

production at two oceanic sites in the Pacific is associated with particles able to pass 1- μm screens. The importance of this fraction increases toward the base of the euphotic zone, a feature that is understandable in terms of the higher effective optical cross section for smaller cells (25), which leads to a higher efficiency of utilization of the available light at depth. We cannot exclude totally the possibility, at least at the Biostat site, that there may be a population of very small pigmented cells that did not survive normal sampling procedures, is invisible to conventional light microscopy, or did not respond to our incubation techniques (that is, did not survive the experimental procedure).

Our results, the time-course measurements in particular, indicate that the picoplankton include photosynthetically active cells. These results are contrary to those reported by Herbland and LeBouteiller (12), who concluded that the size fraction of particles < 3 μm comprised mainly inactive phytoplankton. Their results, however, may not be definitive because the filters they used as terminal screens (effective pore size 2 to 3 μm) may have been too coarse (26).

A probable corollary to our results is that, because the autotrophic cells in the picoplankton fraction are active rather than dormant or inert, they or their aggregates must be grazed by some organism or organisms at about the same rate as they are being produced. These results support a view of the structure of the pelagic ecosystem in which most of the activity (production and metabolism) is carried by very small organisms (27). The significance for quantification of autotrophic biomass and primary production in the ocean is that use of filters not able to trap particles at least 0.2 μm or smaller will lead to results that are too low.

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18. Fresh samples excited at 400 nm (Zeiss BG12) and preserved samples excited at 450 to 490 nm (acridine orange combination) yielded the same counts as preserved samples excited at 365 nm.
19. The discrepancy between cell counts and chlorophyll measurements could be reconciled in terms of "excess chlorophyll" or "invisible photoautotrophs" at Biostat. The excess chlorophyll may represent detrital chlorophyll-like pigments [Gieskes *et al.* in (12)] or fragments of larger algae disrupted during sampling and filtration [Lasker and Holmes, in (12)]. Cyanobacteria that are not visible for direct counting have been reported [Johnson and Sieburth, in (8)]; also, fragile flagellated forms have been observed to "simply vanish" during preparation for enumeration [R. R. Parker and D. J. Tranter, *Aust. J. Mar. Freshwater Res.* **32**, 629 (1981)]. To calculate chlorophyll per cell we used the following constants: specific gravity, 1.0; ratio of dry to wet weight, 0.1; ratio of carbon to dry weight, 0.4; and ratio of carbon to chlorophyll a, 40.
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Sulfide Binding by the Blood of the Hydrothermal Vent Tube Worm *Riftia pachyptila*

Abstract. *The blood of the deep-sea hydrothermal vent tube worm Riftia pachyptila Jones contains a sulfide-binding protein that appears to concentrate sulfide from the environment and may function for sulfide transport to the internal endosymbiotic bacteria contained within the coelomic organ, the trophosome.*

Clusters of the large red vestimentiferan tube worm *Riftia pachyptila* (phylum Pogonophora) occur in association with actively venting warm water at deep-sea hydrothermal vent sites, including the Rise site at 21°N on the East Pacific Rise (1). The worms at this site live where water temperatures average about 10°C (2) and hydrogen sulfide is present (3). *Riftia pachyptila* has internal bacterial symbionts that appear to be capable of oxidizing sulfide to obtain energy (4). The trophosome organ, which contains the bacterial symbionts, is highly vascularized and is linked to the apparent site of gas exchange, the obturacular plume, by dorsal and ventral blood vessels, with a heart located in the dorsal vessel (4, 5). We have examined the role of the hemoglobin-containing blood (6, 7) of this animal in the transport

of sulfide from the obturacular plume to the trophosome. We show that the blood of *R. pachyptila* has a high capacity for sulfide and has the ability to transport sulfide as well as other gases to the internal bacterial symbionts.

The tube worms were collected at 2600 m by the D.S.R.V. *Alvin* from the collapsed pit site (20°50'N, 109°06'W) on the East Pacific Rise at 21°N (1) and were brought to the surface in thermally insulating polyethylene boxes. We collected blood from the freshly recovered living animals. The experiments described in this report were done on fresh vascular blood while we were on board the R.V. *Melville* at the hydrothermal vent site (except in the one case noted). The vascular blood was collected by dissection of the worm to expose the anterior section of the large dorsal vessel

which was drained into a chilled beaker.

