

N. L. Arroyo · M. Maldonado
R. Pérez-Portela · J. Benito

Distribution patterns of meiofauna associated with a sublittoral *Laminaria* bed in the Cantabrian Sea (north-eastern Atlantic)

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Abstract This study deals with meiofauna associated with a sublittoral population of the kelp *Laminaria ochroleuca* located on the northern coast of Spain. By sampling once a year over a 4-year period, we examined patterns of faunal distribution as a function of some environmental factors at the meso-scale level (depth, and exposure to waves and surge). We also examined the relationship between *L. ochroleuca* abundance (as dry weight biomass and number of plants per sampling quadrat) and abundance and diversity of meiofauna. Finally, we investigated patterns of within-plant distribution (algal frond vs. algal holdfast), using also the meiofauna of the adjacent bottom as a referent to estimate the level of “phytal dependence” of the meiofauna collected on *L. ochroleuca*. We found that the bulk of permanent meiofauna consisted of nematodes, copepods, mites, polychaetes, tanaids and ostracods, with copepods being predominant on the fronds of the alga and nematodes in the holdfasts. The temporary meiofauna consisted of juvenile amphipods, bivalves and gastropods, together with barnacle nauplii and cyprids. Abundance and major composition of meiofaunal taxa were unrelated to both depth and hydrodynamic exposure of the sampling quadrats. However, we detected

significant qualitative and quantitative faunal differences as a function of microhabitat. All meiofaunal groups were more abundant in holdfast samples than in frond and bottom samples. The gross taxonomic composition of meiofauna in bottom samples was similar to that in holdfast samples, but substantially different from that of meiofauna associated with the fronds. The *L. ochroleuca* holdfasts, in which dense aggregations of meiofauna can occur, appear to function as ecotone between phytal and rocky-bottom microhabitats. All together, our results suggest that the distribution of meiofauna within the *Laminaria* bed is mostly affected by factors operating at the microhabitat level rather than the meso-scale level.

Introduction

Diverse studies on sublittoral meiofauna associated with macroalgae suggest that the faunal abundance increases significantly with decreasing depth and increasing complexity in alga body shape. In the upper sublittoral zone, maximum abundance and diversity have been reported from shallow algal communities in sheltered areas, typically characterised by species with complex frond structure (Wieser 1952; Hicks 1980). In contrast, minimum values appear to occur in algal populations either established on very exposed shores or composed of species of simple morphology (Hicks 1985; Gibbons 1988a; Hull 1997).

It has been suggested that algae of small, simple fronds offer insufficient protection to most meiofaunal organisms against predation, desiccation and wave abrasion (Coull et al. 1983; Gibbons 1988b). Unlike complex fronds, simple algal forms are also inadequate substrata to accumulate both sediment and potential food for meiofaunal organisms (Whatley and Wall 1975; Hicks 1977a, 1980; Gibbons 1988a, 1988b; Edgar 1990; Hull 1997). Such a deficiency particularly prevents the establishment of many psammic organisms, which are an important component of the meiofauna associated with algae of complex morphology (Dahl 1948; Moore

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N. L. Arroyo (✉) · R. Pérez-Portela · J. Benito
Dpto. de Biología Animal (I), Facultad de Biología,
Universidad Complutense de Madrid,
28040 Madrid, Spain
E-mail: nhailuot@abo.fi
Fax: +358-2-2153428

M. Maldonado
Department of Aquatic Ecology,
Centro de Estudios Avanzados (CSIC),
17300 Blanes, Spain

Present address: N. L. Arroyo
Husö Biological Station Department of Biology,
Environmental and Marine Biology,
Åbo Akademi University,
20520 Åbo, Finland

1971, 1972a). The most accepted view is that the more complex the algal frond, the larger the available surface for colonization by meiofauna (Gunnill 1982a, 1982b, 1983; Gee and Warwick 1994a, 1994b), macroepifauna and epiphytic algae. The presence of the latter epibionts, in turn, will add further intricacy to the microhabitat structure, facilitating the development of meiofaunal communities (Moore 1971; Kangas 1978; Gunnill 1982b; Johnson and Scheibling 1987). Therefore, it is not surprising that several studies have reported that meiofaunal organisms tend to “aggregate” on algae of relatively complex morphology, on which they form richer and more diverse communities than those found on morphologically simpler species from the same geographical area (e.g. Hicks 1977a, 1980; Coull et al. 1983; Gee and Warwick 1994a, 1994b).

The initial view that phytal meiofauna abundance decreases with increasing depth within the sublittoral zone (e.g. Hicks 1985) probably favoured several decades of research focussed on the intertidal and the upper sublittoral zone. Additionally, the increasing complexity of the methods required with increasing depth has traditionally discouraged exhaustive investigations of meiofaunal assemblages associated with deep sublittoral algae. Here, we contribute to reduce this gap in knowledge by investigating the meiofauna associated with a sublittoral *Laminaria* bed, established between 5 and 20 m deep.

