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Meiofauna and the Thiobios in the East Flower Garden Brine Seep

E. N. Powell, T. J. Bright, A. Woods and S. Gittings

Department of Oceanography, Texas A&M University; College Station, Texas 77843, USA

Abstract

Special hydrodynamic-chemical conditions at the East Flower Garden brine seep have provided the opportunity to examine the community structure of the thiobios and the oxybiotic-thiobiotic boundary. The boundary between the thiobios, whose population maxima occur in sulfide-dependent chemoclines and which presumably have an ecologic requirement for sulfide, and the oxybios, which occur in oxidized zones above the chemocline, is controlled by sulfide, not oxygen. The boundary, which may not be at zero sulfide, is determined by a time-concentration phenomenon based on a dynamic interplay of sulfide and oxygen supply rates and the biota's sulfide detoxification capabilities. In Gollum's Canyon, where oxygen is plentiful, the boundary is at 10–40 μg-atoms $\cdot$ l^{-1} sulfide. Total abundances of organisms at thiobiotic stations were comparable to total abundances at oxybiotic stations. Highest thiobiotic abundance was 202 051 organisms per m^2; highest oxybiotic abundance was 240 572 organisms per m^2. The thiobios is dominated by representatives of the lower Bilateria (viz. Gnathostomulida, Platyhelminthes and Aschelminthes). These groups accounted for 50–80% of all the organisms present in the thiobiotic stations but less than 20% of all organisms in the oxybiotic stations. At two thiobiotic stations, over 50% of all organisms were gnathostomulids. Thiobios included macrofaunal as well as meiofaunal components. Peak abundances of amphipods were associated with the thiobiotic environment.

Introduction

Marine sediments, with the exception of wave-stressed beaches and some areas of the deep sea, possess three vertical zones: (1) a surface oxidized layer usually 1 to 10 cm deep, (2) a reduced deeper layer usually characterized by the presence of sulfide (used in this paper to denote total dissolved sulfide: $H_2S+HS^-+S^{-2}$) in the interstitial water and, in clastic sediments, by a distinctive black coloration, and (3) the boundary between the two, which has been termed the redox potential discontinuity or RPD (Fenchel and Riedl, 1970). Since it is the gradients of oxygen and sulfide that are likely to be important here, not the gradient in redox potential, the RPD is termed the chemocline in this paper. The chemocline, for all practical purposes, is chemically identical to the chemocline found in many lakes and stagnant ocean basins where the term has been previously used.

Fenchel and Riedl (1970) described the environmental conditions and biota of the reduced sediments and called this biotope the sulfide system. The interstitial organisms associated with it included various micro-metazoans such as gnathostomulids, gastrotrichs, nematodes and turbellarians. Boaden and Platt (1971) used the term, thiobios, to denote the biota of the sulfide system. Although the discovery of the thiobios was unexpected because the environmental parameters associated with the sulfide system (i.e. high sulfide concentrations and very low to zero O_2 levels) were generally considered inimical to metazoan life, subsequent work has corroborated Fenchel and Riedl's claim that two distinct groups of interstitial organisms are present in most sandy marine sediments. One inhabits the surface oxic sediment. The other, the thiobios, inhabits both the deeper reducing sediment and the chemocline between them (Ott, 1972; Ehlers, 1973; Crezee, 1976). Among the meiofauna, some taxonomic groups, such as the turbellarian groups Solenofilomorphidae (Crezee, 1976) and Catenulida (Sterrer and Rieger, 1974) and the phylum Gnathostomulida (Farris, 1976) are nearly or totally restricted to the thiobiotic environment. Other groups such as the harpacticoid copepods are rarely encountered in it (Fenchel and Riedl, 1970; Wieser *et al.*, 1974).

The chemical-ecological boundaries of the thiobiotic environment and the role of thiobiotic micro-metazoans in meiofauna community structure and function have been

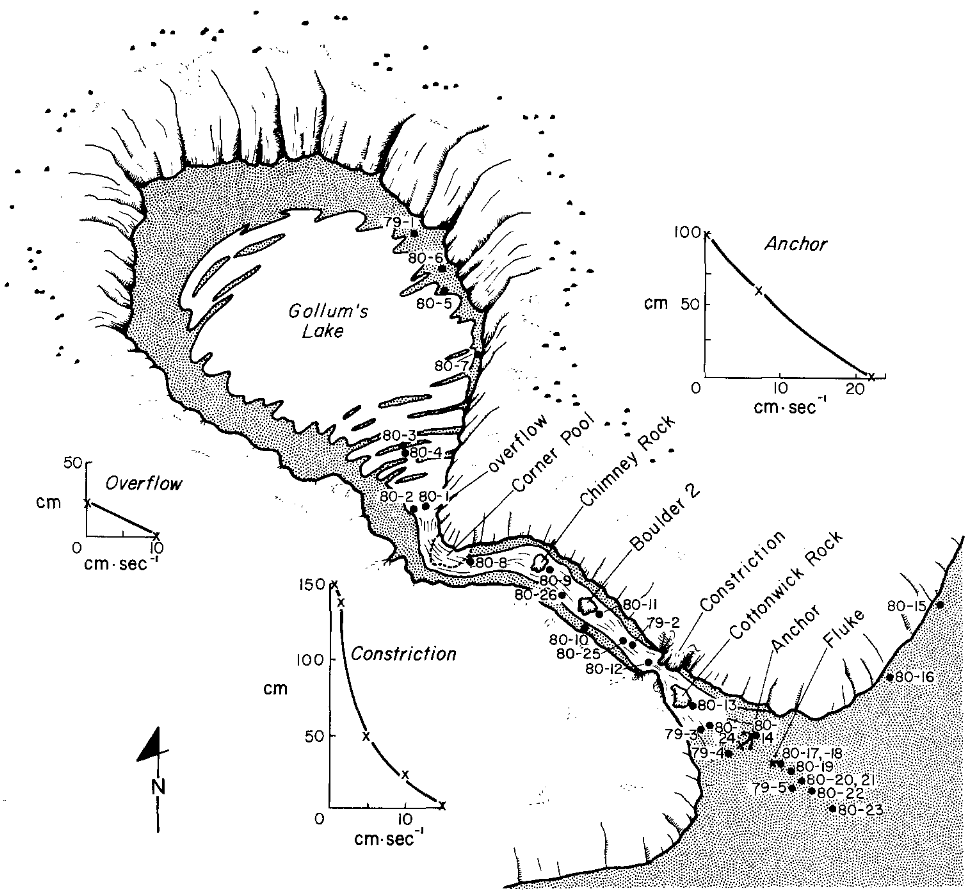

Fig. 1. The East Flower Garden brine seep area with location of the sampling stations and current profiles of the brine stream at three stations as measured by a Savonius rotor placed on the manipulator arm of the submersible "Sea Link"

questioned. Reise and Ax (1979, 1980) and Reise (1981a, b) pointed out that the distributional maxima of most thiobiotic organisms are consistently associated with low oxygen regions such as the micro-oxic zones of animal burrow walls and the redox potential discontinuity at the upper boundary of the sulfide system rather than with the black, reducing sediments below the RPD. Reise and Ax (1980) suggested that the thiobios, as conceived by Boaden (1977) and Fenchel and Riedl (1970), does not exist, that these organisms are merely an extension of the surface oxic biota adapted to life along burrow walls, and that no true community exists which is clearly associated with the reducing environment. Powell and Bright (1981) argued that the thiobios does exist, but redefined it as organisms with an ecologic requirement for sulfide, that inhabit sulfide-dependent chemoclines and which are, therefore, dependent on sulfide as well as oxygen for existence.

A brine seep occurs at 72-m depth near the eastern edge of the East Flower Garden Bank (EFGB) located at Lat. 27°54′N, Long. 93°34′W in the northwestern Gulf of Mexico (Bright *et al.*, 1980a). The sulfide-rich brine, which results from dissolution of the salt diapir underlying the EFGB (Rezak and Bright, 1981), flows by gravity into a basin located about 60 m from the bank's edge to form a brine lake – Gollum's Lake (Fig. 1). The overflow from the lake flows into a 96-m long canyon – Gollum's Canyon – which runs from the brine lake to the edge of the bank. At the canyon mouth, the brine stream spreads out laterally, decreases substantially in height, and slowly dissipates as it moves out across the gently inclined bottom adjacent to the bank. More complete descriptions appear in Bright *et al.* (1980a, b). Powell and Bright (1981) described a unique, gnathostomulid-dominated community from Gollum's Canyon and concluded that it is thiobiotic.

