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Range extension and microhabitat of *Lightiella incisa* (Cephalocarida)

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Abstract

During an intensive meiofauna sampling campaign in intertidal seagrass beds along the Caribbean coast of the Yucatán Peninsula (Mexico), 131 specimens of *Lightiella incisa* (Cephalocarida, Crustacea) were recovered from the sediment. Two-thirds of the specimens were adults, one-third were pre-adults. This collection is the first record of this minute primitive crustacean in the western part of the Caribbean Sea, and extends the known range 3000 km from the type locality of Hastings Bay, Barbados. A detailed sampling protocol and environmental data made it possible to study the microhabitat preferences of this species, and perhaps for cephalocarids in general for the first time. The vertical distribution of *L. incisa* in the sediment showed a maximum density in deeper layers, i.e. 3–4 and 4–5 cm depth. Nitrate and nitrite concentrations seem to be most closely related to the distribution of *L. incisa*. It was clear that *L. incisa* followed polychaetes to deeper sediment layers. In this study we state that *L. incisa* is an endobenthic species occupying anoxic sediments oxygenated by bioturbation (e.g. Polychaeta) rather than being an animal living in the oxygenated top layers.

Key words: Cephalocarida, *Lightiella incisa*, range extension, microhabitat

INTRODUCTION

With at present 10 species, attributed to four different genera, the Cephalocarida are one of the more restricted crustacean taxa. These minute benthic organisms have a world-wide distribution, and have been collected in shallow intertidal localities to > 1500 m deep (Schram, 1986). The systematic position of the Cephalocarida has been subject to much debate as it was long considered as a crucial taxon in speculations on crustacean phylogeny (Sanders, 1955, 1957). Consequently several studies on morphology (Burnett, 1981; Elofsson, 1992; Read, Hessler & Govind, 1994; R. R. Hessler & Elofsson, 1995; R. R. Hessler, Elofsson & Hessler, 1995; Elofsson & Hessler, 1998) and development (Sanders, 1963; Sanders & Hessler, 1964; A. Y. Hessler, Hessler & Sanders, 1970) have been conducted in order to reveal the phylogenetic position of the cephalocarids.

Ecological information on this group is sparse. Only three species have been found in abundant numbers; most other species are known from one to seven specimens obtained only once. From the available information, cephalocarids tend to prefer sediments rich in organic fine particulate matter, a condition which is often encountered in dense seagrass beds. R. R. Hessler & Sanders (1964) reported on maximum densities of *Hutchinsoniella macracantha* of 176.5 individuals/m^2 at Buzzards Bay (off Massachusetts). While McLaughlin (1976) obtained up to 50 individuals of *Lightiella floridana* per site (15×15 cm box corer) off the western coast of Florida. However, the distribution within the sample area is clearly very patchy as has been shown by Saloman (1978) who recovered only 12 specimens in four out of 208 sampling stations along the western coast of Florida.

During an intensive sampling campaign for meiofauna (here defined as Metazoa 38 μm to 1 cm long) along the Caribbean coast of the Yucatán Peninsula (Mexico), many *Lightiella incisa* Gooding, 1963 were detected in the sediments between the roots of seagrasses. This find represents a considerable extension of the range of this species to the westernmost limits of the Caribbean Sea, and the sampling method and the parameters of the sediments allows us to study in detail the ecological preferences of this species, and perhaps for cephalocarids, in general for the first time.