Several species of *Laminaria* are common in the intertidal and rocky subtidal bottoms of many temperate seas, forming either dense mono-specific aggregations or patchy communities along with other organisms (Seoane-Camba 1966; John 1969; Kain 1979). Laminarians are usually large algae. Most species possess a complex system of haptera (the holdfast) for attachment to the substratum. A variously long stalk emerges from the holdfast, bearing distally a relatively extended, flat frond. Therefore, from a morphological point of view, several levels of complexity occur within each plant, making laminarians potentially suitable substrata to host meiofauna. One of the earliest approaches to the meiofauna of laminarians goes back to Colman (1940), who examined and identified the meiofauna of six holdfasts, one frond and one stalk of *L. digitata* (Hudson) Lamouroux, as part of a broader study on phytal communities. In a similar way, several subsequent studies, mostly concerned with macrofauna, have included diverse pieces of information on laminarian meiofauna (Velmirov et al. 1977; Allen and Griffiths 1981; Tzvetlin et al. 1997). One of the earliest studies specifically addressed to phytal meiofauna was published by Hicks (1980), who exclusively investigated the copepods associated with the fronds of *L. digitata*, disregarding the holdfasts. He found relatively low abundances and species numbers compared to other algae from the same area and attributed this finding to the comparatively low micro-spatial complexity provided by the *Laminaria* fronds. Conversely, a study series by Moore

(1971, 1972a, 1972b, 1973, 1978) focussed on the total meiofauna from the holdfasts of *L. hyperborea* (Gunnerus) Foslie, disregarding the fronds. Nevertheless, Moore gave an unprecedented ecological dimension to his approach, investigating the effects of holdfast exposure to waves and on the meiofauna surge. He concluded that these factors affected the meiofauna whenever the quality and quantity of the sediment retained by the holdfast were also affected. After Moore's works, the meiofauna occurring on large macrophytes and on the adjacent bottom has rarely been quantitatively compared (Norton 1971; Sheppard 1976). Yet several recent studies suggest that these latter substrata may function as relevant sources of migrating organisms, enhancing maintenance of phytal meiofaunal communities (Edgar 1983b; Gibbons and Griffiths 1986; Somerfield and Jeal 1996; Atilla and Fleeger 2000). The scarcity of quantitative ecological data in this regard prevents a clear understanding of the dynamics of such meiofaunal communities.

In summary, despite the preliminary evidence that the study of laminarian algae may provide a substantial contribution to current knowledge on the taxonomy and ecology of phytal meiofauna, this meiofaunal habitat has received comparatively little research attention. More importantly, the available information is clearly biased towards the taxonomic approach, quantitative ecological data being scarce. As a consequence, some basic questions, such as the magnitude of differences in taxonomic composition and abundance distribution of meiofaunal groups between both algae belonging to the same population and parts of an alga, remain to be addressed.

From 1996 to 1999, a series of research projects was conducted to characterise the benthic assemblages surrounding the Island of Mouro in the Bay of Biscay (Cantabrian Sea, Spain), in an attempt to obtain scientific information to vindicate the status as a protected marine area for these bottoms. Initial results of these surveys suggested that the spatial distribution of the macrofauna associated with *L. ochroleuca* was affected by meso-scale environmental factors, such as bottom morphology, exposure to waves and surge, and depth of the sampling locations (García-Castrillo et al. 2000b). Interestingly, many of these macrobenthic organisms also showed a consistent preference to occupy a particular microhabitat within each *Laminaria* alga, regardless of the position of the alga within the bed (García-Castrillo et al. 2000b). Several studies involving macrofauna associated with other laminarian species have revealed similar patterns (Norton 1971; McKenzie and Moore 1981; Schültze et al. 1990). The prediction is that animals included in the meiobenthic size range (62 µm–1 mm) are likely to be affected differently than macrofauna by environmental factors that operate at a meso-scale level (Gibbons and Griffiths 1986), as a consequence of body size differences. Likewise, factors controlling within-plant distribution of meiofauna and those controlling the within-plant distribution of macroinvertebrates are likely to be different (Edgar 1983a; Gee and Warwick 1994a, 1994b).

Here we describe the meiofauna associated with a population of *L. ochroleuca* and investigate the faunal distribution as a function of both meso-scale factors (depth, exposure to waves and surge) and micro-scale factors (within-alga microhabitat, substratum type).