This brine seep system provides an opportunity to study the impact of a sulfide system on eukaryotic community structure. The small vertical distance (about 1–10 cm) over which the chemical gradient occurs from the oxic, oxidized environment to the sulfide-rich reduced environment and the presence of animal burrows make biological and chemical investigation of the chemocline difficult in most marine sediments. As the brine spills over the overflow at the canyon's upper end, it mixes with the overlying seawater. Entrainment of increasing amounts of seawater as the stream flows down the canyon produces a > 96-m gradient from a sulfide-rich, anoxic brine lake to a purely oxic environment beyond the canyon mouth. The community under the brine stream exists only in and below the chemocline that begins at the top of the brine stream. No micro-oxic zones of the type described by Reise and Ax (1979) exist because infaunal burrows open into the brine stream rather than into typical oxic seawater. Therefore, there is no true surfaced oxidized zone associated with this system. Since the brine pool's depth, chemistry, and overflow rate appeared similar during five years of observation (1976–1980), it appears that the hydrological-chemical conditions have remained fairly stable over many years.

In this paper, we use the term thiobios to designate the biota whose population maxima are associated with a sulfide-dependent chemocline and which Powell and Bright (1981) suggested have an ecologic requirement for sulfide. No term exists to designate those organisms associated with oxidized regions of the sediment above the chemocline [the surface community of Fenchel and Riedl (1970) and others]. We propose the term oxybios to denote these organisms. We emphasize, following the arguments of Powell and Bright (1981), that the term oxybios does not imply the importance of oxygen in establishing community boundaries vis-a-vis the thiobios, just as the term thiobios does not, but itself, imply the importance of sulfide.

Material and Methods

The East Flower Garden (EFG) brine seep was sampled using the R/V "Johnson" and the research submersible "Johnson Sea Link" in September, 1980. Locations of the sampling stations are given in Fig. 1 and are designated by the prefix 80. For comparison, the five stations sampled by Powell and Bright (1981) are located on the figure and are designated 79. Soft-bottom sampling was accomplished by using a submersible-operated grab sampler. Two sizes of grabs were used; one sampled a 20×20-cm section of bottom, ideally to a depth of 10 cm, the other a 15×15-cm section to 7.5-cm depth. The coarse carbonate sand prevented sampling to the rated depths in many cases. Thus, sample data are reported on a per m^2 and per g (or ml) sediment collected basis. Samples were transferred from the grab to a system of individual containers to accomodate discrete samples after collection and brought to the surface. All stations were photographed before sampling. Three stations (80-1, 80-2, and 80-4) were in areas influenced by the pure brine (refer to Fig. 1). Station 80-4 came from Gollum's Lake in a depression or trough between two sand wave crests; stations 80-1 and 80-2 came from the lake near the point of overflow. Station 80-3 was on a sand wave crest which formed an island in Gollum's Lake; stations 80-5 and 80-7 were at the lake's edge; and station 80-6 was about half way between the lake edge and the rock walls of the basin in which the lake is situated. Stations 80-8 to 80-14 and 80-24 to 80-26 were in the canyon; all but 80-10 were in the brine stream. Station 80-10 was lateral to 80-11 in the sandy sediment between the brine stream and the carbonate bank. The sediment under the brine stream at stations 80-26, 80-25, 80-12, 80-11, 80-9 und 80-8 was covered with a white mat formed by prokaryotic and eukaryotic plants. No mat was present at station 80-10. This mat, composed primarily of *Beggiatoa* spp., *Oscillatoria* spp., diatoms and various bacteria, covered the canyon floor from the Overflow to downstream of the Constriction. In most areas it completely obscured the coarse sandy texture of the sediment on the canyon floor. The mat gradually disappeared below the Constriction. It was poorly developed at station 80-13 near the Cottonwick Rock, evanescent downstream of this point (80-14, 80-24) and completely absent at and below station 80-17. Stations 80-17 and 80-18 were below the canyon mouth at the Anchor Fluke downstream of the Anchor and 80-14. Stations 80-19 to 80-23 were located below the Fluke at 5-m intervals (10 m between 80-22 and 80-23) on the sandy bottom below the canyon. The brine stream spreads out and slowly dissipates as it flows across this area. Stations 80-15 and 80-16 were control stations located at approximately the same depth as 80-17 but near the edge of the EFG bank 40 m and 20 m respectively northeast (lateral) of the canyon mouth and were considered to be beyond the influence of the brine stream. Data analysis suggests that 80-16 may have been influenced by the brine stream to some extent, but that 80-15 was a true control station.

Soft-bottom samples were extracted for meiofauna using the magnesium chloride decantation method (Crezee, 1976). All material caught on the 63-μm screen was preserved immediately at 4 °C using a glutaraldehyde-phosphate buffer preservative (Rieger and Ruppert, 1978). The remainder of each sample was preserved using a Rose Bengal-5% buffered-formalin mixture. All organisms, except ciliates and foraminiferans, which were not satisfactorily sampled by the methods used, were sorted from the small grab sample. Larger grab samples were subsampled randomly until as many organisms were counted as found in a numerically rich small-grab sample. Sediments were wet-sieved for grain size analysis using a 63 μm–16.0 mm sieve size range. The size fraction $< 63\ \mu$m was lost during the extraction procedure and is not reported in the grain-size analyses. Measurements of mean, median, skewness and kurtosis were calculated using the graphic method of Folk (1968).

Water samples were collected in plastic syringes within the submersible using a through-hull sampler. The inlet tube was attached to the submersible's manipulator arm and could be positioned within a few centimeters of the bottom. All values given, except where indicated, are from samples taken as close to the bottom as possible. As significant gradients in chemical concentration occur on this scale, particularly in the canyon, values reported may be only representative of the near-bottom chemical conditions.

Samples for analysis of total dissolved sulfide were pickled immediately with zinc acetate (Goldhaber *et al.*, 1977). Oxygen samples were taken from these samples using the method of Ingvorsen and Jørgensen (1979), and pickled in Winkler reagents. The use of a long tube and syringe prevented taking oxygen samples with precision, so the values reported are approximate only.

All samples were frozen and taken to the laboratory for analysis. Salinity was measured by chloride titration (Strickland and Parsons, 1972). Total dissolved sulfide was measured using the methylene-blue method of Cline (1969). Oxygen was measured by the Winkler method (Strickland and Parsons, 1972).

Results

Chemistry of the EFG Brine Seep System

Salinity, total dissolved sulfide and oxygen values are reported in Table 1. The salinity of the brine lake has remained around 200‰ S over the past seven years (Brooks *et al.,* 1979; Bright *et al.,* 1980a). Salinity in September 1980 was 200.1‰ S. The small Corner Pool in the canyon had a salinity of 220‰ S. A typical seawater salinity for the EFG area at this depth is 36.2‰ S (McGrail and Horne, 1981). Salinities just above the lake-seawater interface approximated this value. The density differential between the brine and seawater inhibits mixing between the lake brine and the overlying seawater, so that the chemical characteristics of the water, at the brine-seawater interface, change greatly over a vertical distance of less than 2 cm. Salinities dropped almost immediately upon entering the overflow to 88.6‰ S, dropped to 41.9‰ S above the Corner Pool, and gradually decreased over the remainder of the canyon's length to 37.4‰ S at the Anchor near the canyon mouth. The decrease in salinity at station 80-10 shows that significant lateral chemical heterogeneity occurred in the canyon in areas where the canyon is wider than the stream. Gollum's Lake brine contributed 1–5% of the total water in the brine stream throughout the canyon (using salinity as a conservative tracer of the brine), with highest values at Corner Pool and values dropping more-or-less constantly to 0.7% at the Anchor. Between-station variability in the salinity measurements in the central part of the canyon may be attributed to either short-term variability in the brine flow or to the extremely steep vertical gradient in salinity in the stream, which required more precise placement of the manipulator arm than could always be accomplished.