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Table 1. Standard field information of the different sampled quadrats

Seagrass species	Quadrat	Locality	Date	Air temperature (°C)	Water temperature (°C)	pH	Salinity (psu)
T. testudinum	I	19°47′06.6″N 87°28′08.2″W	17 July 1998	30.6	33.1	8.28	36.5
T. testudinum	II	19°47′08.5″N 87°28′08.4″W	17 July 1998	30.0	29.6	8.06	36.5
S. filiforme	I	19°47′06.6″N 87°28′08.2″W	17 July 1998	31.2	31.2	8.21	36.6
S. filiforme	II	19°47′08.5″N 87°28′08.4″W	17 July 1998	29.4	31.4	8.19	36.5
H. wrightii	I	19°47′06.6″N 87°28′08.2″W	18 July 1998	30.6	30.0	8.10	36.5
H. wrightii	II	19°47′08.5″N 87°28′08.4″W	18 September 1998	29.3	32	8.29	36.5

MATERIAL AND METHODS

Study site and sampling method

During July 1997, an intensive meiofauna sampling campaign was carried out in Punta Allen (19°47′06″N and 87°28′08″W) on the Caribbean south coast of the Yucatán Peninsula (Quintana Roo State, Mexico). This site is situated in the northern part of the UNESCO biosphere reserve of Sian Ka'an.

Meiofauna samples were taken in the subtidal zone adjacent to 3 seagrass species: *Syringodium filiforme* Kützing 1860, *Thalassia testudinum* Banks ex. König 1805 and *Halodule wrightii* Ascherson 1868. For each seagrass species, 2 quadrats situated on 2 transects were sampled, with 3 replicates per quadrat. All samples were taken while snorkelling as the maximum depth was about 2 m. A standard PVC meiocore with a diameter of 3.6 cm (surface 10 cm^2) was forced into the sediment to a depth of 10 cm, and subsequently divided into 1-cm slices for the upper depth layers, and a 5-cm slice for the rest of the core. No cephalocarids were encountered in the overlying water.

All samples were preserved with warm formaldehyde to a final concentration of 4%. In the laboratory, samples were decanted over a 38 μm sieve, centrifuged with Ludox HS40 at a specific density of 1.18, and stained with Rose Bengal (modified after de Jonge & Bouwman, 1977). Meiofauna was sorted and counted at the higher taxon level using a Wild M5 binocular. Cephalocarids were picked out with a needle and stored in 75% ethanol. The appendages of 3 specimens were dissected and mounted in glycerine on slides. The body shape and appendages conformed closely with the original detailed description of Gooding (1963). Voucher specimens were deposited in the Invertebrate Collection of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium; no. IG 28700), the Zoology Museum of the University of Gent, Belgium (nos MDCC 0001- 0010) and the Zooplankton Collection at El Colegio de la Fontera Sur (Cheturnal, Mexico; no. ECO-CH ZOO497).

Abiotic data

The following abiotic variables were measured for each sampling quadrat: air and water temperature, salinity, pH and conductivity of the water using a pH meter (type Sentix 97T, Sentix 50, TFK 325/HC) or a conductivity meter (type LF 323-325, Tetracon 325). The exact location of each quadrant was determined by GPS (type GPS 45 Personal Navigator™ Garmin).

Two macrocores (diameter 6.2 cm) per quadrat were taken for sediment and nutrient analysis; they were subdivided into 6 depth layers as described for the meiofauna cores. These samples were stored frozen until nutrient analysis of the interstitial water; concentrations of $NO_2^- - N$, $NO_3^- - N$, $NH_4^+ - N$, $PO_4^{3-} - P$ and SiO_2 were determined with an A_{II} automatic chain (SANplus Segmented Flow Analyser, SKALAR). Part of the remaining sediment was dried for 4 h at 110 °C and used for organic matter analysis (total organic matter, TOM) as determined by weight loss upon ignition for 120 min at 550 °C.

A few grams of the sediment were dried for 24 h at 60 °C and used for grain size analysis on a particle size analyser (type Coulter® LS100). The yielded standard sediment characteristics are median grain size, percentage silt (< 63 μm), percentage coarse sand (850–2000 μm) and percentage gravel (> 2000 μm).

