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Distribution of Trace Elements in *Callichirus laurae* Burrows and Nearby Sediments in the Gulf of Aqaba, Jordan (Red Sea)

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ABSTRACT

In nearshore waters of the Jordanian sector of the Gulf of Aqaba, the distributions of Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb and Zn, as well as Ca and Mg, were determined in the mucus-rich burrow lining made by the locally abundant Crustacea Callichirus laurae *(Thalassinidea: Callianassideae), and compared with concentrations obtained in surface sediments surrounding the burrows. The highest concentrations of trace elements were observed in a sewage affected area. At uncontaminated stations, a marked increase from surface sand values was observed in the burrow lining. The correlations between the concentration of trace elements in this biogenic micro-environment and both the concentration of organic carbon and the mean granulometric diameter were highly significant.*

This study shows that the C. laurae *burrow acts as a chemical reservoir that may reach several meters deep into the sediment. This special reservoir is created as an indirect consequence of the building of a mucus-rich, metal-reacting lining. It is demonstrated that the absolute quantity of trace elements*

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incorporated in the lining is much higher (c. 85 to 250 times more, depending on the element) than in the dense and healthy Halophila stipulacea *seagrass bed covering the surface.*

The environmental significance of large lined burrows for the distribution of trace elements is discussed.

INTRODUCTION

The distribution of trace elements in various sedimentary environments and their correlation with either a high organic content or a fine grain size are well documented (Nissenbaum & Swaine, 1976; Swinbanks & Shirayama, 1984; Rashid, 1985). In the Jordanian sector of the Gulf of Aqaba (Red Sea), the distribution of cadmium (Cd), cobalt (Co), chromium (Cr), copper (Cu), iron (Fe), manganese (Mn), nickel (Ni), lead (Pb) and zinc (Zn) was recently analyzed in nearshore surface sediments, showing a general distribution parallel to that of organic carbon (Abu-Hilal, 1987). However, when considering the vertical distribution of trace elements in the sediment, an eventual redistribution by infaunal organisms had to be taken into consideration, as the elements can become adsorbed on tridimensionally distributed biogenic substrata such as burrow linings (Anderson & Meadows, 1978; Aller & Yingst, 1978; Aller *et al.*, 1983). This is especially true in Aqaba where dense monospecific populations of the burrowing Crustacea *Callichirus laurae* de Saint Laurent 1984 (Decapoda, Thalassinidea, Callianassideae) are a characteristic feature of extensive surfaces of sediment (Vaugelas, 1984; Vaugelas & Saint Laurent, 1984). The deep (vertical extension >2 m deep into the soft substratum) and large burrows (several meters of 2·5 to 3·0 cm diameter open tunnels for a single network), inhabited by 12- to 14-cm long adult *C. laurae*, are lined with a 0·5- to 1·5-cm thick burrow lining, made of a mixture of fine particles cemented by an organic mucus.

This investigation was conducted to examine the distribution of the above trace elements in *C. laurae* burrows, as it was demonstrated in a separate work (Buscail & Vaugelas, submitted), that the lined walls contain a significant proportion of humic substances, biopolymers known for their complexation effect towards trace elements (Nissenbaum & Swaine, 1976; Faguet, 1982; Rashid, 1985).

It was recently hypothesized that *C. laurae* from the Red Sea and its closely related species *C. armatus* from the Indo-Pacific zone, could in fact be synonymized with *Glypturus acanthochirus*, an abundant species in the Caribbean (Manning, 1987 and pers. comm.). *Glypturus acanthochirus* would therefore be a species distributed world wide, giving the preliminary results exposed in this study a larger scope than initially thought when we started our study in the Gulf of Aqaba on the locally abundant *C. laurae.*

STUDY AREA

The position of the four sampling stations along the Jordanian sector of the Gulf of Aqaba is shown in Fig. 1.