We analyzed the gas content of the blood immediately after the worms were brought to the surface to determine whether sulfide was present in their blood in their natural environment. The gases in this freshly collected blood were stripped by the carrier gas flow into a gas chromatograph that measured sulfide and carbonate concentrations (8). The vascular blood of the tube worms contained high concentrations of sulfide (up to 1.1 mM) (Table 1). This finding indicates that substantial quantities of sulfide are available to these animals in the vent environment. The presence of sulfide in the blood also suggests that an appreciable supply of sulfide is available to the bacterial symbionts in the trophosome organ, supporting the hypothesis that the endosymbiotic bacteria use sulfide as an energy source (4). The elevated carbonate levels and low pH values of the blood probably are a result of anoxic conditions in the collection box during the approximately 2-hour recovery from the bottom (Table 1).

Although sulfide levels immediately around the worms have not been measured (because of the instability of sulfide and the dilution of the vent waters before they reach the worms), it seems unlikely that ambient sulfide would approach the higher concentrations found inside the worms. The dilution of the "end-member" water at this site, which is at 350°C and contains 6.5 mM H₂S (3), to the 10°C water found around the worms (2) would suggest an upper limit for sulfide of about 0.19 mM in this area. This suggests that the blood of *R. pachyptila* may concentrate sulfide from the environment in a manner analogous to the O₂-concentrating properties of blood respiratory proteins. To characterize this sulfide accumulation, we placed vascular blood with a low initial sulfide content in dialysis tubing (molecular

Table 1. Initial blood gas concentrations. All measurements were done on freshly collected vascular blood, and pH values were determined at 5°C.

Animal number	pH	Sulfide (mM)	CO ₂ (mM)
1214-6A	6.70	0.86	3.65
1214-6B	6.36	0.03	2.13
1214-6C	6.08	0.57	2.95
1214-6D	6.21	1.12	2.57
1214-6E	7.30	0.12	3.84

weight retention of 10,000) and dialyzed in a tris buffer (pH 7.76 at 5°C) containing a low sulfide concentration. In two parallel experiments, bovine serum albumin and human hemoglobin solutions of comparable protein concentrations were tested for possible sulfide accumulation at the same time as the *R. pachyptila* blood (Fig. 1, A and B). The sulfide levels of each solution were monitored over time with the gas chromatograph. This experiment tested for binding, but not for the rate of binding, since uptake of sulfide was limited by the dialysis apparatus.

The vascular blood of *R. pachyptila* showed marked accumulation of sulfide over time (Fig. 1, A and B). In *R. pachyptila* blood, sulfide levels rose as high as 3 mM in a 0.10 mM sulfide solution, whereas bovine serum albumin and human hemoglobin solutions showed no sulfide accumulation. Thus the high capacity for sulfide concentration of *R. pachyptila* blood is not a general protein or hemoglobin phenomenon, but rather is a previously undescribed, distinct property of this animal's blood. This accumulation appears to be reversible, since lowering the blood pH to 5 resulted in the release of virtually all sulfide (9). In experiments in which the blood was dialyzed with a membrane of 15,000 molecular weight retention, the binding component was retained, indicating that

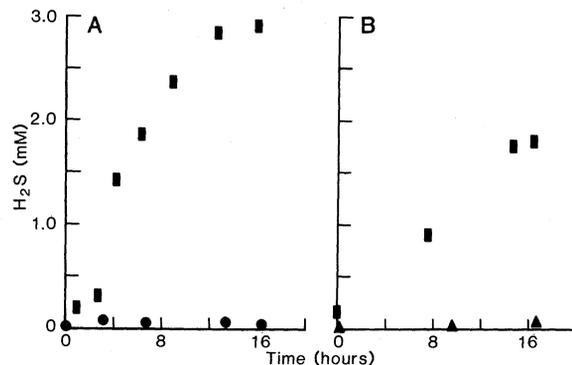
the molecular weight of the binding component is probably greater than 15,000.