Total dissolved sulfide was 1 607 μg-atoms $\cdot$ l^{-1} in Gollum's Lake. This is distinctly lower than the value obtained by Brooks *et al.* (1979) and suggests a greater year-to-year variability in sulfide concentration than in salt concentration. Corner Pool had a higher sulfide concentration, 2 173 μg-atoms $\cdot$ l^{-1} (Table 1). Sulfide was detected above the lake-seawater interface and decreased with distance from the lake. Sulfide concentration at station 80-6 was approximately one-third of the value recorded at the other two stations. The data indicate that molecular diffusion at the brine-seawater interface is sufficiently rapid to add 1–5 μg-atoms $\cdot$ l^{-1} sulfide to the normal seawater above the lake. Advection then distributes this throughout the basin.

Sulfide concentrations, even near the lake-seawater interface, were distinctly lower than those in the canyon, where sulfide decreased from 80 μg-atoms $\cdot$ l^{-1} just downstream of Corner Pool to 32 μg-atoms $\cdot$ l^{-1} at the Anchor. Through most of the canyon's length, sulfide values fluctuated around 80 μg-atoms $\cdot$ l^{-1} in the brine stream. Lateral to it, sulfide concentrations were considerably lower (e.g. station 80-10).

As with salinity, total dissolved sulfide in the brine stream decreased considerably at two places during the stream's travel down the canyon; one between Gollum's Lake and Corner Pool in the overflow, where sulfide concentration dropped by about 95%; and the second just downstream of the Constriction and Cottonwick Rock area, where sulfide concentration dropped by a factor of about two. Elsewhere in the canyon, sulfide concentration and salinity were remarkably stable considering the flow and mixing regimes present.

If one assumes that the only significant source of sulfide in the EFG brine seep area is Gollum's Lake, and that no losses occur, so that changes in sulfide concentrations are effected only by dilution with seawater, then sulfide can be used as a conservative tracer of Gollum's Lake brine in the system. Calculations of brine input based on salinity or sulfide as a tracer (Table 1) are sufficiently similar to suggest that dilution is the only significant factor controlling sulfide concentration in the canyon. No quantitatively important additions from biological sulfate reduction or removal by biological or chemical oxidation could be resolved. Current speeds in the canyon ranged from 5–10 cm $\cdot$ s^{-1} at the Overflow to 25 cm $\cdot$ s^{-1} at the Anchor (Fig. 1). Residence time (or travel time) for brine in the canyon, which is less than 15 min, is sufficiently short to make chemical oxidation insignificant even with quantities of oxygen available because of the slow rate at which sulfide is oxidized (Cline and Richards, 1969; O'Brien and Birkner, 1977) relative to the hydrodynamics involved.

Calculations of the amount of pure brine required to produce the mixtures observed in the canyon based on salinity and total dissolved sulfide are consistently off by a factor of 1.5 (Table 1, Stations 80-8 to 80-11), when based on the sample of Gollum's Lake brine analyzed (Station 80-1, Table 1). These differences probably are not due to sampling error, but more likely indicate that Station 80-1 was not completely representative of the brine feeding the canyon brine stream. The topography of Gollum's Lake suggests that certain portions might be partially isolated by the system of longitudinal sand ridges present (Fig. 1). Local spatial heterogeneities are clearly present since Corner Pool (Table 1) had higher salinity and sulfide concentrations than station 80-1 in Gollum's Lake.

Oxygen concentration was zero in Gollum's Lake, but was similar to typical seawater oxygen concentrations at this depth in the EFGB area just above the lake-seawater interface (approximately 5 ml $\cdot$ l^{-1}). Oxygen concentrations were generally lower in the brine stream of Gollum's Canyon. In no case did values in the stream drop below 50% of normal seawater. The ratios of brine to seawater, predicted from salinity and sulfide data, show that brine stream water contains no more than 5% brine from the lake (i.e. > 95% is oxic seawater). Thus, even if all of the sulfide was oxidized in the brine stream, significant concentrations of oxygen would still remain. Therefore, it is unlikely that oxygen concentrations ever fall much below 50% saturation anywhere in the canyon below Corner Pool.

Table 1. Chemistry of the East Flower Garden brine seep system. Locations of sampling stations are in Fig. 1

	SALINITY				SULFIDE			
Station	Oxygen (ml·l^{-1})	Salinity (‰)	Mixture [n parts brine: 1 part seawater (36‰)]	% Pure Brine in Mixture	Total Dissolved Sulfide (µg-atoms·l^{-1})	Mixture [n parts brine: 1 part seawater (36‰)]	% Pure Brine in Mixture	$\frac{\text{\% Brine (Sulfide)}}{\text{\% Brine (Salinity)}}$
80-1	0	200.1	--	100.0	1607	--	100.0	
Corner Pool		220.0			2173			
80-2	4.77	88.6	0.47	32.0	761.9	.9016	47.41	1.48
80-3	4.88				4.5	.0028	0.28	--
80-5	4.83	36.8	0.0037	0.37	5.1	.0031	0.31	0.86
80-6	5.11	36.1	0	0	1.7	.0011	0.11	∞
80-7	5.31	36.2	0	0	3.5	.0022	0.22	∞
80-8	4.32	41.9	0.0360	3.47	80.1	.0525	4.99	1.44
80-9	3.35	40.1	0.0244	2.38	63.9	.0414	3.98	1.67
80-10	3.61	37.9	0.0105	1.04	26.5	.0168	1.65	1.59
80-11	3.60	41.9	0.0360	3.47	83.9	.0551	5.22	1.50
80-12	3.06	37.0	0.0049	4.88	83.2	.0546	5.18	1.06
80-13	3.31	38.9	0.0167	1.64	45.2	.0289	1.84	1.12
80-14	2.50	37.4	0.0074	0.73	32.3	.0205	2.01	2.75

The hydrodynamic process in the canyon dictates that sulfide, salinity and oxygen concentrations be strongly coupled in the canyon since brine enters the canyon from a point source at the Overflow, the hydrodynamic process adds oxygen as salinity and sulfide are diluted, and travel time down the canyon is too fast for biological or chemical processes to greatly change concentrations. Any deviation from this pattern in Table 1 probably can be attributed either to measurement error or to horizontal and vertical heterogeneities in the brine stream which occurred on a time scale shorter than the sampling regimen used.

Sediment Texture of the EFG Brine Seep System

Most sediments in the brine lake basin were very coarse to granular, poorly sorted sands (Tables 2, 3). Sediment mean-size in the canyon was somewhat lower than in the brine lake basin. Most stations taken below the canyon mouth, and canyon stations 80-10, 80-14 and 80-26 had lower mean-sizes than other stations. Overall, sediments were quite uniform over the entire sampling area; all being composed of very coarse to granular, poorly sorted sands.

Biota of the EFG Brine Seep System

Numbers of organisms collected in the soft-sediment samples are shown in Tables 4 and 5. Based on Bray-Curtis cluster analyses on log-transformed and untransformed data (Fig. 2), these stations can be divided into four community types: (1) stations adjacent to Gollum's Lake and the control stations;. (2) stations below the Cottonwick Rock – two subgroups can be distinguished, one composed primarily of stations at the canyon mouth, the other of stations farther downstream; (3) middle canyon stations between Chimney Rock and the Cottonwick Rock – two subgroups may be present, one between Chimney Rock and Boulder Two, the other between Boulder Two and the Cottonwick Rock; (4) upper canyon stations above Chimney Rock. Groups one and two are oxybiotic; groups three and four are thiobiotic.