Sediment

Stations 1 and 3 are similar terrigenous, fine, muddy-sand facies (Table 1 and Gabrié & Montaggioni, 1982), 90% covered with a *Halophila stipulacea*

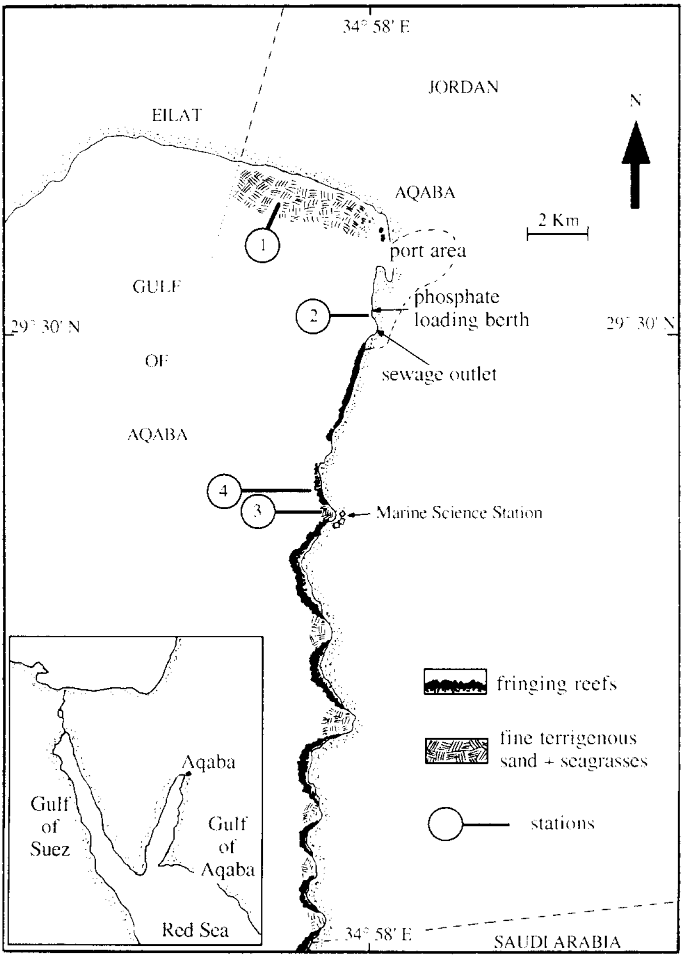

Fig. 1. Location of the stations along the Jordanian coast of the Gulf of Aqaba (Red Sea).

TABLE 1
Granulometric and Redox Characteristics of the Surface Sediment at Stas 1–4 and in *Callichirus laurae* Burrow Lining

Origin	*Stas 1 & 3*	*Sta. 2*	*Sta. 4*	*Burrow lining*
Type	*Terrigenous*	*Terrigenous + phosphate mud*	*Coralline*	*Mixed*
Md (μm)	125	80	400	100
Q1 25% (μm)	75	13	220	60
Q2 75% (μm)	200	140	700	220
So (Trask)	1·63[b]	3·28[a]	1·78[b]	1·30[c]
% < 40 μm	10	40	< 5	6·3
% carbonates	10–20	10–20	80–95	30–60
eH: +350 mV	surface	surface	surface	—
eH: RPDL	−1 cm	−1 cm	−3 to −4 cm	—
eH: 0 mV	−2 cm	−2 cm	−3 to −5 cm	—
eH: −150 mV	> 3 cm	> 3 cm	> 5–6 cm	—

[a] Poorly sorted; [b] well sorted; [c] very well sorted; —, no data.

seagrass bed (Hulings, 1979; Wahbeh, 1982). They represent the main sedimentary environment in terms of surface area along the Jordanian coast.

The main characteristic of Sta. 2, located in Aqaba Port Area, is the presence of a 5- to 15-cm-thick layer of phosphate (apatite) mud dumped from a loading berth (Fig. 1), covering an original sediment similar to Sta. 1 (Table 1). Also affecting Sta. 2 is a sewage outlet discharging untreated effluents from the city of Aqaba (Abu-Hilal, 1987).

Station 4 is a medium-to-coarse coralline sand scattered among coral patches of the outer reef slope (Table 1 and Gabrié & Montaggioni, 1982).