Materials and methods

Study site

We investigated a *Laminaria ochroleuca* population established around Mouro Island (Fig. 1; 43°28'24"N; 3°45'22"W; Bay of Santander, north coast of Spain). The island is a 200-m-long rocky outcrop located about 1 km offshore, emerging from a submerged rocky shelf that extends up to a maximum depth of 25 m. Most of the rocky bottom is covered by the encrusting coralline alga *Mesophyllum lichenoides* (Ellis) Lemoine. The individuals of *L. ochroleuca* attach to either the bare rock or the *M. lichenoides* crusts. Various amounts of sediment accumulate between successive growth layers of *M. lichenoides* and between these and the rhizomes of *L. ochroleuca*, depending on substratum orientation. A detailed description of bottom topography and algal communities in the area is given elsewhere (Garcia-Castrillo et al. 2000a, 2000b; Puente 2000).

The host alga

At Mouro Island, *L. ochroleuca* showed a relatively homogeneous distribution, though slightly more abundant in the exposed areas of the island. It was consistently found on the top of boulders or

rocky surfaces, presenting the greatest abundance in the 10–15 m depth range. After the first 2 years of study, the population of *L. ochroleuca* experienced an unexplained, drastic decline, which initially affected only the vitality of fronds but ended in a substantial mortality of plants, its status changing from being the dominant macrophyte to presenting only scattered plants, with poorly developed fronds and small holdfasts.

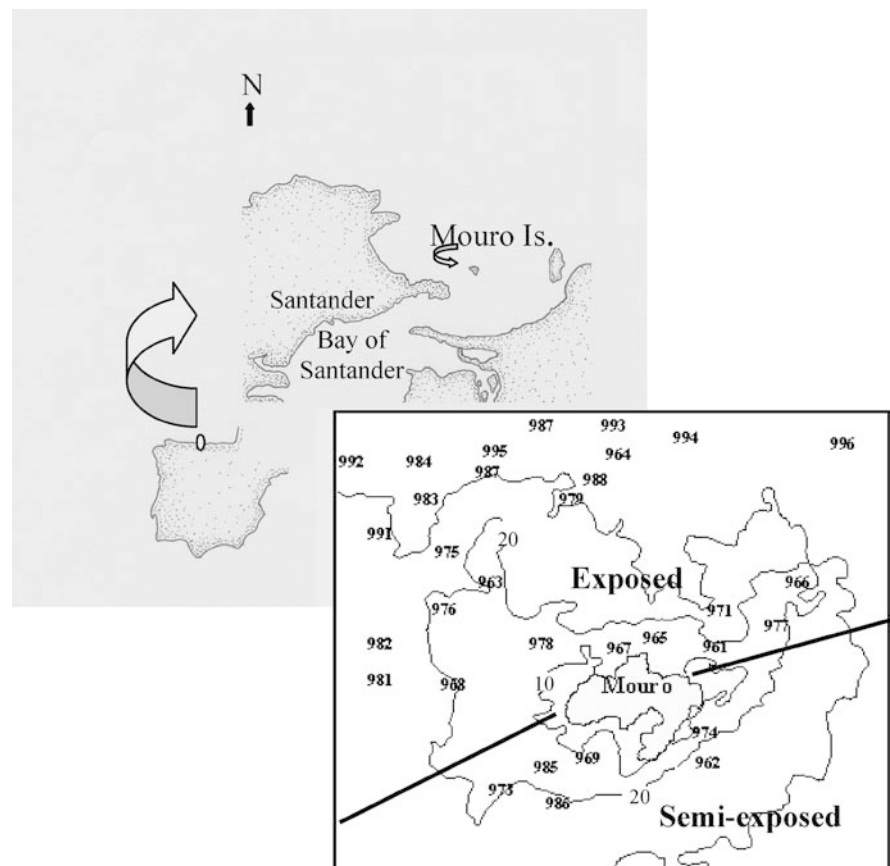
The mean density in the years in which the population showed a healthy appearance was ca. 12 plants m⁻², with a maximum density of 18 plants m⁻². In subsequent years, following algal decline, mean density was reduced, reaching an average of ca. 5 plants m⁻² in 1999.

L. ochroleuca shows the typical morphology of other species in the digitate section of the genus, that is, a wide, digitate lamina (the frond), a long, erect stipe and a complex system of haptera by which the alga attaches to the substrata (the holdfast). Unlike *L. hyperborea*, the rugose stipe of which favours settlement of numerous epiphytes, *L. ochroleuca* has a very smooth stipe, virtually lacking epiphytes. Nevertheless, the holdfast usually harbours a dense assemblage of epiphytes, typically sub-canopy algae, barnacles, sponges and other sessile macrofauna. The fronds may be colonised by a few species of bryozoans or hydrozoans and grazed by the gastropod *Patina pellucida* (L.), which occasionally feed on the lower portions of the alga as well (Braud 1974).