The control stations and stations associated with the sandy-bottom between Gollum's Lake and the carbonate bank were dominated by copepods, with numerous turbellarians, nematodes, and annelids. Figs. 3, 4, and 5 show the change in faunal composition of the sandy-bottom from Corner Pool down canyon and below the canyon's mouth. Throughout the upper canyon, from below Corner

Table 2. Grain size analysis at the stations sampled for biota in the East Flower Garden brine seep system. Fractions are percents of total amount collected. Total weight is the total amount of sample (dry wt in g) collected

	STATION												
SIZE CLASS (%)	80-1	80-2	80-3	80-4	80-5	80-6	80-7	80-8	80-9	80-10	80-11	80-12	80-13
63 μ	0.2	0.2	0.2	0.8	0.4	0.7	1.5	0.4	0.4	0.8	0.1	0.4	0.3
120 μ	0.4	2.3	1.2	3.2	2.3	3.2	6.1	1.5	1.8	5.2	1.9	1.2	1.3
250 μ	2.2	7.8	7.0	9.8	7.2	7.1	9.4	7.1	7.4	19.1	3.9	5.5	6.8
500 μ	14.1	29.6	20.4	16.7	13.8	11.9	11.9	18.4	17.0	25.7	28.5	20.0	18.7
1000 μ	24.6	26.8	25.4	18.6	17.0	20.4	18.7	21.2	24.9	26.2	37.5	27.4	23.6
2000 μ	27.7	16.1	19.1	24.6	36.9	39.7	28.1	20.4	22.4	11.9	21.0	24.1	19.7
4000 μ	22.4	8.6	17.1	9.9	12.6	11.1	11.6	15.6	18.2	9.1	6.0	12.9	18.1
8000 μ	7.1	4.6	9.6	11.5	6.4	2.9	6.1	15.4	7.9	2.0	1.4	8.5	8.1
16000 μ	1.3	4.0	0.0	4.9	3.4	3.0	6.6	0.0	0.0	0.0	0.0	0.0	3.4
TOTAL WEIGHT (g)	133.9	180.6	292.1	230.0	231.7	253.7	267.3	214.9	278.0	342.1	137.3	179.2	228.8

	STATION												
SIZE CLASS (%)	80-14	80-15	80-16	80-17	80-18	80-19	80-20	80-21	80-22	80-23	80-24	80-25	80-26
63 μ	0.6	1.0	0.9	0.9	0.4	1.2	1.0	0.7	0.9	0.6	0.4	0.5	0.2
120 μ	3.5	2.8	3.2	3.8	4.0	4.2	3.7	2.0	3.0	1.3	2.6	0.8	1.5
250 μ	13.4	9.0	21.5	16.0	17.6	15.1	12.5	7.0	11.7	7.9	8.3	4.9	13.3
500 μ	30.8	20.5	29.6	34.0	32.9	28.1	33.4	25.2	30.7	25.7	22.2	19.4	33.6
1000 μ	30.8	22.9	21.6	27.3	29.3	29.1	31.0	32.7	27.2	26.8	31.8	29.1	31.0
2000 μ	10.8	18.1	11.3	8.5	9.9	14.0	12.4	19.6	13.7	18.0	20.3	24.2	11.5
4000 μ	6.8	9.2	5.7	2.9	5.0	5.3	6.0	10.2	9.1	11.4	11.2	13.2	5.4
8000 μ	3.4	6.6	3.9	5.8	0.9	1.2	0.0	2.6	3.6	4.1	3.2	7.9	3.5
16000 μ	0.0	9.9	2.3	0.8	0.0	1.7	0.0	0.0	0.0	4.3	0.0	0.0	0.0
TOTAL WEIGHT (g)	309.7	632.2	1178.0	958.7	22.4	813.4	731.2	618.0	857.6	1039.8	833.6	1073.9	1149.0

Table 3. Statistical parameters of grain size

Station	Median (0)	Mean (0)	Mean (mm)	Standard Deviation	Skewness	Kurtosis
80-1	-1.30	-1.27	2.41	1.26	0.02	0.91
80-2	-0.37	-0.58	1.49	1.51	-0.25	1.15
80-3	-0.84	-0.95	1.93	1.45	-0.07	0.83
80-4	-1.05	-1.03	2.04	2.02	-0.01	0.98
80-5	-1.24	-1.06	2.08	1.52	0.12	1.17
80-6	-1.15	-0.90	1.87	1.41	0.23	1.26
80-7	-1.08	-0.89	1.85	1.89	0.11	1.14
80-8	-1.07	-1.16	2.23	1.58	-0.01	0.78
80-9	-0.94	-0.95	1.93	1.44	0.02	0.89
80-10	0.03	-0.05	1.04	1.42	-0.09	0.99
80-11	-0.41	-0.46	1.38	1.02	-0.08	1.04
80-12	-0.84	-0.91	1.88	1.36	-0.06	0.94
80-13	-0.97	-1.05	2.07	1.56	-0.08	0.90
80-14	-0.05	-0.13	1.09	1.31	-0.12	1.20
80-15	-0.73	-1.00	2.00	1.84	-0.17	0.98
80-16	0.17	0.14	0.91	1.48	-0.16	1.19
80-17	0.13	0.04	0.97	1.38	-0.19	1.36
80-18	0.14	0.13	0.91	1.17	-0.06	1.09
80-19	-0.07	-0.07	1.05	1.13	0	1.11
80-20	0.03	0	1.00	1.12	0.04	1.18
80-21	-0.48	-0.53	1.44	1.22	-0.06	0.99
80-22	-0.14	-0.29	1.22	1.36	-0.16	1.13
80-23	-0.57	-0.76	1.69	1.42	-0.20	1.07
80-24	-0.53	-0.57	1.48	1.32	-0.11	1.02
80-25	-0.87	-1.06	2.08	1.38	-0.08	0.93
80-26	-0.04	-0.15	1.11	1.13	-0.14	1.16

Pool to the Constriction, the fauna was dominated by gnathostomulids, nematodes, annelids, gastrotrichs and turbellarians. These stations comprise the thiobios of the canyon. Stations near Boulder Two and Chimney Rock had relatively more gastrotrichs and copepods while stations just above the Constriction had more gnathostomulids and amphipods. Stations of the upper canyon above Chimney Rock were depauperate. No living organisms were collected at station 80-2 and only a few turbellarians were collected at station 80-8.

Below the Constriction, the fauna was composed primarily of annelids, ostracods, copepods, tanaids, amphipods, turbellarians and nematodes. As with the middle canyon stations, significant station-to-station variability in the numerically dominant groups characterized these stations. Stations 80-13, 80-14 and 80-24 mark the ecotone between the downstream stations and the canyon thiobios. Some gnathostomulids were still present at station 80-13. Tanaids and annelids comprised a larger portion of the total fauna in this area than at most stations farther downstream because copepods and ostracods were less abundant than at most downstream stations. Stations below the canyon mouth were dominated by one or more of the following groups; copepods, ostracods, tanaids, amphipods, and annelids. Molluscs (which were more abundant at these stations than elsewhere), turbellarians, and nematodes were also present in large numbers. Stations 80-17 to 80-23 resembled the control stations and stations located in the brine basin

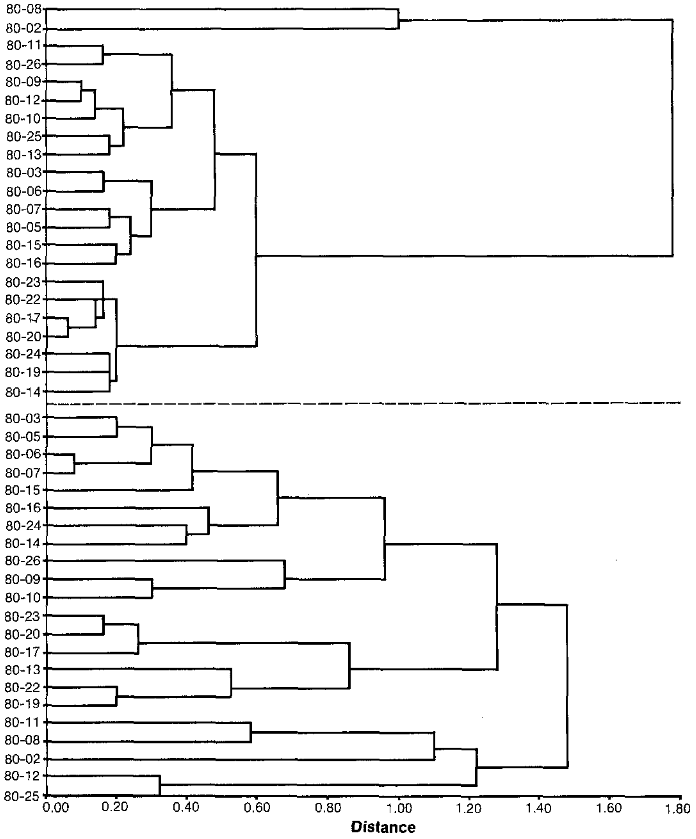

Fig. 2. Bray-Curtis cluster analysis of the stations from the East Flower Garden brine seep system. Lower analysis used untransformed data, upper analysis used log transformed data

