circ}\text{C}$ at their posterior ends at 15 cm depth. The anterior part is exposed to about -1.5°C bottom water.

Most data concerning the influence of temperature come from hydrothermal vent studies at high-temperature sulfide edifices. Various experiments show that the temperature, as well as the time of exposure, influences survival (Fisher 1998). Compared with the maximum temperatures an animal can be exposed to during short time spans, the maximum sustained body temperature is much lower. For example, on the basis of physiological studies, it was concluded that the hydrothermal vent crab *Bythograea thermydron* can tolerate sustained temperatures $\sim 25^{\circ}\text{C}$, and alvinellids at the East Pacific Rise can withstand body temperatures of $\sim 30\text{--}35^{\circ}\text{C}$ (Fisher 1998). Thus, our observations that *Sclerolinum* sp. occurs in sediments with temperatures as high as 20°C and is absent from sediments that are influenced by warmer fluids of up to 49°C (NBP-TVG 68, Fig. 3) indicate that temperature could be the limiting factor.

In addition, siliceous crusts are formed by precipitation when the high-temperature fluids mix with low-temperature bottom water, which might physically exclude *Sclerolinum* from such sites. To our knowledge, this effect has not been observed at other hydrothermal systems.

Advection rates—In general, hydrothermal vents are considered to have higher fluid outflow rates than cold seeps. This is obviously true when looking at smoker-type vents. However, when sediments are present, the hydrothermal flow is much lower; thus, we were interested in how the advection rates at Hook Ridge compare with other reducing environments and whether this could influence species distribution.

The multicorer recovered undisturbed sediment surfaces from which we obtained high-resolution pore-water profiles. We modeled the advection rates for these samples by fitting a one-dimensional transport-reaction model to the measured chlorinity profiles. Chloride was chosen because, first, at low temperature, chloride is an inert tracer that is controlled by advection and diffusion; thus, the reaction term can be eliminated. Second, the hydrothermal fluids are considerably depleted in chloride because of phase separation at high temperature and pressure with end member concentrations $< 100\text{ mmol L}^{-1}$ (Dählmann et al. 2001). The model curves were fitted to the measured concentrations by adjusting the advection rates (Fig. 5). The rates are similar at sites with and without *Sclerolinum*, ranging from 18 to 40 cm yr^{-1} .

The published data on habitats at vents and seeps did not evidence a consistent relationship between advection rates and the occurrence of chemosynthesis-based species. Advection rates of the same order of magnitude are encountered at sites without chemosynthesis-based species at a sediment-covered ridge flank hydrothermal vent (20 cm yr^{-1} ; Maris

and Bender 1982), with vesicomyid clams at a sediment-hosted hydrothermal vent at Chowder Hill, Middle Valley, Juan de Fuca Ridge (50 cm yr⁻¹; Grehan and Juniper 1996), and with bacterial mats at cold seeps with gas hydrate deposits at Hydrate Ridge (Oregon Margin) and average flow rates in the range of 10–100 cm yr⁻¹ (Tryon et al. 1999). This comparison emphasizes that the flow velocities at sediment-hosted hydrothermal vents can be compared with cold seeps. Thus, when sediments occur at hydrothermal vents, the habitat conditions for the chemosynthetic community are more similar—at least with respect to the advection rate—to cold seeps than to the bare-rock hydrothermal vents.

Source, concentration, and flux of hydrogen sulfide—We discuss the source of hydrogen sulfide that is assumed to be the energy-yielding chemical compound used by the endosymbionts in *Sclerolinum* sp. in our samples. This assumption is based on transmission electron micrograph images of the endosymbiotic bacteria in the trophosome that show similarities to other well-studied siboglinids with sulfur-oxidizing chemoautotrophic bacteria (E. Southward and L. Beck pers. comm.). However, further studies are needed to confirm this.