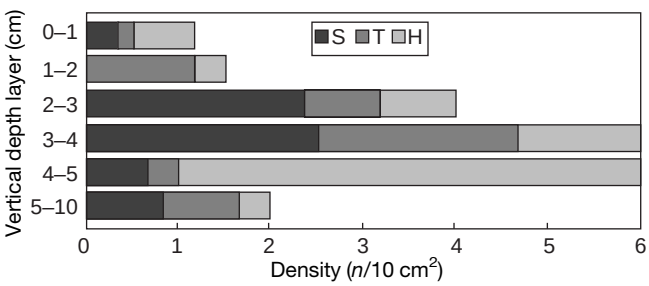

Fig. 1. Vertical distribution of *Lightiella incisa* (average density of three replicates and two transects) from sediment surrounding three seagrass species: *Syringodium filiforme* (S), *Thalassia testudinum* (T), *Halodule wrightii* (H).

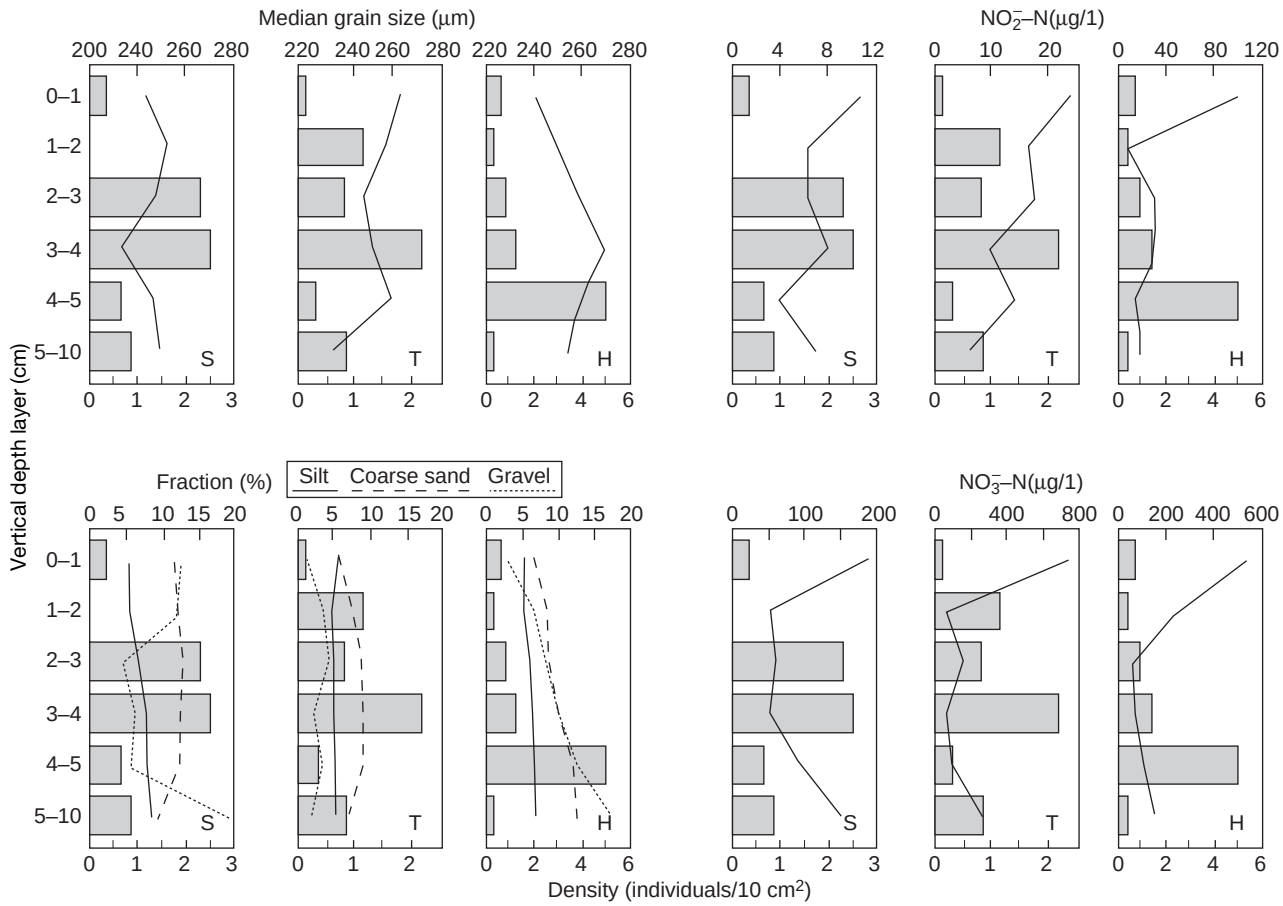

Fig. 2. Vertical distribution of *Lightiella incisa* (bars, bottom scale) and median grain size, silt fraction, coarse sand fraction, gravel fraction, $NO_2^- - N$, $NO_3^- - N$ (lines, top scale) for three seagrass species: *Syringodium filiforme* (S), *Thalassia testudinum* (T), *Halodule wrightii* (H).

In addition, triplicate small (~1 ml) sediment samples were taken from the different depth layers with a syringe (distal top removed) and stored frozen. They were used for pigment analysis (chlorophyll *a* and fucoxanthin) on a Gilson HPLC-chain (fluorometrical and visible detection) using a modified protocol of Mantoura & Llewellyn (1983).

RESULTS

Range extension

One hundred and thirty-one specimens of *L. incisa* were found in benthic meiofauna samples from Punta Allen (Quintana Roo State, Mexico). The species was found in five out of six stations and in 10 out of 18 analysed replicates.