Table 4. Numbers of individuals per m² of sandy bottom. Values for station 80–18 may be anomalous because the small size (Table 3) suggests that the grab did not take a complete sample. The category "Other" includes primarily larvae and eggs plus unidentifiable fragments of organisms. Parentheses indicate numbers of dead individuals pickled by the pure brine of Gollum's Lake

Taxonomic Group (#/m^2)	80-1	80-2	80-3	80-4	80-5	80-6	80-7	80-8	80-9	80-10	80-11	80-12	80-13	80-14	80-15	80-16	80-17	80-18	80-19	80-20	80-21	80-22	80-23	80-24	80-25	80-26
Cnidaria	--	--	--	--	--	--	--	--	--	--	--	--	--	133	--	--	--	--	--	--	--	--	--	--	--	--
Platyhelminthes																										
Turbellaria	(444)	--	2044	(178)	2756	1644	1333	978	6667	3111	1022	3111	1289	6133	250	450	3119	125	2585	1380	2303	288	1561	3910	1392	27197
Nemertea	--	--	--	--	--	--	--	--	--	--	--	--	--	44	--	--	--	75	--	--	128	144	--	--	--	--
Gnathostomulida	--	--	--	--	--	178	--	--	13022	2400	178	88489	1022	400	--	--	297	--	108	1553	384	721	--	290	124630	145
Aschelminthes																										
Nematoda	(578)	--	9956	(178)	3111	6933	5467	89	4133	3689	844	23067	3289	5689	1250	8250	6386	375	1723	6386	640	1441	780	2317	5430	436
Gastrotricha	--	--	44	--	89	89	--	--	13289	9867	--	4489	44	400	75	750	891	--	323	1553	128	--	--	434	--	--
Ectoprocta	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50	--	--	--	--	--	--	--	--	--	--	--
Annelida	(6444)	--	4444	(978)	6133	5733	7067	--	7644	10000	1556	1822	3600	13778	7196	20625	58360	1600	19172	23698	4862	10957	36424	49384	12114	8872
Mollusca																										
Polyplacophora	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	25	--	--	--	--	--	--	--	--	--	--
Gastropoda	--	--	--	(311)	44	--	44	--	--	--	--	--	--	978	250	25	1188	75	1292	1208	1535	1441	260	1014	--	--
Bivalvia	--	--	--	(311)	311	--	--	--	44	222	--	178	89	133	25	375	1040	25	969	1898	513	721	780	290	--	--
Sipunculida	(44)	--	--	--	89	44	400	--	--	89	--	--	--	267	50	225	--	--	108	--	--	--	--	--	--	--
Arthropoda																										
Copepoda	(12489)	--	27689	(2089)	21156	14489	14578	44	1111	2222	133	444	1067	13822	9850	33400	60440	1925	--	65939	5118	6776	73629	15785	1114	5381
Ostracoda	(222)	--	267	(1422)	489	1333	1156	--	356	444	89	889	1156	5067	250	225	41877	1950	14756	19505	4478	9516	17431	5648	1392	290
Cumacea	--	--	--	(133)	44	--	44	--	--	--	--	--	--	44	--	--	--	--	--	--	--	--	--	--	--	--
Tanaidacea	(356)	--	622	(133)	444	1600	311	--	89	2667	--	44	14889	7511	200	225	31185	1000	28758	32796	10108	28836	22895	--	7659	145
Amphipoda	(400)	--	133	--	222	844	444	--	222	222	622	13644	10000	8356	100	25	21087	400	9909	5005	2431	2883	1041	2462	47345	145
Isopoda	(756)	--	--	(89)	--	--	133	--	--	89	--	--	--	311	--	75	8613	--	3662	4315	1024	2451	780	579	975	--
Decapoda	(89)	--	--	--	--	--	--	--	--	--	--	--	44	267	25	50	--	--	--	2071	256	144	--	--	--	--
Acarina	(89)	--	44	--	89	133	44	--	--	--	--	--	--	--	25	--	--	--	--	--	--	--	--	--	--	--
Echinodermata	(89)	--	--	--	--	--	44	--	--	--	--	--	--	--	75	--	--	--	--	--	--	--	--	--	--	--
Hemichordata																										
Enteropneusta	--	--	89	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Chordata																										
Urochordata	--	--	44	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Other Chordata	(133)	--	--	--	89	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Other	(89)	--	3511	(2267)	1378	1378	1067	44	44	356	--	--	44	89	350	650	6089	175	--	1725	256	--	1040	579	--	145
Total	(22222)	0	48887	(8089)	36444	34398	32132	1155	46621	35378	4444	136177	36533	63422	19771	65375	240572	7725	83365	169032	34165	66319	156621	82742	202051	42756

Table 5. Numbers of individuals per 100 g dry wt of sediment. Parentheses indicate the numbers of dead individuals pickled by the pure brine in Gollum's Lake. * indicates an individual's presence in numbers below 1 per 100 g sediment. Number of individuals per 100 ml sediment can be obtained by multiplying by 2.26 (see Powell and Bright, 1981)

Taxonomic Group (#/100 gm sediment)	80-1	80-2	80-3	80-4	80-5	80-6	80-7	80-8	80-9	80-10	80-11	80-12	80-13	80-14	80-15	80-16	80-17	80-18	80-19	80-20	80-21	80-22	80-23	80-24	80-25	80-26
Cnidaria	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--
Platyhelminthes																										
Turbellaria	(7)	--	16	(2)	27	15	11	10	54	20	17	39	13	46	2	2	13	22	13	8	19	2	6	19	5	95
Nemertea	--	--	--	--	--	--	--	--	--	--	--	--	--	*	--	--	--	13	--	--	1	1	--	--	--	--
Gnathostomulida	--	--	--	--	--	2	--	--	105	16	3	1111	10	3	--	--	1	--	1	8	3	3	--	1	465	1
Aschelminthes																										
Nematoda	(10)	--	77	(2)	30	61	46	1	33	24	14	290	32	41	8	28	33	67	8	35	5	7	3	11	20	2
Gastrotricha	--	--	*	--	1	1	--	--	108	65	--	56	*	3	1	3	4	--	2	8	1	--	--	2	--	--
Ectoprocta	--	--	--	--	--	--	--	--	--	--	--	--	--	--	*	--	--	--	--	--	--	--	--	--	--	--
Annelida	(108)	--	34	(10)	60	51	59	--	62	66	25	23	35	100	45	70	243	286	70	137	39	51	140	237	45	31
Mollusca																										
Polyplacophora	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	*	--	--	--	--	--	--	--	--	--	--
Gastropoda	--	--	--	(3)	*	--	*	--	--	--	--	--	--	7	2	*	5	13	6	7	12	7	1	5	--	--
Bivalvia	--	--	--	(3)	3	--	--	--	*	1	--	2	1	1	*	1	4	4	5	10	4	3	3	1	--	--
Sipunculida	--	--	--	--	1	*	3	--	--	1	--	--	--	2	*	1	--	--	1	--	--	--	--	--	--	--
Arthropoda																										
Copepoda	(210)	--	213	(20)	205	128	123	1	9	15	2	6	10	100	62	113	252	344	--	361	41	31	283	76	4	19
Ostracoda	(4)	--	2	(14)	5	12	10	--	3	3	1	11	11	37	2	1	175	348	72	107	36	44	67	27	5	1
Cumacea	--	--	--	(1)	*	--	*	--	--	--	--	--	--	*	--	--	--	--	--	--	--	--	--	--	--	--
Tanaidacea	(6)	--	5	(1)	4	14	3	--	1	18	--	*	146	55	1	1	130	179	141	179	82	134	88	--	28	1
Amphipoda	(7)	--	1	--	2	7	4	--	2	1	10	171	98	61	1	*	88	71	49	27	20	13	4	12	176	1
Isopoda	(13)	--	--	(1)	--	--	1	--	--	1	--	--	--	2	--	*	36	--	18	24	8	11	3	3	4	--
Decapoda	(*)	--	--	--	--	--	--	--	--	--	--	--	*	2	*	*	--	--	--	11	2	1	--	--	--	--
Acarina	(1)	--	--	*	1	1	*	--	--	--	--	--	--	--	*	*	--	--	--	--	--	--	--	--	--	--
Echinodermata	(1)	--	--	--	--	--	*	--	--	--	--	--	--	--	*	--	--	--	--	--	--	--	--	--	--	--
Hemichordata																										
Enteropneusta	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Chordata																										
Urochordata	--	--	*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Other Chordata	(2)	--	--	--	*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Other	(1)	--	28	(22)	15	12	9	1	1	3	--	--	1	1	2	2	25	31	--	10	2	--	4	3	--	1
Total	(370)	0	378	(79)	352	304	269	13	378	234	72	1709	357	462	126	222	1009	1378	386	932	275	308	602	397	752	152