Vascular *R. pachyptila* blood was saturated with ammonium sulfate and centrifuged at 13,000 rev/min for 45 minutes. The blood initially contained 2.89 mM sulfide. The precipitated protein fraction retained 0.64 mM sulfide, and the supernatant contained no sulfide. The carrying through of sulfide in the precipitated protein fraction during ammonium sulfate treatment and the sulfide-concentrating effect (Fig. 1, A and B) suggest that *R. pachyptila* blood actually binds sulfide. The form of sulfide bound is most likely to be either H₂S or HS⁻ (with a dissociation constant, *pK*, of 7.04) at the pH values that occur inside the animals.

The fraction precipitated at 50 percent saturation with ammonium sulfate (this fraction contained both the binding molecule and the hemoglobin) was divided into three portions; one portion was boiled for 10 minutes, another was digested with proteolytic enzymes (protease K, trypsin, and chymotrypsin for 30 minutes at pH 4), and the third was untreated. These three fractions together with the supernatant were titrated to pH 7 and tested for sulfide accumulation by dialysis against a deoxygenated 50 mM tris buffer containing 0.27 mM sulfide at pH 7 for 20 hours at 5°C. The untreated precipitated fraction accumulated sulfide up to 2.54 mM, whereas the sulfide concentration in the supernatant and both the boiled and the enzyme-treated fractions remained similar to that of the medium (0.12 mM, 0.27 mM, and 0.13 mM, respectively). These data indicate that the sulfide-accumulating component of *R. pachyptila* blood is a protein, because it was precipitated by ammonium sulfate and subject to denaturation by heat and destruction by proteolytic enzymes.

Our data show that *R. pachyptila* has the ability to concentrate sulfide from the medium and the potential for transporting it in substantial quantities to its bacterial endosymbionts. This is important because, regardless of the metabolic capacities of the endosymbionts, their metabolism of any given substrate will be limited by supply. The apparent capacity of *R. pachyptila* vascular blood for sulfide (1.5 to 3 mM) approaches its capacity for O₂, that is, about 4 mM (6). *Riftia pachyptila* blood may also reduce the rate of spontaneous oxidation of sulfide internally since it showed sustained high levels of sulfide over time in the presence of O₂ (10). The apparent lack of sulfide oxidation is a further indication that the sulfide is bound and unavailable

Fig. 1. Sulfide accumulation in *Riftia pachyptila* vascular blood, bovine serum albumin, and human hemoglobin solution. (A) *Riftia pachyptila* blood (■) protein concentration was estimated at 140 mg/ml, pH 7.45; bovine serum albumin (●) protein concentration was 68 mg/ml, pH 7.61; and the dialyze was 50 mM tris buffer with 0.10 mM sulfide, pH 7.65, deoxygenated by bubbling with N₂. (B) *Riftia pachyptila* blood (■) protein concentration was estimated at 140 mg/ml, pH 7.23; human hemoglobin solution (▲) protein concentration was estimated at 200 mg/ml after lysis of packed erythrocytes with twice-distilled water, pH 7.63; and the dialyze was 50 mM oxygenated tris buffer with 0.04 mM sulfide, pH 7.61.



for interaction with O₂, thus enabling the persistence of sulfide in the animal and the simultaneous transport of both sulfide and O₂ by the blood to internal symbionts. This further supports the proposed sulfide-based chemoautotrophy hypothesis (4).

The hemoglobin of *R. pachyptila* accounts for more than 90 percent of the total protein present in the blood (11) and is therefore a likely candidate for the sulfide-binding protein. Vertebrate methemoglobin (ferric hemoglobin produced by treatment with nitrite or ferricyanide) can form complexes with sulfide (12). The sulfide binding by *R. pachyptila* blood does not appear to involve the formation of methemoglobin, however, as substantial levels of methemoglobin have not been detected in *R. pachyptila* blood (fresh blood showed no spectral indication of methemoglobin or sulfhemoglobin formation when exposed to sulfide levels as high as 5.3 mmHg of H₂S gas) and determinations of methemoglobin in fresh blood were low (13). In addition, vertebrate methemoglobin does not occur naturally in high concentrations and is nonfunctional for O₂ transport, whereas *R. pachyptila* sulfide-binding protein is present in high concentrations and the blood has a high O₂ capacity simultaneously.