Collection and preservation procedures

The *Laminaria* bed was sampled by SCUBA once a year over a 4-year period (1996–1999). We sampled during July–August in 1996, May in 1997, July–August in 1998 and May–June in 1999. Between-year variability in sampling date was due to weather conditions, as underwater work was conducted in a high-risk diving zone. Sampling sites were selected at random on the island

Fig. 1 Location of the study area. Framed plot indicates the two areas of different exposure to waves and surge, and the position of samples during the 4 years of study. First two digits indicate sampling year and third digit stands for sample number



shelf, and their positions were identified by using a portable Magellan GPS (Fig. 1). At each sampling site, we recorded diving depth by using an ALADIN PRO diving computer, then corrected depth according to local tidal tables to average the effect of tidal oscillations. At each site, we sampled two different substrata. First, we marked 0.5×0.5 m quadrats and collected all individuals of *L. ochroleuca* in each quadrat, storing holdfasts and fronds separately in plastic bags. Then, we scraped a 0.25×0.25 m bottom area within each quadrat to collect whatever potential substratum for meiofauna occurred, i.e. the sediment veneer, the crusts of *Mesophyllum*, the soft algal canopy and the biofilm. All the elements of each bottom sample were stored together in a plastic bag.

During the first 2 years of study (1996 and 1997), we collected nine samples a year. In subsequent years, due to the decline in the *L. ochroleuca* population, only eight quadrats contained *L. ochroleuca* in 1998 and six in 1999 (Fig. 1).

Once in the laboratory, samples (including *L. ochroleuca* tissue, their associated fauna and the sediment retained among the rhizomes) were wet-weighed, then frozen until subsequent faunal extraction. Macrofaunal organisms were picked out by using forceps under a binocular microscope. Then, we sieved *L. ochroleuca* and bottom samples through 1-mm and 62- μ m meshes, collecting the animals retained and preserving them in 4% buffered formalin with rose-bengal until taxonomic study. For samples containing important amounts of sediment or debris, we used an alternative method to isolate the meiofauna. Such samples were suspended in Ludox (colloidal silica polymer, density 1.15) and, after a 40-min settlement period, the supernatant fraction was filtered through a 62- μ m mesh. The sediment was then re-suspended in Ludox, and the whole process was repeated three times. During each round, we examined sub-samples of sediment to determine whether or not the meiofauna had been extracted appropriately. We realised that the efficiency of this separation method was still low for ostracods, bivalves and gastropods. Therefore, in samples in which these taxa prevailed, the organisms were extracted manually under a binocular microscope. These latter groups were preserved in 70% alcohol until taxonomic study.

For the taxonomic study, we considered all meiobenthic organisms, except Protozoa, classifying them at fairly high taxonomic levels. Organisms were also assigned to the category of either temporary (organisms only transitorily in the meiofauna, such as developmental macrofaunal stages, etc.; sensu McIntyre 1969) or permanent (usually consisting of adult life-cycle stages) meiofauna. Because we sampled in different seasons each year and this may have had an effect on the abundance of temporary meiofauna, only the permanent meiofauna was considered for the ecological analyses.

Effects of depth on meiofauna

We investigated potential effects of depth on the abundance of meiofauna by examining the correlation (Pearson product moment correlation coefficient) between depth of each sampling quadrat and number of organisms in the quadrat.

We also examined potential differences in meiofaunal community structure as a function of depth by means of multivariate techniques. Faunal affinity based on permanent meiofaunal taxa was calculated between samples by Bray–Curtis distances on fourth-root transformed data. Matrices of pairwise faunal distances were then processed by applying non-metric multidimensional scaling (NMDS). Samples were assigned to a depth rank (6–10 m = 1, 11–15 m = 2 and 16–20 m = 3), and this factor was used as a label for the different samples. Significance tests for predicted differences in the distribution of taxa according to these depth ranks were performed using the ANOSIM permutation test (Clarke 1993).

Preliminary analyses detected no between-year differences in abundance or community structure of meiofauna per sampling quadrat (Arroyo 2002); hence, samples from all years ($n=32$) were pooled for these analyses.

Effects of surge on meiofauna

The prevailing direction of waves approaching Mouro Island is N–NE. According to wave regime (height and frequency of the waves provided by the Asheville National Climatic Data Center, N.C., USA) and island topography (García-Castrillo et al. 2000a), most of the bottom surrounding the island is clearly exposed to surge. Nevertheless, the E–SW sector, located on the lee side, can be considered semi-exposed (Fig. 1).