Burrows

Thalassinid mud-shrimps are known to produce the deepest and largest burrows recorded in the actual marine environment, with penetrations of 3 m or more (Pemberton *et al.*, 1976; Tudhope & Scoffin, 1984). The average abundance of *Callichirus laurae* burrows at Stas 1 and 3 was 0·2 to 0·3 m^{-2} (i.e. 20 to 30 burrows in a square 10 × 10 m), 0·05 to 0·1 m^{-2} at Sta. 2 and lower than 0·05 m^{-2} at Sta. 4. *Callichirus laurae* lines its tunnels with a mixture of fine particles (Table 1) and mucus as described in detail by Thompson (1972) for the Thalassinid crustacean *Upogebia pugettensis*. All burrow lining samples were collected in the upper network of tunnels (between 20 and 60 cm deep) where the mud-shrimp spends most of its time, (Vaugelas, 1984). The first 2 mm of the inner burrow lining, in contact with the O_2-rich irrigation water, is of a light brown colour characteristic of oxidized substrata, contrasting with deeper parts of the lining and the surrounding sediment which are dark grey and reduced.

MATERIALS AND METHODS

Sampling procedure

All samples from the uppermost layer of sediment (*c.* 0–2 cm layer) were collected with polyethylene bags. Upon collection, samples were freed from coarse shell fragments, visible organisms, seagrass leaves and roots when present. The samples were then washed with deionized distilled water, oven dried at 80°C for at least 72 h, ground and homogenized using a grinding mill equipped with a corundum pestle and mortar. The fine powder was then stored in plastic or glass containers until analysis.

Samples of *C. laurae* burrow lining were obtained while excavating the burrows with an all-plastic sediment sucker (Vaugelas, 1984), then treated in the same way as the surface sediment samples. Calculations of burrow surface area, depth and morphology were made after *in situ* casting of burrows with polyester resin (adapted from Shinn, 1968). The surface area of the inner lining was measured following Hutchings (1978), after coating the resin cast with a peel of silicone glue and using a digital polar planimeter.

Specimens of *C. laurae* were collected at Sta. 3 (Vaugelas, 1985). After drying to constant weight, they were treated in the same way as sediment samples.

Redox was measured on perforated cores (30 cm long, 7 cm internal diameter), with a thin-wire platinum electrode (Vaugelas *et al.*, 1983 and unpublished data). The analysis of the redox curves emphasized the 0 mV and the redox potential discontinuity (RPD) level.

Analysis

Total element concentration was determined after complete dissolution of the samples by the use of concentrated ultra-pure HNO_3, $HClO_4$ and HF acids (Agemain & Chau, 1976, 1977). Analyses were carried out by aspiration into a Perkin-Elmer atomic absorption spectrometer Model 3030, equipped with a premix burner and simultaneous background corrector. Analytical blanks and sediment samples were analyzed in duplicate using the same reagents and procedures. The analytical blanks obtained were Ca = 0·60, Cd = 0·00, Co = 0·00, Cr = 0·01, Cu = 0·01, Fe = 0·06, Mg = 0·09, Mn = 0·02, Ni = 0·02, Pb = 0·00, Zn = 0·01 μg litre^{-1}.

Organic carbon was measured following the standard method of Walkley and Black, as described in Buchanan & Kain (1971). Humic and fulvic acids were determined following the procedure of Debyser & Gadel (1983).

The grain-size distribution of the sand and burrow walls was carried out using an AFNOR sieve column ($r = \sqrt[10]{10}$). The cumulative grain-size curves were used to determine mean diameter (Md) and Trask sorting index (So). Carbonate content was determined following the method of Anwar & Mohammed (1970).

All concentrations are expressed as dry weight.