The binding of sulfide by vertebrate methemoglobin protects against sulfide poisoning both in vitro and in vivo (14). The binding protein in *R. pachyptila* has been shown to protect against sulfide poisoning in this species (15).

In conclusion, *R. pachyptila* blood contains a sulfide-binding protein that may, in analogy to oxygen-binding proteins, allow the animal to concentrate sulfide from its environment and transport sulfide to the point of utilization within the animal's body. The unloading of sulfide to the trophosome could occur in response to lower pH or lower sulfide concentrations. This protein may also have an important function in protecting the animal against sulfide toxicity.

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9. *Riftia pachyptila* blood with an initial sulfide concentration of 2.62 mM was titrated with 0.5M HCl to pH 5. Blood sulfide concentration dropped to 0.44 mM after 3 hours, 0.18 mM after 5.5 hours, and 0.03 mM after 11.5 hours.
10. Blood dialyzed against oxygenated 50 mM tris buffer (pH 7.76 at 5°C) that contained 0.74 mM sulfide accumulated and retained 3 mM sulfide for 5 days.
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13. Treatment with H₂S gas at 5.3 mmHg failed to produce peaks at 635 nm or at 520 nm; the relative heights of the α and β peaks were approximately equivalent, and no spectral shift of any kind was indicated. Fresh *R. pachyptila* blood showed low methemoglobin (coelomic, 0.03 g/100 ml; vascular 0.13 g/100 ml), determined spectrophotometrically by the method of K. A. Evelyn and H. T. Malloy [*J. Biol. Chem.* 126, 655 (1938)]. The hemoglobin of the annelid *Abarenieva affinis* has also been shown to be insensitive to sulfide [R. M. G. Wells and N. W. Parkhurst, *Comp. Biochem. Physiol. C*, 66, 255 (1980)].
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Blood Components Prevent Sulfide Poisoning of Respiration of the Hydrothermal Vent Tube Worm *Riftia pachyptila*

Abstract. *Respiration of plume tissue of the hydrothermal vent tube worm Riftia pachyptila is insensitive to sulfide poisoning in contrast to tissues of animals that do not inhabit vents. Permeability barriers may not be responsible for this insensitivity since plume homogenates are also resistant to sulfide poisoning. Cytochrome c oxidase of plume, however, is strongly inhibited by sulfide at concentrations less than 10 μM. Factors present in blood, but not in cytosol, prevent sulfide from inhibiting cytochrome c oxidase. Avoidance of sulfide poisoning of respiration in Riftia pachyptila thus appears to involve a blood-borne factor having a higher sulfide affinity than that of cytochrome c oxidase, with the result that appreciable amounts of free sulfide are prevented from accumulating in the blood and entering the intracellular compartment.*

The dense communities of organisms at the deep-sea hydrothermal vents are believed to be highly dependent on primary production that is driven by the oxidation of hydrogen sulfide (1). The sulfide that is produced by reduction of seawater sulfate in the hot basaltic rocks of the sea floor (2) is oxidized by chemolithotrophic bacteria that are either free-living or contained as symbionts within specialized tissues of certain vent animals (3, 4). The vent tube worm *Riftia pachyptila* Jones (5), which lacks a mouth and digestive system, harbors symbiotic bacteria at densities of approximately 10⁹ cells per gram (fresh

weight) in its trophosome tissue (3). Studies of enzyme systems (4, 6, 7) and stable carbon isotope ratios (8) of *R. pachyptila* indicate that reduced carbon compounds generated in the trophosome may supply a major share of the organism's needs for these materials.

While supplying an abundant source of energy for primary production in the vent ecosystem, hydrogen sulfide creates a potential problem for the vent organisms as a result of its extreme toxicity. With the exception of certain animals from sulfide-rich sediments (9), the animals that have been studied are killed by sulfide concentrations of a few micro-