We investigated differences in the abundance of both *L. ochroleuca* and its associated meiofauna as a function of the hydrodynamic exposure (exposed vs. semi-exposed) of sampling site. Patches of *L. ochroleuca* were more abundant at the exposed side of the island, which was sampled more intensively ($N_{\text{exposed}} = 14$ quadrats) than the semi-exposed side ($N_{\text{semi-exposed}} = 4$). Because the population of *L. ochroleuca* experienced epidemic mortality during the last 2 years of study, the analysis only involved data from the first 2 years (1996 and 1997). This analysis included samples from all the depth ranges mentioned above (5–20 m), under the assumption that the magnitude of the effect of depth on exposure may be considered negligible when compared with that between the lee and the exposed side of Mouro Island.

In these conditions, we examined differences in *L. ochroleuca* biomass (dry weight) per sampling quadrat as a function of exposure to surge by using the unpaired *t*-test after confirming that data met the assumptions of normality and homoscedasticity. We also examined differences in the distribution of taxonomic abundance of meiofauna as a function of exposure to surge by using ordination techniques. First, we conducted classification analyses of exposed and semi-exposed sampling quadrats using as descriptors fourth-root transformed abundance data of the most relevant meiofaunal groups. Pairwise faunistic similarities between quadrats were calculated by using the Bray–Curtis similarity index. Similarity matrices were submitted to an NMDS analysis, and the output was plotted in bi-dimensional space. A gross significance test for the level of faunal similarity detected between the two predicted areas of exposure was performed by using the ANOSIM permutation test. We also examined potential differences in mean abundance (number of individuals per sampling quadrat) of meiofauna as a function of hydrodynamic exposure of sampling site. Analyses were made for abundance values of total meiofauna, as well as for the major meiobenthic groups ($N_{\text{exposed}} = 14$, $N_{\text{semi-exposed}} = 4$). We used the *t*-test for parametric data sets and the Mann–Whitney *U*-test for data that did not fit the parametric model after transformation.

Effect of algal biomass on meiofauna

We investigated the relationship between *L. ochroleuca* biomass and meiofaunal abundance. Algal biomass was estimated as dry weight (65°C for 48 h in a drying oven) of *L. ochroleuca* per sampling quadrat, also considering separately holdfast and frond values per quadrat for some analyses. Meiofaunal abundance was estimated as the number of individuals per sampling quadrat. Additionally, we examined the relationship between *L. ochroleuca* biomass and meiofaunal diversity per sampling quadrat and algal tissue fraction (holdfast vs. frond) by using Pearson product moment correlation. Different estimates of faunal diversity were considered, such as the number of taxa, the Shannon–Wiener diversity index (H' , log base 2), and its evenness component (J), calculating their values for frond and holdfast samples separately. We also examined the correlation between the number of *L. ochroleuca* individuals per quadrat and abundance of meiofauna per quadrat, as well as between the former and meiofaunal diversity per sampling quadrat. A methodological mistake in sample labelling and storage caused a loss of data on holdfast and frond biomass per quadrat, as well as on number of algal individuals per quadrat for all quadrats collected in 1996 and half of those collected in 1997. Therefore, a total of just 18 quadrats ($N=4$ in 1997, $N=8$ in 1998, $N=6$ in 1999) was used for these analyses.

Within-plant distribution of meiofauna

We investigated differences in gross taxonomic composition and abundance of meiofauna as a function of within-alga microhabitat (frond vs. holdfast). Due to significant between-year differences in frond–meiofauna abundance and community structure (Arroyo 2002), analyses were run separately for each of the study years. The faunal affinity between frond and holdfast samples was evaluated by an ordination approach. First, we used the Bray–Curtis similarity index to calculate pairwise faunal similarities between holdfast and frond samples. The index was applied to fourth-root transformed data of numerical abundance per plant fraction and quadrat for each of the most relevant meiofaunal groups. The similarity matrix was then submitted to a NMDS analysis, and the output was plotted in bi-dimensional space. A one-way ANOSIM was used as a gross significance test for predicted differences between fractions in each of the 4 years of study.

We also investigated differences in mean meiofaunal abundance (number of individuals per quadrat) as a function of algal tissue fraction (holdfast vs. frond) in each of the 4 years. These analyses were run separately for total meiofauna and for each of the major taxa. Comparisons of mean abundances were made by using the Mann–Whitney *U*-test, due to non-compliance of the data with parametric assumptions. Due to the high number of comparisons involved in these analyses, the sequential Bonferroni procedure for adjusting significance levels was used in order to control the type I error rate (Quinn and Keough 2002).

Effects of algal epibiosis on meiofauna

We examined the hypothesis that the heavier the epiphytic load on *L. ochroleuca* the richer its associated meiofauna. Given that the *L. ochroleuca* population experienced a drastic decline in 1998 and 1999 and that the presence of epibionts on the algal fronds is extremely rare, we constrained this test to involve just the meiofauna found on the holdfasts collected during the first 2 years of study (1996–1997). First, we identified the main epiphytes associated with the holdfasts of all samples. Then, we obtained dry weight values for both total epibionts and each major epiphytic taxa in each sampling quadrat ($N=18$). We examined the relationship between weight of epibionts and numerical abundance of each major meiofaunal group by using the Pearson product moment correlation coefficient. We also examined the correlation between the abundance of each major meiobenthic taxon and the biomass of each of the most abundant epiphytic organisms. All data were $\log(n+1)$ transformed prior to analysis.