Our data show that significant hydrogen sulfide concentrations of ~150 μmol L⁻¹ are present at the posterior end of *Sclerolinum* sp. at a depth of 15 cm (Fig. 3). The sulfide concentrations decrease in the multicorer (SO-MUC 32 and 33) as well as the gravity corer samples (SO-GC 37) at deeper sediment depths (Figs. 3, 4). This decrease is very likely an artifact that occurred during sampling and analytical procedure. The low pH and high temperatures of the sediment cores favor the loss of H₂S gas from the porewater. As we processed and analyzed the cores from the top downward, we assumed that the first samples were not significantly biased. Despite the similarity of the hydrogen sulfide profiles obtained from the two *Sclerolinum* sediment cores, we can not rule out that ex situ oxidation occurred. Therefore, the sulfide concentrations and fluxes given below are minimum values.

Hydrogen sulfide is possibly enriched in the fluids because of seawater–basalt interaction at high temperatures (Von Damm 1995). This is indicated by the hydrogen sulfide concentrations that are much higher in the hottest sediments that also showed the strongest hydrothermal fluid signatures (i.e., lowest pH, chloride, and sulfate concentrations and highest silicate concentrations; Fig. 3). Dählmann et al. (2001) estimated that the fluids at Hook Ridge contained >4.5 mmol L⁻¹ of hydrogen sulfide before they became diluted by seawater entrainment.

At Hook Ridge, the fluids flow through sediments before they reach the sediment–water interface; therefore, sulfate reduction could also contribute to the hydrogen sulfide pool. Sulfate reduction is caused by the anaerobic oxidation of methane at cold seeps (Boetius et al. 2000) or the anaerobic oxidation of organic matter. Anaerobic oxidation of methane can only have a minor influence because methane concentrations (<25 μmol L⁻¹, Figs. 3, 4) are too low to account for hydrogen sulfide concentrations of >150 μmol L⁻¹. Anaerobic organic matter degradation leads to an increase in nutrients like ammonia. This is observed in core SO-GC 11.

Because the fluid-influenced core SO-GC 37 shows almost the same ammonia concentration, we conclude that no enhanced amounts of organic matter are degraded as a result of the hydrothermal setting. This is in accordance with the sediment organic matter content that is not enriched at the *Sclerolinum* sites (values ~0.6–1%, Web Appendix 1). Furthermore, the concentration profiles of ammonia did not further increase with sediment depth after the concentration reached its maximum around 350 μmol L⁻¹ (SO-GC 37, Fig. 4), which indicates that anaerobic organic matter degradation is not a significant process at depth. We conclude that the major source of hydrogen sulfide in the *Sclerolinum* habitat is the hydrothermal fluid. The original high sulfide concentration is lost on the way through the sediment column from dilution by seawater entrainment and removal as metal sulfide precipitates. The remaining hydrogen sulfide concentrations to which *Sclerolinum* is exposed is further oxidized by the species itself.

The flux of sulfide in the *Sclerolinum* habitat can be estimated roughly by taking into account the concentration of hydrogen sulfide and the advection rates. For example, at a given advection rate of 40 cm yr⁻¹ (SO-MUC 33), 400 dm³ of porewater is seeping through an area of 1 m² yr⁻¹. The fluids contain 136 μmol L⁻¹ of sulfide at ~20 cm sediment depth, but zero sulfide at the sediment–water interface, resulting in a sulfide flux of 0.054 mol m⁻² yr⁻¹ into the *Sclerolinum* habitat (SO-MUC 33). The same calculation yields ~0.03 mol m⁻² yr⁻¹ for SO-MUC 32.