This is the first record of *L. incisa* in the western part of the Caribbean Sea, extending the known range westward by *c*. 3000 km with regard to the type locality, i.e. Hastings Reef in Barbados (Gooding, 1963), and by more than 2000 km with regard to Puerto Rico, the second locality where the species was reported (Sanders & Hessler, 1964).

Two-thirds (65.6%) of the specimens were adults and one-third (34.4%) were pre-adults belonging to different development stages. Some of the adults bore a single egg sac.

Microhabitat characterization

Collection dates, localities and standard abiotic variables measured in the field are listed in Table 1. No important differences were recorded between the different samples. Salinity (36.5 psu) and temperature of the overlying water ($31.2 \pm 0.5\,^{\circ}C$) were stable. The intertidal depth ranged between 0.5 and 1.5 m.

The vertical distribution of *L. incisa* in the sediment surrounding the three seagrass species is shown in Fig. 1. No preference for a specific seagrass species was found. A striking pattern of higher density at intermediate depth was observed with a maximum of five individuals/10 cm^2 at 4–5 cm depth in the *H. wrightii* samples. Additional data on sediment characteristics about the microhabitat the specimens were recovered from are given in Fig. 2.

The vertical distribution of *L. incisa* for the different seagrass species is shown in Figs 2 & 3 together with the abiotic variables for the corresponding depth layers.