Substratum specificity of phytal meiofauna

To investigate substratum specificity of meiofauna associated with *L. ochroleuca*, we examined the faunal similarity among three different substrata on which meiofauna was collected: fronds and holdfasts of *L. ochroleuca*, and the underlying bottom. This latter substratum consists of a heterogeneous mix of elements, including a thin veneer of unclassified debris and sediment, hard fragments of *M. lichenoides*, the bacterial biofilm and the filamentous algal canopy that covers the rocks.

We conducted a joint classification analysis of holdfasts ($N=32$), fronds ($N=28$) and bottom samples ($N=21$) using as descriptors the presence–absence of the major meiofaunal groups in each sample during the 4 years of study. Pairwise faunal similarities between substratum samples were obtained by using the Sørensen similarity index. The resulting similarity matrix was then processed by the un-weighted arithmetic average algorithm of clustering to produce a hierarchical dendrogram. We also performed ordination by submitting the similarity matrix to NMDS analysis and plotting the output in bi-dimensional space. The ANOSIM permutation test was used as a gross significance test for predicted levels of faunal similarity between substrata. Utilisation of presence–absence data

allowed comparisons considering samples from the 4 years of study, since quantitative differences between years and differences due to variation in sample size were obviated by this procedure.

Results

Taxonomic composition

We collected a total of ca. 172,000 individuals belonging to 12 phyla, including permanent and temporary meiofauna (Table 1). Permanent meiofauna accounted for 79% of total organisms, while temporary meiofauna represented 21%. Mean density of total meiofauna per quadrat was $4,895.45 \pm 4,774.3$ individuals, which means about 10,000 organisms m^{-2} of *Laminaria ochroleuca* bed.

Of the major meiofaunal taxa, nematodes were the most abundant group (52%), followed by copepods (29%) and polychaetes (15%). Other relevant groups were mites (2%), ostracods (1%) and tanaids (1%). For the temporary forms, barnacle nauplii dominated in abundance (65%), followed by polychaete posttrochophoran stages (11%), and juveniles of bivalves (8%) and gastropods (5%).

Effects of depth on meiofauna

There was no significant association between depth and abundance values of meiofauna (Pearson correlation, $P>0.05$). The ANOSIM test did not detect significant differences in the level of faunal similarity between samples from the different ranks of depth ($R=-0.001$, $P>0.05$; Fig. 2).

Effects of surge on meiofauna

We found no significant difference in the mean biomass of *L. ochroleuca* per sampling quadrat between hydrodynamically exposed and semi-exposed sampling sites ($t=-1.075$, $df=16$, $P>0.05$). The ANOSIM test did not show significant differences ($R=0.169$, $P>0.05$) in the level of faunal similarity between samples from the exposed and the semi-exposed areas. The ordination analyses based on permanent meiofauna (Fig. 3) show that samples were grouped irrespective of sampling year and exposure factor. Similarly, no significant differences were found in mean abundance of each major meiofaunal taxon between exposed and semi-exposed quadrats ($P>0.05$).

Effect of algal biomass on meiofauna

The abundance of meiofauna showed significant positive correlation with frond biomass ($r^2=0.69$, $P<0.001$). However, no significant association was found between

Table 1 Meiofauna associated with *Laminaria ochroleuca* at Mouro Island. Abundance values are mean number of individuals per sampling quadrat (2,500 cm² for frond and holdfast, 625 cm² for the substrate), pooled for the 4 years of study. Number of taxa, Shannon–Wiener diversity and evenness values are represented as the mean and standard deviation (N number of quadrats on which the above estimates of faunal diversity were calculated)

Taxa	Frond	Holdfast	Substrate
Acari	7	81	30
Amphipods	8	53	17
Bivalves	10	79	60
Caprellids	2	13	6
Cirripedes		20	
Cyprids	4	34	4
Copepods	97	1,066	205
Cumaceans		1	1
Entoprocts		2	9
Gastropods	3	50	81
Insects		1	1
Isopods	1	1	6
Nauplii	29	732	104
Nematodes	59	1,967	301
Oligochaetes		1	1
Ostracods	18	33	19
Picnogonids	1	1	2
Picnogonid larvae		1	1
Polyplacophorans		1	3
Polychaetes	40	547	280
Polychaete larvae		123	186
Sipunculans	1	3	2
Tanaids	2	42	13
Tardigrades		2	2
Total	279	5,089	1,134
Number of taxa	8.4 ± 3.39	13.9 ± 3.14	12.71 ± 2.64
Diversity [$H'(\log^2)$]	2 ± 0.69	2.13 ± 0.29	2.44 ± 0.28
Evenness (J)	0.56 ± 0.07	0.56 ± 0.07	0.67 ± 0.07
N	28	32	31

abundance of meiofauna and holdfast biomass ($r^2 = 0.09$; $P > 0.05$).