RESULTS

Chemistry, grain size and organic carbon

The pattern of trace elements distribution observed in the present study for surface sediments is similar to the one previously reported (Abu-Hilal, 1987). However, when looking at the vertical distribution, we observed for all uncontaminated samples, either from terrigenous (Stas 1 and 3) or coralline (Sta. 4) origin a marked increase in the concentration of organic carbon (OC) and all trace elements in the burrow lining (with Fe, Mn, Cr and Zn most concentrated, Table 2 and Fig. 2). Burrows possess finer grain size, greater

TABLE 2

Distribution of Trace Elements, Organic Carbon (OC), Ca and Mg in Surface Sediments, Burrow Linings and *Callichirus laurae* at Stas 1 to 4. Each value is an Average of Two Determinations. — = No data

Sta.	*Sediment type*	*Trace metals (ppm, dry wt.)*									*OC* (%)	*Ca* (%)	*Mg* (%)
		Fe	*Mn*	*Pb*	*Zn*	*Cr*	*Ni*	*Co*	*Cu*	*Cd*			
1	Sup. sediment	14 600	263	102	35·2	70·4	45·7	27·7	10·0	4·0	0·17	3·8	0·45
1	Burrow lining	29 600	426	165	72·0	100	61·7	42·6	17·0	6·0	1·16	8·6	1·45
2	Sup. sediment	12 500	212	168	195	123	62·1	38·1	24·0	13·7	0·62	36·0	0·59
2	Burrow lining	19 900	332	178	182	138	61·1	39·0	27·7	10·5	1·56	14·0	0·82
3	Sup. sediment	10 900	185	96·3	32·3	46·3	30·0	23·1	11·5	3·9	0·16	4·0	0·40
3	Burrow lining	21 600	316	161	74·8	108	70·0	42·7	16·2	6·2	1·39	16·5	1·75
4	Sup. sediment	3 400	68·2	182	24·0	11·7	34·1	42·5	7·1	7·1	0·18	18·4	0·66
4	Burrow lining	10 300	169	212	47·5	22·5	49·8	54·7	11·2	8·4	0·82	24·1	1·32
Callichirus laurae													
	Full animal	970	15·8	23·9	131	3·2	38·7	9·4	263	1·7	—	5·6	0·98
	Large cheliped	100	10·4	43·4	64·2	3·6	97·4	26·5	30·0	4·7	—	21·3	1·89

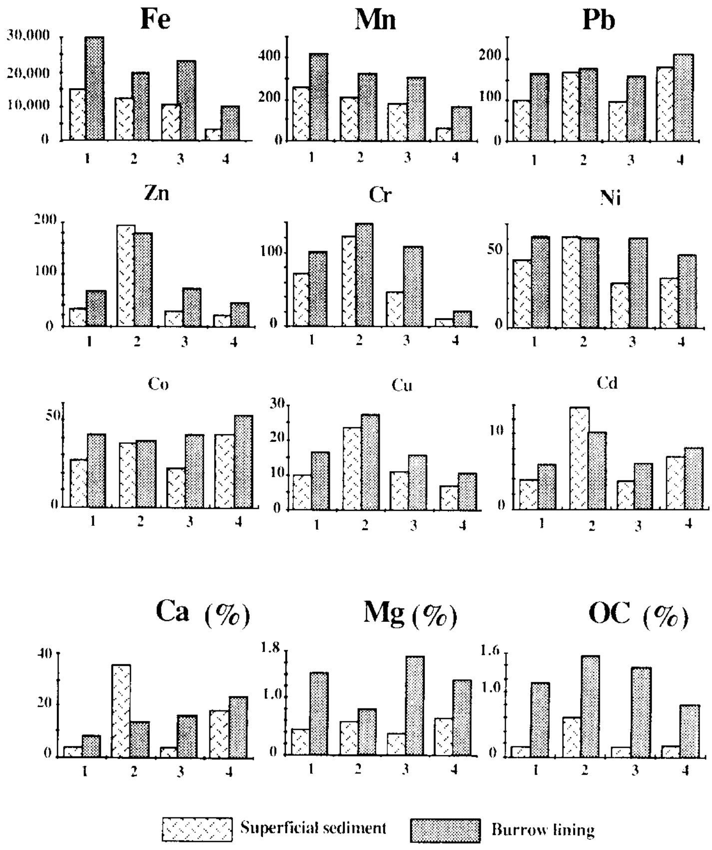

Fig. 2. Distribution of individual elements (ppm), Ca, Mg and organic carbon (%) in sediments and *Callichirus* burrows at Stas 1 to 4. Trace elements are ranged according to decreasing concentrations.

OC and enhanced trace metals. The average increase in trace elements associated with the burrow lining ranged between 1·76 and 2·34 times (Fig. 3).