(copepods were usually the dominant groups and annelids, turbellarians, and nematodes were common), but are readily distinguished by the presence of high numbers of ostracods, tanaids and amphipods which were practically absent from the brine basin and control stations.

No living metazoans were collected from Gollum's Lake, although numerous dead and "pickled" organisms were collected from sediments and rocks in the lake (80-1, 80-4, Tables 4, 5).

Changes in total numbers of organisms (Fig. 5, Tables 4, 5) were closely associated with community boundaries. The abundance of thiobios reached a peak in mid-canyon at the Constriction and was generally lower upstream. Ecotone stations 80-13, 80-14, and 80-24 also had lower abundances. Thiobios were no longer abundant at these stations, but only a portion of the oxybios, the tanaids and the annelids, were present in high numbers. The abundance of oxybios reached a peak at station 80-17 with the increase in abundance of copepods and ostracods and the continued importance of the tanaids and annelids. Total faunal abundance gradually decreased downstream of station 80-17, but total numbers at the farthest downstream station (80-23) were still high in comparison to most brine basin and control stations.

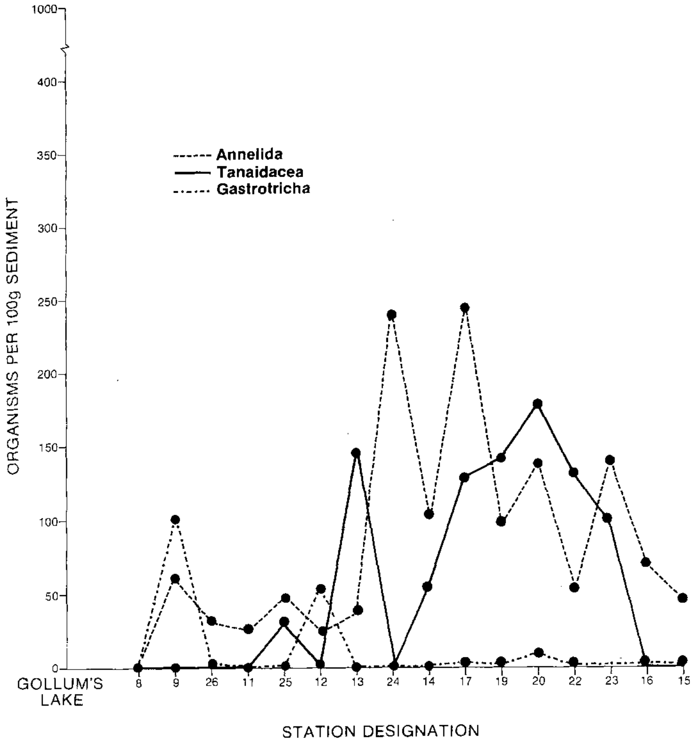

Fig. 3. Numbers of individuals of annelids, tanaids, and gastrotrichs along a transect from Gollum's Lake down Gollum's Canyon to the Anchor and out onto the sandy bottom adjacent to the canyon mouth

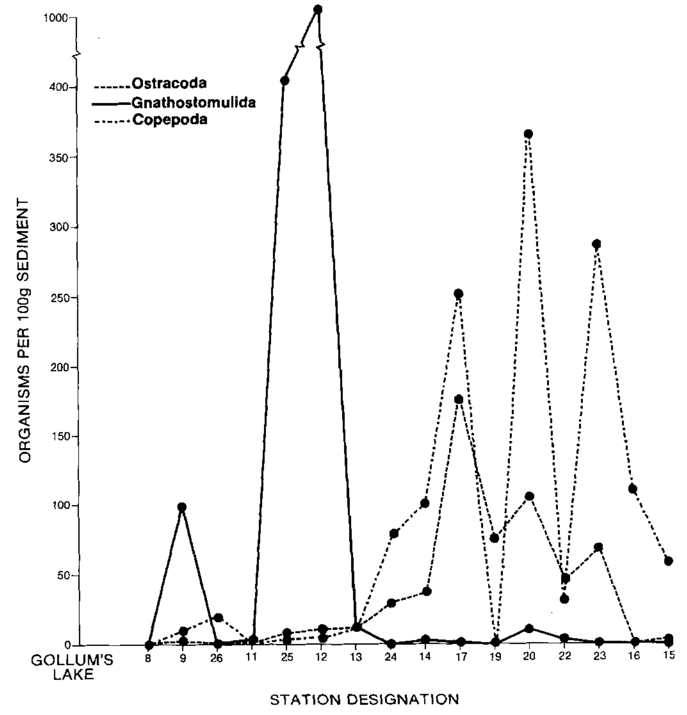

Fig. 4. Numbers of individuals of coepods, ostracods and gnathostomulids along a transect from Gollum's Lake down Gollum's Canyon to the Anchor and out onto the sandy bottom adjacent to the canyon mouth

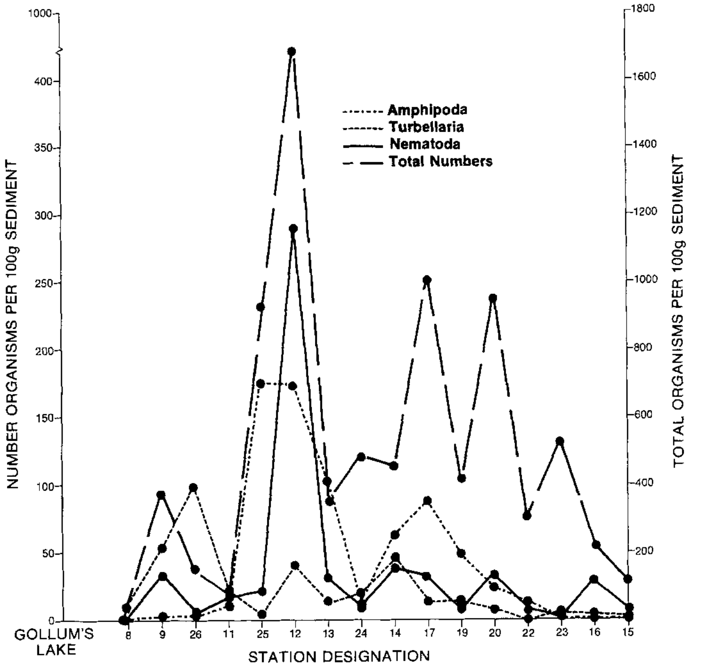

Fig. 5. Numbers of individuals of turbellarians, nematodes, amphipods, and total biota along a transect from Gollum's Lake down Gollum's Canyon to the Anchor and out onto the sandy bottom adjacent to the canyon mouth

Discussion

The Thiobios Hypothesis

The community structure of the EFG brine seep area is dominated by sulfide and the presence of a sulfide system in the Gollum's Lake and Canyon area. Powell and Bright (1981) suggested that thiobiotic communities are delimited from oxybiotic communities by a set of environmental conditions based primarily on the presence of sulfide and a sulfide-dependent chemocline. Thus, the thiobios exists in a gradient system, and the gradient system is required for its existence. In this view, thiobiotic organisms would have an ecologic requirement (but not necessarily a metabolic requirement) for sulfide, whereas oxybiotic organisms would not. This definition is contrary to previous views which placed great importance on the presence or absence of oxygen (Boaden, 1975, 1980; Reise and Ax, 1979, 1980) to determine the existence of and boundaries for the thiobios, and which emphasized the chemical environment present above and below rather than in the chemocline.