Data on mean number of taxa, diversity, evenness of meiofauna per quadrat and per plant fraction (frond vs. holdfast) are summarised in Table 1. The number of taxa found on fronds and holdfasts, respectively, correlated with the biomass of *L. ochroleuca* in each of the plant fractions ($r^2_{\text{fronds}} = 0.51$, $P < 0.01$; $r^2_{\text{holdfasts}} = 0.39$, $P < 0.01$). In contrast, for meiofauna, the Shannon–

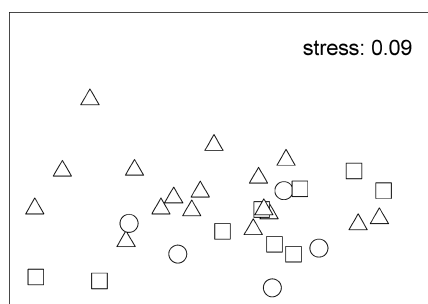


Fig. 2 Non-metric multidimensional scaling (NMDS) ordination of the samples of the 4 years using abundance data of permanent meiofauna and the Bray–Curtis similarity index. Symbols indicate the depth rank in which each sample was located (circles 6–10 m; squares 11–15 m; triangles 16–20 m)

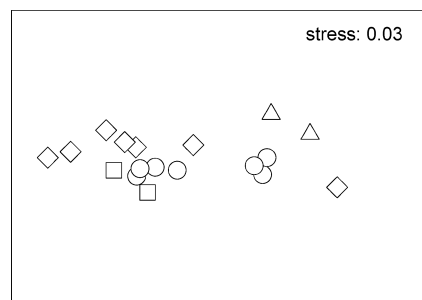


Fig. 3 NMDS ordination of samples from 1996 and 1997 using abundance data of permanent meiofauna. In the ordination space, circles and squares refer to 1996 exposed and semi-exposed locations, respectively, and diamonds and triangles refer to 1997 exposed and semi-exposed locations, respectively

Wiener diversity index did not correlate with biomass values of any algal fraction ($r^2_{\text{fronds}} = 0.18$, $P > 0.05$; $r^2_{\text{holdfasts}} = 0.12$, $P > 0.05$).

The number of *L. ochroleuca* individuals per quadrat did not correlate with abundance of meiofauna ($r^2 = 0.074$, $P > 0.05$). Neither, did it correlate with number of meiobenthic taxa ($r^2_{\text{fronds}} = 0.064$, $P > 0.05$; $r^2_{\text{holdfasts}} = 0.0006$, $P > 0.05$), or Shannon–Wiener diversity ($r^2_{\text{fronds}} = 0.034$, $P > 0.05$; $r^2_{\text{holdfasts}} = 0.0125$, $P > 0.05$).

Within-plant distribution of meiofauna

The algal holdfasts consistently hosted higher abundance of meiofauna than the fronds. All permanent taxa were significantly more abundant on holdfasts than on fronds in the 4 years of study (Tables 1, 2; Figs. 4, 5), with some groups showing only occasional presence in frond samples. Barnacles, cumaceans, entoprocts, insect larvae, oligochaetes, picnogonid larvae, polyplacophorans, polychaete larvae and tardigrades were exclusive to the holdfasts.

The taxonomic analysis of the permanent meiofauna on fronds indicated that copepods were the most abundant organisms (45%), followed by nematodes (25%), polychaetes (18%), ostracods (8%), mites (3%) and tanaids (1%). On the holdfasts, nematodes predominated (53%), followed by copepods (28%), polychaetes (15%), mites (2%), ostracods (1%) and tanaids (1%).

The results of the one-way ANOSIM for each of the 4 years clearly corroborate the above-mentioned faunal differences, indicating differences in community structure between frond and holdfast samples, in the 4 years of study (Fig. 5).