Except for Cd and Zn at Sta. 2 (i.e. terrigenous sediment contaminated by a phosphate mud layer and untreated sewage effluent—Abu-Hilal, 1985), we noted a high correlation between the concentration of trace elements and OC (Table 3). Similarly, a high correlation between trace elements and the granulometric mean diameter was observed (Table 4), except for Cr, Fe and Mn at Sta. 2.

The pattern of trace elements distribution is similar in the uncontaminated Sta. 1 and Sta. 3. Organic carbon is highly concentrated in the lining, especially at Sta. 3, where it is 8·65 times higher than in the surface sediment (Fig. 3).

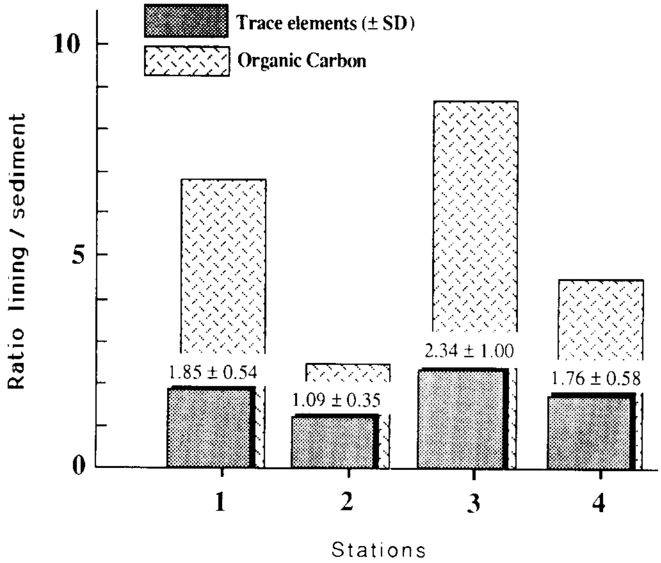

Fig. 3. Average increase of trace elements and organic carbon concentrations between surface sediment and burrow lining, as expressed by the 'lining/surface sediment' ratio.

TABLE 3

Correlation Coefficients Between Individual Elements and Organic Carbon Content

Element	*Calcareous sed.* (*Sta. 4*) (*n* = *12*)	*Terrig. sed.* (*Stas 1 & 3*) (*n* = *8*)	*Terrig. sed. + Phosphate* (*Stas 1, 2 & 3*) (*n* = *12*)
Cd	0·92***	1·00***	0·37 (ns)
Co	0·95***	0·97***	0·87***
Cr	0·99***	0·94***	0·80**
Cu	0·99***	0·95***	0·66*
Fe	0·98***	0·86**	0·72**
Mn	0·99***	0·77*	0·72**
Ni	0·90***	0·89**	0·78**
Pb	0·91***	0·98***	0·87***
Zn	0·99***	0·99***	0·47 (ns)
Ca	0·95***	0·91**	0·23 (ns)
Mg	0·99***	1·00***	0·75**

All r are statistically different from 0 (* $0{\cdot}01 < p < 0{\cdot}05$; ** $0{\cdot}001 < p < 0{\cdot}01$; *** $p < 0{\cdot}001$), except when followed by ns (not significant, $p > 0{\cdot}05$). n = Number of samples.

TABLE 4

Correlation Coefficients between Organic Carbon (OC), Individual Elements and the Granulometric Median

Element	*Calcareous sed.* (*Sta. 4*) (*n = 10*)	*Terrig. sed.* (*Stas 1 & 3*) (*n = 8*)	*Terrig. sed. + phosphate* (*Stas 1, 2 & 3*) (*n = 12*)
OC	−0·99***	−0·99***	−0·55 (ns)
Cd	−0·98***	−1·00***	−0·88***
Co	−0·98***	−0·98***	−0·79**
Cr	−0·97***	−0·93***	−0·32 (ns)
Cu	−0·98***	−0·98***	−0·79**
Fe	−1·00***	−0·85**	−0·36 (ns)
Mn	−1·00***	−0·84**	−0·22 (ns)
Ni	−1·00***	−0·90**	−0·84***
Pb	−1·00***	−1·00***	−0·88***
Zn	−1·00***	−1·00***	−0·83***
Ca	−0·92***	−0·84**	−0·90***
Mg	−0·99***	−0·98***	−0·36 (ns)

All r are statistically different from 0 (* $0{\cdot}01 < p < 0{\cdot}05$; ** $0{\cdot}001 < p < 0{\cdot}01$; *** $p < 0{\cdot}001$), except when followed by ns (not significant, $p < 0{\cdot}05$), n = Number of samples.