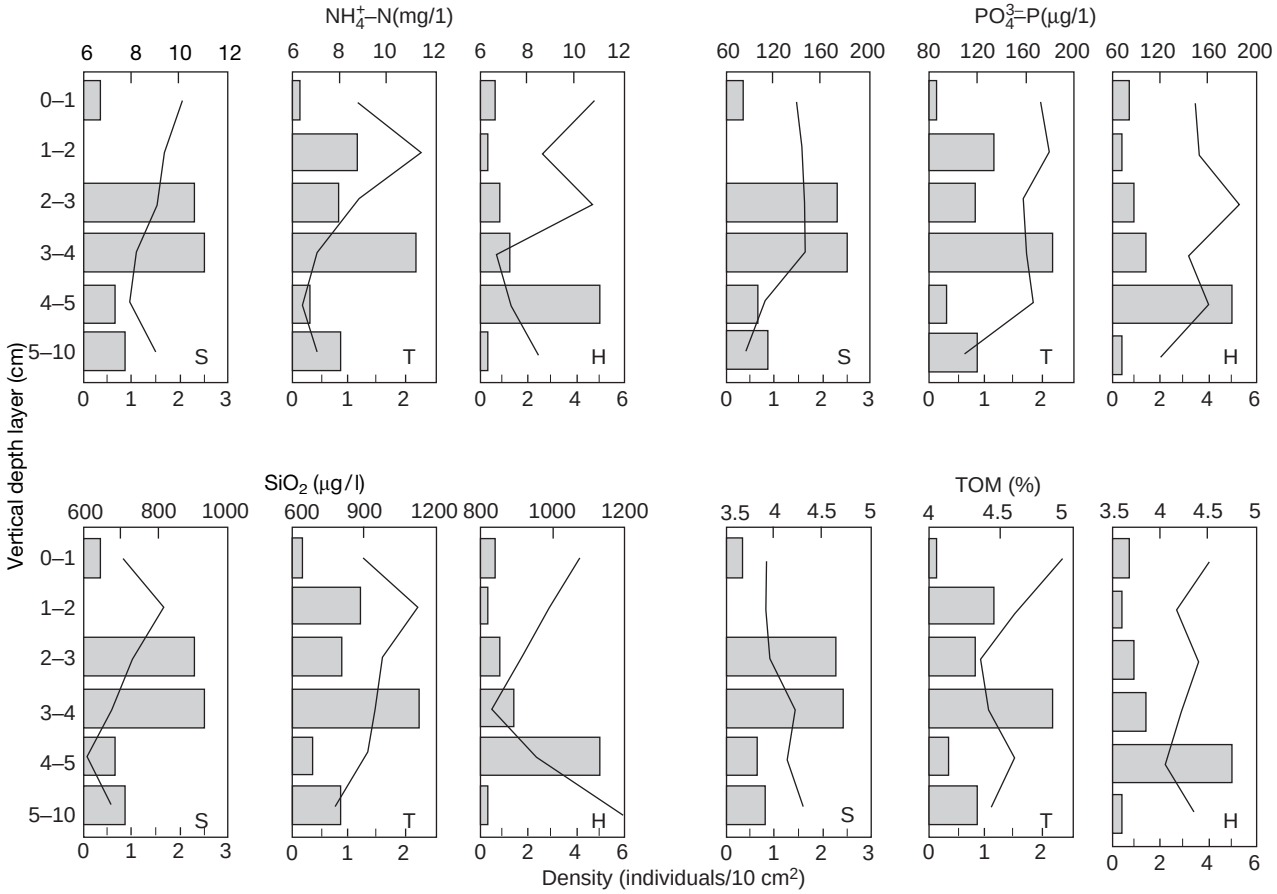

Fig. 3. Vertical distribution of *Lightiella incisa* (bars, bottom scale) and NH_4^+-N, SiO_2, $PO_4^{3-}-P$, TOM (lines, top scale) for three seagrass species: *Syringodium filiforme* (S), *Thalassia testudinum* (T), *Halodule wrightii* (H).

The main sediment characteristics (Fig. 2) are similar for the different seagrass species. The preferred median grain size was between 230 and 260 µm. The highest densities of cephalocarids in the *S. filiforme* corresponded to sediments with a low fraction of gravel in combination with 10–15% coarse sand. No clear preference was found in the *T. testudinum* and *H. wrightii* samples.

The distribution of *L. incisa* was strongly related to nitrite and nitrate concentrations (Fig. 2), suggesting that the species peaks in layers characterized by the lowest $NO_3^- - N$ concentration (< 60 µg/l $NO_3^- - N$) and an intermediate $NO_2^- - N$ concentration(< 15 µg/l for $NO_2^- - N$).