Comparison with other habitats—To our knowledge, there are no chemical environmental data published for other *Sclerolinum* species, except for *S. contortum* (Smirnov 2000) from Håkon Mosby Mud Volcano. However, this species is stated to live in symbiosis with methanotrophic bacteria (Pimenov et al. 1999; Lein et al. 2000). Methane concentrations in these sediments are two orders of magnitude higher than in the Hook Ridge *Sclerolinum* habitat (>50 ml dm⁻³, corresponding to approximately >2.2 mmol L⁻¹; Lein et al. 2000). The only other siboglinid for which methanotrophy has been demonstrated, *Siboglinum poseidoni*, lives at similar high methane concentrations (0.3–3.3 mmol L⁻¹; Dando et al. 1994). The availability of methane in the habitat appears to influence the type of symbiotic bacteria and the physiological capabilities of the symbiosis.

All other siboglinids that have been studied in detail appear to live in symbiosis with sulfur-oxidizing bacteria (Fisher 1990). Most *Siboglinum* species (Frenulata) depend on sulfur-oxidizing bacteria, although they can occur in sediments with hydrogen sulfide concentrations below the analytical or olfactory detection limit (Southward et al. 1986, 1988). We found *Siboglinum plumosum* on the Sakhalin shelf in the Sea of Okhotsk (Sahling et al. 2003) at hydrogen sulfide concentrations of ~250 μmol L⁻¹ (Sahling unpubl. data). Calculation of the sulfide flux on the basis of a simple diffusion equation revealed a flux of ~0.006 mol m⁻² yr⁻¹. The sulfide concentration and flux for *S. plumosum* (Frenulata), as well as for the Antarctic *Sclerolinum* (Monilifera), is in the same range, which could indicate that the small siboglinids (Frenulata and Monilifera) are able to live in habitats with low sulfide availability.

Table 1. Comparison of the physicochemical habitat of selected sediment-living species that are chemoautotrophic or depend on chemoautotrophy of their symbionts.

Species	Area/Physicochemical environment	Sulfide concentration (mmol L ⁻¹)/ [Sediment depth (cm)]	Sulfide flux (mol m ⁻² yr ⁻¹)
<i>Beggiatoa</i>	Guaymas Basin, sediment-hosted hydrothermal vent, 2,000 m water depth 2.8°C (bottom water), >100°C (25 cm sediment depth) (Jørgensen et al. 1990; Weber and Jørgensen 2002)	7–15 [5]	70*
<i>Beggiatoa</i>	Hydrate Ridge/Cascadia margin, gashydrate deposits at cold seep, 780 m water depth Advection rate 10–100 cm yr ⁻¹ ~4°C (bottom water) (Tryon et al. 1999; Boetius et al. 2000; Sahling et al. 2002)	8–20 [5]	51* 23‡
<i>Calyptogena pacifica</i> , <i>C. kilmeri</i>	Hydrate Ridge/Cascadia margin, gashydrate deposits at cold seep, 780 m water depth Fluid in- and outflow ~4°C (bottom water) (Tryon et al. 1999; Sahling et al. 2002)	7–20 [10]	6.6‡
<i>Calyptogena phaseoliformis</i>	Aleutian trench, cold seep, ~4,900 m water depth Advection rates 3.4 m yr ⁻¹ ~1.5°C (bottom water) (Wallmann et al. 1997)	>1 [20]	19‡
<i>Calyptogena</i> sp.	Middle Valley, sediment-hosted hydrothermal vent, ~2,400 m water depth Advection rate ~0.5 m yr ⁻¹ 2°C (bottom water) to 4–10°C (10 cm sediment depth) (Juniper et al. 1992; Grehan and Juniper 1996)	~0.5 [4–8]	0.25‡
<i>Lamellibrachia</i> sp.	Hydrocarbon seep, Gulf of Mexico, ~700 m, ~8°C (bottom water) (Julian et al. 1999)	>1.5 [10–20]	No data
<i>Siboglinum atlanticum</i>	Santander Canyon, Bay of Biscay, organic matter degradation, ~1,440–2,200 m water depth 3.5–4.5°C (bottom water) (Southward and Dando 1988)	<0.0001	No data
<i>Siboglinum fjordicum</i>	Ypresund, Norway, organic matter degradation, 25 m water depth 4–12°C (bottom water) (Southward et al. 1986)	<0.001	No data
<i>Siboglinum plumosum</i>	Sakhalin Shelf, Sea of Okhotsk, organic matter degradation, 400 m water depth –1.7 to ~2°C (bottom water) (Sahling et al. 2003, unpubl. data)	~0.250 [15]	0.006‡
<i>Sclerolinum</i> sp.	Bransfield Strait, Antarctica, sediment-covered hydrothermal vent, 1,045 m water depth Advection rates 18–40 cm yr ⁻¹ –1.8°C (bottom water) to 20°C (15 cm sediment depth) (This study)	~0.150 [15]	0.003–0.054‡