The concentration of organic carbon is much higher in the surface layer of the phosphate mud (0·60% OC) than in all other stations (average 0·18% OC), which is probably due to the combined effects of a finer granulometry and sewage input. Organic carbon is 1·56% in the burrow lining, which is slightly higher but remained in the range observed for uncontaminated Stas 1 and 3 (Table 2: OC = 1·16 and 1·39%, respectively). This may indicate that, whatever the level of OC at the surface, the shrimp will incorporate the same amount of OC in its lining. In the phosphate mud area, the order of enrichment in the lining was similar to that in the surface layer (Fe > Mn > Zn > Pb > Cr > Ni > Co > Cu > Cd), which might be explained by the small differences in particle size (Table 1: Md = 80 μm in the surface sediment and 100 μm in the lining). In these contaminated sediments, Zn, Cu and Cd were higher than in all other samples, as the phosphate dust contains high concentrations of these elements (Abu-Hilal, 1987).

In the coralline sediment, the order of enrichment in lining and surface sand was Fe > Pb > Mn > Co > Ni > Zn > Cr > Cu > Cd. The Co and Cd contents were higher than in the terrigenous sand, indicating that the two elements are easily leached by the acid treatment of the coralline sediments. However, Fe > Mn > Cr > Zn, Ni and Cu were lower in the surface sediment and lining of the coralline area compared with the terrigenous area, which is mainly due to the dilution effect of $CaCO_3$.

Callichirus laurae

Trace elements were measured in *Callichirus laurae* to compare with concentrations in the sediment. Full animals (2 adult specimens) and three isolated large chelipeds were used for this purpose, all samples coming from uncontaminated Sta. 3.

All trace elements concentrations were in the same range, or even less concentrated, in full animal samples compared with those in the surface sand, except for Cu, which increased 22·8 times with respect to the surface sand and 8·7 times when compared with large cheliped values (Table 2). Keeping in mind that soft tissue analyses are notoriously variable, this latter difference could indicate that Cu is highly incorporated in organs which are neither carapace, nor muscle, the two main constituents of the cheliped. It could be the digestive tube or, more probably, the voluminous digestive glands, organs known for accumulating trace elements (Bryan, 1976). Results from a study on acute toxicity indicated that Cu, mainly located in the abdomen, was more toxic than either Zn or Cd to *Callianassa australiensis* (Ahsanullah *et al.*, 1981). It was not possible in this study to check the potential toxic effect of Cu on *C. laurae*, but the high Cu observed at contaminated Sta. 2 in both surface sediment and burrow lining did not seem to be lethal to *Callichirus laurae*.

DISCUSSION

This study represents the first report of trace elements distribution in a Callianassid burrow. Our data indicate a significant increase for all trace elements in the lining. These preliminary results are consistent with previous observations on the distribution of trace elements in other Thalassinid burrows: Pemberton *et al.* (1976), studying *Axius serratus* (Thalassinidea: Axiidae), showed accumulations of Pb, Zn, Cu and Fe in the burrow infilling, while Aller *et al.* (1983) found a selective incorporation of Fe in the mucus Fe-oxide-laden inner burrow wall of the Thalassinid *Upogebia affinis*, and Mn concentration around the lining. Similarly, Aller & Yingst (1978), studying the polychaete worm *Amphitrite ornata*, demonstrated the existence of marked increases in the concentration of both solid and aqueous phases Mn and Fe in the mucus-rich walls, with Fe^{++} and Mn^{++} in pore waters decreasing with distance from the burrow. It must be mentioned that both Thalassinid mud-shrimps and *A. ornata* build their lining with small bricks of fine sediment soaked in a mucopolysaccharidic substance (compare Thompson's and Aller & Yingst's descriptions in that respect).