For ammonia (Fig. 3), a trend similar to that for $NO_3^- - N$ was found: a maximum density of *L. incisa* at the lowest concentration $NH_4^+ - N$ concentrations (< 10 mg/l $NH_4^+ - N$). The same was true for silicate (SiO_2), with highest *L. incisa* numbers at the lower concentrations, i.e. between 600 and 1000 µg/l. The opposite trend was found for phosphate: maximal densities corresponded to the highest $PO_4^{3-} - P$ concentrations (between 145 and 160 µg/l).

The data on total organic matter (% TOM, Fig. 3) showed only minor variation with depth, with a range from 3.9 to 4.5%. The maximum density of *L. incisa* was found at an intermediate value (4–4.5% TOM).

The pigments fucoxanthin (Fig. 4a) and chlorophyll *a* (Fig. 4b) showed a common pattern with high values in the top layer (0.6–1.1 µg/g fucoxanthin, 1.5–2.5 µg/g chlorophyll *a*) and a decrease with increasing depth (decreasing sunlight).

DISCUSSION

The number of specimens recovered from the seagrass bed sediments is low compared with overall meiofauna densities. However, when we recalculate the densities to individuals/m^2 (as was done for *Hutchinsoniella macracantha* by R. R. Hessler & Sanders, 1964), we find *L. incisa* to be quite important in this habitat, with densities up to several thousands per square metre. This high abundance and the presence of juveniles indicate that the species was found in its natural habitat.

Gooding (1963) and Sanders & Hessler (1964) found *L. incisa* in turtle seagrass beds at intertidal depths of 1–2.5 m. Our samples were taken in a shallow (0.5–2 m) and extensive intertidal and subtidal zones with dense seagrass beds between the coastline and a nearby coral reef.

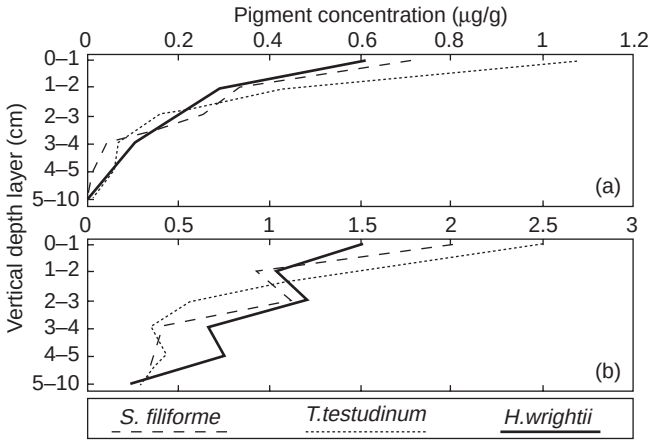

Fig. 4. Vertical distribution of pigments for the three seagrass species: (a) fucoxanthin, (b) chlorophyll *a*.

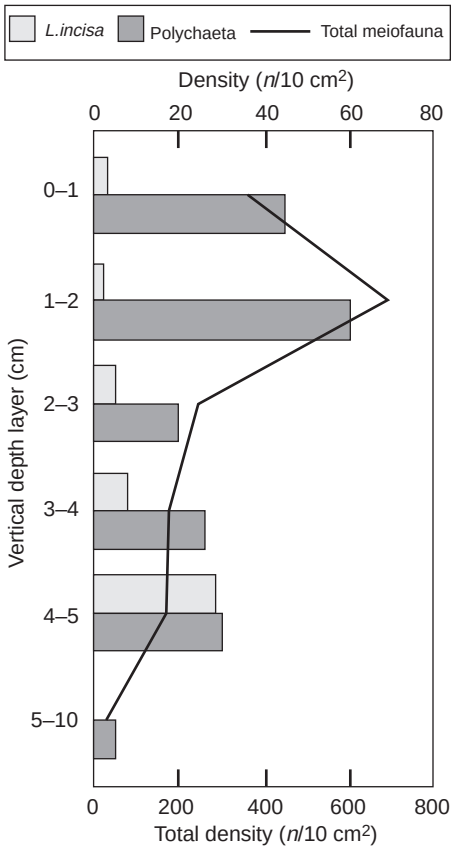

Fig. 5. Vertical distribution of *Lightiella incisa* (light grey bars, top scale), Polychaeta (dark grey bars, top scale) and total meiofauna densities (line, bottom scale).