Powell and Bright (1981) concluded that the brine stream community above the Constriction in Gollum's Canyon is thiobiotic. Three stations, 80-9, 80-12 and 80-25 (and 79-2, Powell and Bright, 1981) are dominated by gnathostomulids. A community dominated by gnathostomulids is unique. Communities are known where one or more species of gnathostomulids are numerically important, particularly at certain seasons (Riedl, 1970a, b; Müller and Ax, 1971; Farris, 1976), but in none of these is gnathostomulid dominance as high as in Gollum's Canyon. Reise (1981a), however, found comparable gna-

Table 6. Changes in community composition in the stations of the East Flower Garden brine seep system

	% Lower Invertebrates (Below Annelida)	Nematode-Copepoda Ratio	Gnathostomulid-Copepod Ratio
80-1	4.6	.048	0
80-2	--	--	--
80-3	24.6	.362	0
80-4	5.1	.100	0
80-5	16.2	.146	0
80-6	25.7	.477	.016
80-7	21.2	.374	0
80-8	84.6	.500	0
80-9	50.8	3.667	11.667
80-10	25.6	1.600	1.067
80-11	47.2	7.000	1.500
80-12	84.3	48.333	185.167
80-13	15.4	3.200	1.000
80-14	19.7	.410	.030
80-15	8.8	.129	0
80-16	13.4	.247	0
80-17	4.7	.131	.004
80-18	7.4	.195	0
80-19	5.7	∞	∞
80-20	6.4	.097	.024
80-21	10.5	.125	.075
80-22	3.9	.213	.106
80-23	1.5	.011	0
80-24	8.4	.147	.018
80-25	65.1	4.874	111.816
80-26	65.0	.081	.027

thostomulid densities around some polychaete burrows, but they are outnumbered by other micro-metazoans, such as nematodes, in this case (Reise, 1981b). In contrast, copepods are consistently associated with the oxybios. They are rare in Gollum's Canyon although present in large numbers elsewhere in the area. A gnathostomulid-copepod ratio (Table 6) over 1.0 coincides with the middle canyon area where sulfide concentrations are above about 40 μg-atoms $\cdot$ l^{-1}, for example. Community composition compares well enough with Fenchel and Riedl's (1970) original biotic composition of the sulfide system to conclude that Gollum's Canyon above the Constriction harbors a sulfide system with a well developed thiobiotic community of metazoans (Powell and Bright, 1981).

The Thiobios Hypothesis – Factors Affecting Faunal Distribution

The stations sampled fall into three main groups: (1) stations adjacent to Gollum's Lake and the control stations, (2) middle canyon stations, and (3) stations at and below the canyon mouth. The third group can be divided into two subgroups: one, the ecotone subgroup, is located between the Cottonwick Rock and the Anchor; the other subgroup is located from the Anchor downstream. These observations based on the taxonomic groups enumerated do not imply, of course, that all species within the groups have similar distributions. The data are sufficient, however, to delineate the major faunal boundaries present in the system.

Although sediment grain size is commonly observed to be an important factor determining faunal boundaries in micro-metazoan and macrofaunal communities (McNulty *et al.*, 1962; Pollock, 1971; Hulings and Gray, 1976), it is unlikely that shifts in grain size distribution can explain any of the faunal shifts observed here. All stations were coarse to very coarse sands. Between-station variability is small and is not associated with changes in faunal composition. For example, the sediments of the brine canyon and brine basin are similar but the faunal compositions are distinctly different. Lower canyon stations and control station 80-16 have finer grain sizes than other stations, but the faunal compositions of the two are dissimilar. The two control stations have dissimilar sediment textures but similar faunal compositions.

Water movement itself is not responsible for the biotic boundaries observed. The currents at the brine basin stations (80-5, 80-6, 80-7) and at the canyon mouth

(80-17) are quite dissimilar, but copepods are important members of the community in both cases, while gnathostomulids are not. Highest current speeds occur at stations 80-14 and 80-24 below the Constriction. Nevertheless, the amphipods which are dominant just upstream of the Constriction are also abundant at the Anchor and downstream of it at station 80-17 and the copepods, which characteristically dominate communities downstream of the canyon mouth, begin to increase in abundance between the Cottonwick Rock and the Anchor. Although current speed is higher at the canyon mouth than below the canyon, the faunal compositions are very similar relative to stations farther upstream in the canyon. Thus, the hydrodynamic regime, though of substantial importance in maintaining the system, is not the primary causative factor establishing the major faunal boundaries observed.

Data on the hydrodynamic regime and chemistry of the brine stream indicate that the principal changes in brine-stream chemistry are effected by dilution of the brine with overlying seawater. Any substantial change in salt, sulfide, or oxygen concentration (assuming errorless synchronous measurements) should always be accompanied by a change in the other two. To determine which is primarily responsible for the faunal distributions observed requires a consideration of the magnitude of change in the concentration observed, coupled with an assessment of its potential for ecological effect.

Although salinity is important in structuring benthic communities (Kinne, 1964; Carpelan, 1967), changes in salinity are unlikely to have produced the faunal boundaries observed in this system except in the brine lake and in the overflow region where salinities remain high enough to prevent most metazoan life. The significant changes in community composition in the canyon below Corner Pool occur over a salinity range of no more than 2‰ S in an area that may have yearly salinity changes of that magnitude (McGrail and Horne, 1981). Low abundances in the canyon near Corner Pool and Boulder Two occur at salinities essentially equivalent to that of the high abundance stations near the Constriction (80-12). Salinity change between the Constriction and the canyon mouth, where the greatest change in faunal composition occurs, is no more than 1‰ S, whereas sulfide concentration changes by over 50%. Since most of the taxa involved have euryhaline representatives in hypersaline areas, changes in taxonomic composition, at the taxonomic levels dealt with here, induced by such small variations in salinity should not even be expected.

The data allow a choice between oxygen and sulfide as the component chiefly responsible for the faunal boundaries observed. Oxygen is not limiting in the brine-seep area exclusive of Gollum's Lake. Typically, oxygen concentration must drop below 1 ppm to cause significant changes in community composition of the type observed here (Rhoads and Morse, 1971; Gallardo, 1977; Rosenberg, 1977; Jørgensen, 1980). Values in Gollum's Canyon below Corner Pool never drop low enough to produce such changes since over 95% of the brine stream is entrained oxic seawater. Thus, although there probably is an oxygen gradient in the canyon, it is not ecologically meaningful.

Changes in sulfide concentration, on the other hand, are ecologically meaningful. Loss of the gnathostomulids as a principal component of the community coincides with a substantial drop in sulfide concentration in the area between the Constriction and the Cottonwick Rock. Gnathostomulids are present throughout the canyon where sulfide concentrations are above 40 μg-atoms $\cdot$ l^{-1}. Nematodes, gastrotrichs, and amphipods show peak abundances in this region as well. Copepods and ostracods are found in significant numbers only where sulfide concentrations are considerably lower (e.g. 1–5 μg-atoms $\cdot$ l^{-1} at stations 80-3, 80-5, 80-6 and presumably below the Anchor at stations 80-17 to 80-23 – $[S^{-2}] \sim 2$ μg-atoms $\cdot$ l^{-1} in this area; Brooks *et al.,* 1979). Between the Cottonwick Rock and the Anchor, where sulfide drops by a factor of at least 3, there is a transition community. Tanaid and annelid abundances in this area are near the peak values found downstream, but neither the gnathostomulids nor the copepods are as common as elsewhere. Thus, in the area of transition from thiobios to oxybios, the only ecologically meaningful change in brine stream chemistry is the change in sulfide concentration. This contrasts with views that stress the importance of oxygen and suggests that the concept of the thiobios to date rests on a false assumption that the capability to withstand low to zero oxygen levels is the primary prerequisite for sulfide system life. It is likely that the ability to detoxify sulfide is of more adaptive importance (Powell *et al.,* 1979, 1980).