In order to estimate the representativity of *C. laurae* burrows as a significant reservoir for trace elements, we compared Sta. 3 values with concentrations previously measured at the same station by Wahbeh (1984), for a dense *Halophila stipulacea* seagrass bed whose leaves, rhizomes and roots represent the most conspicuous biogenic structure at the surface of Sta. 3 (Fig. 4).

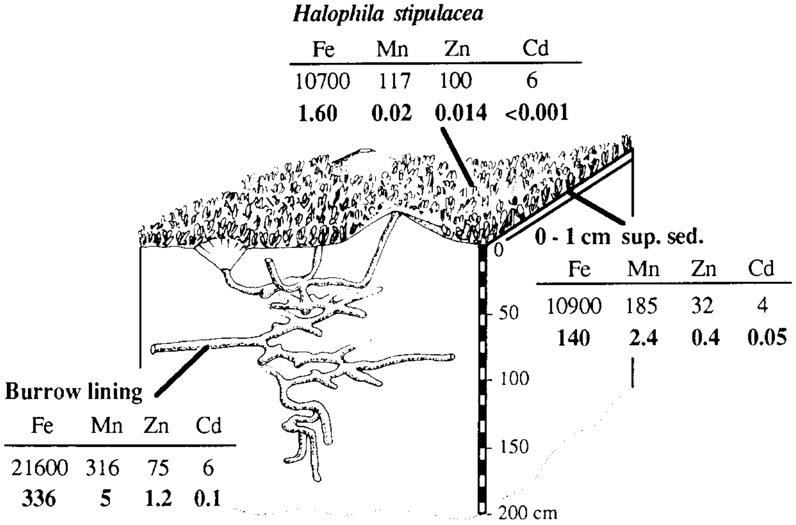

Fig. 4. Comparison of the trace elements distribution (upper line = ppm; lower line = g m^{-2}) in a *Halophila stipulacea* seagrass bed, the first centimeter of surface sediment and *Callichirus laurae* burrow lining at Sta. 3. Details of calculations in the text.

On a square meter basis, we compared concentrations of Cd, Fe, Mn and Zn in the 1 cm thick burrow lining with concentrations in the 0–1 cm layer of surface sand and in *H. stipulacea.* We took averaged values for leaves, rhizomes and roots of Cd = 6, Fe = 10700, Mn = 116·80 and Zn = 100 ppm (Wahbeh, 1984) and a summer maximum biomass of 150 g m^{-2} (Hulings, 1979; Wahbeh, 1982). Assuming an homogeneous composition of the burrow lining at all levels in the burrow network, a specific weight of 1·56 g cm^{-3} ($n = 5$) and a surface area of the inner lining of 1·72 ± 10% m^2 for the burrow displayed on Fig. 4, the amount of lining material is 26·8 ± 10% kg. With 1·28 g cm^{-3} ($n = 5$) as specific weight for the 0–1 cm layer of surface sand, we calculated the distribution of trace elements in these three biota, two of them (*Halophila* and the lining) being of biogenic origin. The results showed that, while the ppm contents were in the same range for the three biota, the absolute quantity of trace elements in 1 m^2 of burrow lining is much higher (*c.* 85 to 250 times more, depending on the element) than in 1 m^2 of a dense and healthy seagrass bed.

This simple comparison gives an idea of the environmental significance of large lined burrows for the distribution of trace elements. These can impart a profound three-dimensionality to the pattern of element distribution. This observation is totally compatible with data obtained for annelids' burrow linings (Anderson & Meadows, 1978; Aller & Yingst, 1978) and leads us to the hypothesis that most trace elements are probably linked to macroinfauna biogenic structures enriched in mucus, rather than randomly dispersed in the sediment. Therefore, it is most important in studies on element distribution to consider deep and large burrows as special reservoirs resulting from a biologically-mediated transport mechanism. Unfortunately, conventional sampling strategies, using either hand or box corers, cannot be applied to these burrows as they can only sample the first 50 cm layer.