Seagrass beds act as a 'sediment trap' that allows fine particles and low density matter to settle out of suspension and form a flocculent-like sediment (Sanders & Hessler, 1964). From a functional morphology study of *Hutchinsoniella*, Sanders (1963) stated that this cephalocarid is limited to those sediments having an organic, flocculent-like superficial layer, and that it is unlikely that cephalocarids could feed in any other substratum. The samples from the current study were taken in dense seagrass beds, which supports this statement, although this first detailed microhabitat description provides some interesting new views.

Our observations on the microdistribution of *L. incisa* do not tally with classic distribution patterns of meiofauna, having maximum densities in the top layers coinciding with the oxygenated part of the sediment column and with the highest concentrations of fresh organic matter. The measured nutrient values are an indirect indication for the redox potential discontinuity (RPD) layer. A pronounced decline in nutrients at 2 cm depth in the sediment was observed. *Lightiella incisa* seems to follow this pattern, showing its maximum densities below the RPD layer, i.e. under conditions of low oxygen concentration.

Three of the four specimens of *L. incisa* obtained by Gooding (1963) were from water aspirated from callianassid and thalassinid burrows. The fourth specimen was collected from surface silt. In his original description, Gooding (1963) stated that presence of *L. incisa* in crustacean burrows is probably insignificant. The limited material and the lack of juveniles led to the suggestion that the specimens represented strays from other environments (Gooding, 1963).

It has been amply demonstrated (e.g. Meyers, Fossing & Powell, 1987; Meyers, Powell & Fossing, 1988) that tubes of burrowing macrofauna can create oxygenated microhabitats in otherwise anoxic sediment layers, resulting in enhanced bacterial activity and increased meiofaunal densities (J. Y. Aller & Aller, 1986; Thomson & Altenbach, 1993).

In the present study, the occurrence of such oxygenated microenvironments was not supported by the distribution pattern of other meiofauna taxa in the same samples (M. De Troch, pers. obs.). Only Polychaeta seemed to be more abundant in these deeper layers (Fig. 5). Polychaeta and total meiofauna densities in a *H. wrightii* sample where the highest number of *L. incisa* was found are shown in Fig. 5. As in the other samples, it was clear that *L. incisa* seemed to follow Polychaeta to deeper sediment layers. In view of the size of *L. incisa*, between 2.0 and 2.6 mm, it is possible that the animal itself provides an oxygenated tube to live in. It is unclear why densities of other meiofauna taxa, as shown by the total meiofauna density (Fig. 5), dropped down to a minimum with increasing depth and did not use the oxygenated tubes.

Areas of steep gradients between oxygenated and sulphide layers are preferred habitats of rich bacterial stocks (R. C. Aller & Yingst, 1978). Whether *L. incisa* can feed directly on bacterial stock or on labile organic components from degradation of organic matter remains unknown, and more information on *L. incisa* feeding ecology is needed to understand its vertical distribution.

We can state that *L. incisa* seems to be an endobenthic species occupying anoxic sediments oxygenated by bioturbation rather than an animal living in the oxygenated

top layers. We think that the species does not belong to the real thiobios (characteristic group of animals from oxygen-free, reducing sediments rich in H_2S) (Fenchel, 1969; Ott, 1972), but *L. incisa* is probably a remnant of the oxibios (animals reliant to oxygen) living at its limits nearby oxygenated tubes.

Further detailed studies on the ecology of Cephalocarida in general are necessary. The indispensability of standardized measurements of oxygen and the RPD-layer must be recognized and integrated in future studies.

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