* Sulfate reduction rate method.

‡ Modeling of pore water profiles.

‡ Estimate based on advection rate and sulfide concentration. The flux estimate in Grehan and Juniper (1996) used in incorrect sulfide concentration; recalculation with 0.5 mmol L⁻¹ results in 0.25 mol m⁻² yr⁻¹.

Sediments with high sulfide concentrations and fluxes sustain prolific communities consisting of large Vestimentifera (e.g., *Lamellibrachia* sp.), vesicomyid clams, or filamentous sulfur-oxidizing bacteria (e.g., *Beggiatoa*; Table 1). All these species have been reported from sediments with sulfide concentrations in the millimolar range (e.g., >1.5 mmol L⁻¹ around *Lamellibrachia* “roots” [Julian et al. 1999], 0.5–20 mmol L⁻¹ in the vesicomyid habitat [Grehan and Juniper 1996; Barry et al. 1997; Wallmann et al. 1997], and 1–20 mmol L⁻¹ at sites with *Beggiatoa* [Jørgensen et al. 1990;

Sahling et al. 2002; Weber and Jørgensen 2002]). In addition, the flux of hydrogen sulfide in these habitats is three to four orders of magnitude higher than in the Hook Ridge sediments inhabited by *Sclerolinum* (Table 1). Vesicomyid clams occur at sulfide fluxes of 0.25–19 mol m⁻² yr⁻¹ and *Beggiatoa* at sites with 23–70 mol m⁻² yr⁻¹ (Table 1).

This compilation of data suggests that sulfide availability in the different habitats is one key factor that matches well with the distribution of sulfide-based symbiotic species. Siboglinids that live in thin tubes and, thus, have a high sur-

face-to-volume ratio and low biomass, occur when sulfide availability is very low. Typical seep and vent species in soft sediments, like vestimentiferans, vesicomyid clams, or bacterial mats, occur at higher sulfide concentrations and fluxes. We propose a threshold in sulfide concentration ($> \sim 500 \mu\text{mol L}^{-1}$) and sulfide flux ($> 0.1 \text{ mol m}^{-2} \text{ yr}^{-1}$) that is required to sustain typical vent and seep species. These values can be tested in future studies, for example at sites influenced by large food falls, where the fauna resembles seep- and vent-type taxa (Smith et al. 1989) but with largely different chemical processes producing the reduced sulfide compounds. We conclude that the geochemical habitat at Hook Ridge is not favorable for typical vent and seep species: At sites inhabited by *Sclerolinum*, the sulfide availability is too low, whereas at sites with higher sulfide availability, the temperatures are too high, siliceous crust precipitation precludes their occurrence, or both.

This is a comparative study with two major limitations: (1) it only includes sulfur-based chemosynthetic species that (2) occur in soft sediment settings. We propose that sulfide availability is a better parameter than—although directly dependent on—the geological setting and fluid advection rates to understand sulfur-based chemosynthetic species distribution. Other abiotic influences and biological interactions are also relevant for observed distribution trends. Further combined biological and geochemical studies are needed to refine the habitat preferences of species in greater detail (e.g., to answer the question of why Frenulata and Monilifera have been not sampled in the same habitat).

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