Fixation routes

Both a finer granulometry and a higher organic content in the lining are sufficient to explain the observed increase in trace elements (Rashid, 1985). As the results showed that the mud-shrimp itself does not accumulate metals (Cu excepted?), we assume that it cannot produce a metal-rich mucus. It is therefore most probable that the trace elements become adsorbed into the wall after its construction, as it was demonstrated for *A. ornata* (Aller & Yingst, 1978). The dominant mechanism in control of concentration for most trace elements appears to be adsorption on biologically produced particulate matter, particularly on reactive humic compounds (Nissenbaum & Swaine, 1976; Faguet, 1982). It has been demonstrated for Sta. 3 burrows that humic substances represent 30 to 48% of organic carbon (OC) and that their distribution pattern is highly correlated to that of OC (Buscail & Vaugelas, submitted). However, trace metals are relatively depleted in the walls when normalized to OC, and the metal/C ratio is higher in surface sediments than in burrow walls, which is probably related to differences in organometallic associations. Buscail & Vaugelas (submitted) have shown through IR analysis that the humic acids' functional groups are different between surface and walls. Humic compounds, because of their high geochemical reactivity through surface adsorption, cation exchange, chelation and complexing processes, adsorb and accumulate metallic trace elements to form organometallic complexes of various stabilities (Rashid, 1985). Based on the correlations reported therein, our hypothesis is that humic substances present in the lining are a key factor for the observed accumulation of trace elements. Similar conclusions were reached for the distribution of uranium in *C. laurae* burrows (Whitehead *et al.*, 1988).

The permanent irrigation of the burrow network brings O_2-rich waters at depth and pumps nutrients and various solutes back to the superjacent water (Gust & Harrison, 1981; Waslenchuk *et al.*, 1983). Trace elements may be adsorbed to the wall (i) either through a direct scavenging when the elements in solution in the superjacent water are moved into the burrow through irrigation and come in contact with the lining (Aller & Yingst, 1978, proposed that intense decomposition processes in the burrow wall create highly reactive surfaces, promoting the scavenging of metals from irrigation water), or (ii) when metal-carrying pore water transits from the surrounding sediment to the burrow water (Whitehead *et al.*, 1988). This latter route might be significant when the residence time of the burrow is considered. The ages of the burrows investigated in this study are not known, but intact open callianassid burrows were observed *in situ* at depths greater than 5 m in the sediment, indicating ages greater than a few thousand years (Shinn, 1968; Tudhope & Scoffin, 1984). In addition, indurated callianassid burrows are well known in the fossil record (Weimer & Hoyt, 1964; Curran, 1984), indicating an even longer period of residence. This tends to increase the capacity of the burrow to act as a sink for various elements, including metals. Despite the fact that the chance for a large burrow to be preserved in the fossil record is much greater than for the numerous tiny burrows produced by various worms in the 0–30 cm layer, little attention has been focused on this aspect of metal distribution.

CONCLUSION

The present study showed that *Callichirus laurae* burrows impart a pronounced three-dimensionality to the distribution of Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb and Zn on the meter scale. In accordance with Aller & Yingst (1978) and Swinbanks & Shirayama (1984) conclusions, there is every reason to believe that comparable heterogeneity exists in the distribution of other elements, both chemical and biological, and that future sampling strategies should be designed to seek such heterogeneity in and around burrow structures (infilled and unfilled). Only then will it be possible to progress from simple one-dimensional steady-state views of the sediment, to more realistic non-steady-state multi-dimensional models in which the effects of deep burrowing organisms are fully taken into account. We share the opinion of Gust & Harrison (1981) and of Waslenchuk *et al.* (1983), that burrowing shrimps and their deep burrow systems constitute a major link for pore water–seawater exchange, probably overriding gradient-controlled physical fluxes. However, this statement is only valid for situations where the reaction rates of the solute of interest are sufficiently high at depth to support relatively substantial fluxes into the burrows. The fluxes of constituents whose reactions are strongly attenuated below the sediment–water interface will not be influenced by deeply penetrating burrows, except in situations where the period of residence of the burrow is long enough to allow for late-stage migrations.

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