Certain members of the oxybios, such as the tanaids and annelids, approach the thiobiotic-oxybiotic boundary closer than others. The decrease in total abundance at the canyon mouth is caused by the reduction of thiobiotic organisms and the failure of all groups of the oxybios to be well represented. Jacubowa and Malm (1931), Theede *et al.* (1969) and Powell *et al.* (1979) demonstrated substantial variability in sulfide tolerance among oxybiotic metazoans. Some oxybiotic organisms withstand relatively high concentrations of sulfide, particularly for short time periods. Thus the thiobiotic-oxybiotic boundary is not necessarily at 0 μg-atoms $\cdot$ l^{-1} sulfide, but probably at some value above it, as determined by the oxygen and sulfide flux rates and the biota's sulfide detoxification capabilities. Since many factors, such as temperature, bacterial activity and bottom currents, affect the sulfide flux in most marine sediments (e.g. Ankar and Jansson, 1973; Goldhaber and Kaplan, 1974; Reimers, 1977; Demaison and Moore, 1980), the exact chemistry of the boundary may vary temporally and spatially. In Gollum's Canyon, where the boundary conditions are likely to be stable, the faunal shift takes place at around 20–40 μg-atoms $\cdot$ l^{-1} sulfide. Since temporal changes in the flow regime of the canyon may occur and since the chemistry of the interstitial water within the white mat of the canyon may be quite different from that of the brine stream (Jørgensen, 1982), a more precise characterization is impossible at this time.

Values for total dissolved sulfide in the brine stream are within the 96-h lethal dose values for many oxybiotic organisms (Oseid and Smith 1974 a, b). Since higher oxygen concentrations increase the oxybiota's ability to detoxify sulfide (Oseid and Smith, 1974a; Powell *et al.,* 1980), it is likely that the sulfide concentration at the thiobiotic-oxybiotic boundary in Gollum's Canyon is higher than in most areas. In marine sediments where oxygen concentrations may be considerably lower in the chemocline (Revsbech *et al.,* 1980 a, b), the sulfide concentration may also be considerably lower at the boundary. Thus, the importance of oxygen in determining the oxybiotic-thiobiotic boundary may not be as a terminal electron acceptor – many oxybiotic organisms are euryoxic (e.g. von Brand, 1944; Warren and Dales, 1980; Pionetti and Toulmond, 1980; Hammen, 1980 and references therein) – but that the oxygen supply determines (1) through inorganic reactions with sulfide, the extent of and chemistry of the chemocline and its position in the sediment or water column, and (2) the relative concentration of sulfide which can be tolerated for varying lengths of time by the oxybios, since the principal oxybiotic detoxification pathway leading to sulfate is oxygen intensive, whereas the thiobiotic pathway to elemental sulfur is not (Powell *et al.,* 1980).

It is less obvious what limits thiobiotic life, since oxygen is certainly a metabolic requirement for them as well as for the oxybios (Reise and Ax, 1979; Powell and Bright, 1981). Four possibilities are: (1) Sulfide or reducing conditions may be a metabolic requirement. Recent evidence for autotrophy in the vestimentiferan worms of the Galapagos Rift (Felbeck, 1981) and in some organisms from shallow-water habitats (Felbeck *et al.,* 1981), the apparent concentration of sulfide by gnathostomulids (Powell *et al.,* 1979), and certain bacterial symbioses in the thiobios (Fenchel *et al.,* 1977; Powell *et al.,* 1979; Cavanaugh *et al.,* 1981) suggest a metabolic requirement for sulfide in some species. (2) High oxygen concentrations may be deleterious (Wieser *et al.,* 1974), possibly due to a loss of oxygen detoxification capabilities. (3) Sulfur-requiring prokaryotes may be an obligate trophic base. They are almost certainly an important one (Reise and Ax, 1979; Powell and Bright, 1981). The oxybiotic-thiobiotic boundary in Gollum's Canyon approximately coincides with the downstream extent of the white prokaryotic mat characteristic of the middle and upper canyon floor. (4) Competitive or predatory interactions may exclude some species from oxybiotic environments.

Characteristics of Thiobiotic Communities

The thiobios is generally considered to be micro-metazoan:microfaunal in composition. In most marine sands this must be so, since the sulfide system is entirely interstitial. In the canyon, however, (and in many sulfureta, Fenchel, 1969; Reimers, 1977) it is not, and thiobiotic macrofauna could be present. Evidence from the mid-ocean rift valley suggests that such organisms do exist (Felbeck, 1981; Cavanaugh *et al.,* 1981). In Gollum's Canyon, annelids and amphipods are important macrofaunal components of the thiobiotic community. In fact, amphipods have a population maximum coincident with that of the gnathostomulids, although, as a group, they are certainly not known for their sulfide detoxification capabilities or euryoxia (e.g. Wieser and Kanwisher, 1959; Oseid and Smith, 1974b). Whether these macrofauna are true thiobiota or oxybiota capable of living in the canyon despite the high sulfide concentrations because of the simultaneous presence of high oxygen concentrations is unknown, but their presence at most stations suggests that a broader definition of thiobiotic life is needed.

The sulfide system is not a homogeneous environment as has sometimes been claimed. Although buffered from many physical parameters affecting oxidized sediments (Wieser, 1975), the fact that it is a gradient system must introduce heterogeneity. Variability in the specific distribution patterns (e.g. location of population maxima) of the various taxa probably exists, since both variability in the detoxification capabilities of the various species and temporal and spatial variability of the chemistry in the chemocline can be expected. In Gollum's Canyon, the thiobiotic stations have significant faunal differences even though identifications were only at the higher taxonomic levels. This suggests that thiobiotic community structure is more complicated than previously believed.

There is a profound difference in faunal composition between oxybiotic and thiobiotic communities. The lower invertebrate groups (platyhelminths, aschelminths and gnathostomulids) make up a small percentage of the oxybios at most stations, but are 50–80 percent of the thiobiotic community (Table 6). Within the oxybios, the percent contributions by these invertebrate groups to the total biota is generally lower at stations with lower sulfide concentrations. Lower invertebrate phyla are able to exploit sulfide system life to a significantly greater degree than other phyla. It might be argued that these groups are predominantly micro-metazoan and that this alone is the reason, but micro-metazoan annelids, ostracods and, particularly, copepods, are also important components of the meiofauna. Yet, these groups are not well represented in the thiobios.

A number of recent hypotheses and models of Precambrian and Paleozoic community structure implicate the sulfide system as a particularly important component (Fenchel and Riedl, 1970; Boaden, 1975, 1977) of the early Phanerozoic benthos since oxygen levels were considerably lower than today in many areas of the ocean (Cloud, 1968; Berry and Wilde, 1978). Fenchel and Riedl (1970) suggested that an unexpectedly high number of thiobiotic organisms were phylogenetically primitive and Boaden (1975) proposed that the sulfide system played an important role in metazoan evolution. The phylogenetic position of these taxa remains an area of intense interest (Rieger, 1976; Rieger and Rieger, 1976; Salvini-Plawen, 1978; Rieger and Mainitz, 1977). Certainly within the phyla, Fenchel and Riedl's hypothesis is open to question (Reise and Ax, 1979; Powell *et al.*, 1980). On the other hand, at the phylum level, the dominance of the lower invertebrate groups (exclusive of Porifera and Coelenterata) in the thiobios is striking. These groups in general must possess some adaptive advantage for sulfide system life.

The present study expands and supports the definition of the thiobios proposed by Powell and Bright (1981). Thiobiotic organisms should have an ecologic requirement for sulfide, have population maxima in the chemocline, and be important members of the biota only where sulfide is present. Sulfide, more than oxygen, is the important chemical determinant of their community structure. Oxybiota should have population maxima above the chemocline and be important members of the biota where sulfide is not present, though oxybiota may be important in sulfide systems characterized by high oxygen concentrations. A considerably better understanding of the ecological and physiological capabilities of micro-metazoans is required, however, to confirm these points of view.

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