Effect of algal epibiosis on meiofauna

Mean dry-weight values of epiphytes per sampling quadrat (Fig. 6A) represent a moderate percentage of the total phytal weight per quadrat. The most abundant

Table 2 Results of Mann–Whitney *U*-tests for differences between frond and holdfast meiofaunal abundances in the 4 years of study. The original significance values are provided. All values were significant after adjustment using the Bonferroni correcting procedure

Taxa	1996 (<i>n</i> =9)	1997 (<i>n</i> =9)	1998 (<i>n</i> =8)	1999 (<i>n</i> =6)
Mites	$Z = -3.223, P = 0.001$	$Z = -3.593, P < 0.001$	$Z = -3.451, P = 0.001$	$Z = -2.989, P = 0.003$
Copepods	$Z = -2.605, P = 0.009$	$Z = -2.341, P = 0.019$	$Z = -3.371, P = 0.001$	$Z = -2.882, P = 0.004$
Nematodes	$Z = -3.401, P = 0.001$	$Z = -3.400, P = 0.001$	$Z = -3.451, P = 0.001$	$Z = -2.908, P = 0.004$
Polychaetes	$Z = -3.488, P < 0.001$	$Z = -3.576, P < 0.001$	$Z = -3.590, P < 0.001$	$Z = -2.908, P = 0.004$
Total	$Z = -3.311, P = 0.001$	$Z = -3.4, P = 0.001$	$Z = -3.386, P = 0.001$	$Z = -2.882, P = 0.004$

epibionts were four species of algae (Fig. 6B), *Cryptopleura ramosa* (Hudson) Kylin ex Newton, *Plocamium cartilagineum* (Linnaeus) Dixon, *Pterosiphonia complanata* (Clemente) Falkenb. and *Rhodymenia pseudopalmeta* (Lamoroux) P. Silva.

Neither total meiofauna abundance nor that of any of the major groups was correlated with biomass of total epiphytes. In contrast, correlation analyses considering each epiphyte separately revealed a weak negative correlation (not shown) between abundance of copepods and ostracods and biomass of *C. ramosa* (Pearson: $r^2 = 0.40, P < 0.05$ and $r^2 = 0.30, P < 0.05$, respectively). The abundance of the remaining taxa and that of total

meiofauna did not correlate with the biomass of any epiphyte.

Substratum specificity of phytal meiofauna

Classification and ordination analyses (Fig. 7) consistently detected higher faunal affinities between holdfast and bottom samples than between bottom and frond samples. In consistency with these results, the ANOSIM test detected significant faunal differences between frond and holdfast samples ($R = 0.252, P < 0.01$) and between frond and bottom samples ($R = 0.073, P < 0.05$), but not between holdfast and bottom samples ($R = -0.002, P > 0.05$). The analysis of relative abundances shows that nematodes (36%) are the predominant permanent taxon in bottom samples, followed by polychaetes (33%) and copepods (24%). Mites (4%), ostracods (2%) and tanaisids (1%) were clearly less abundant in bottom samples than in *L. ochroleuca* samples (Fig. 4), particularly regarding the holdfasts. Among the temporary meiofauna, barnacle nauplii (30%) dominated in bottom samples, followed by juvenile gastropods (26%), polychaete larvae (19%), juvenile bivalves (18%), gammaridean (6%) and caprellid amphipods (1%).

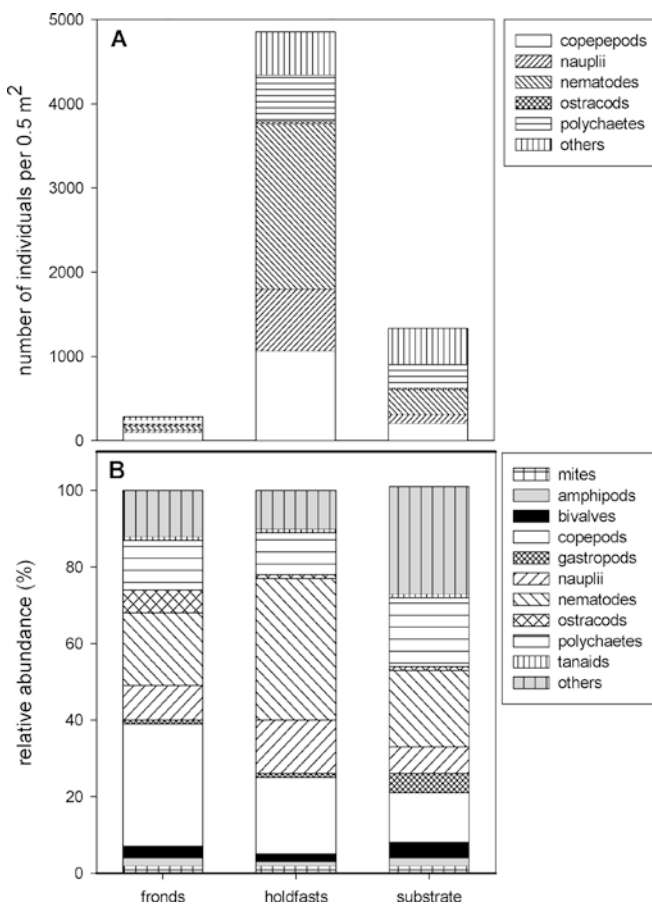


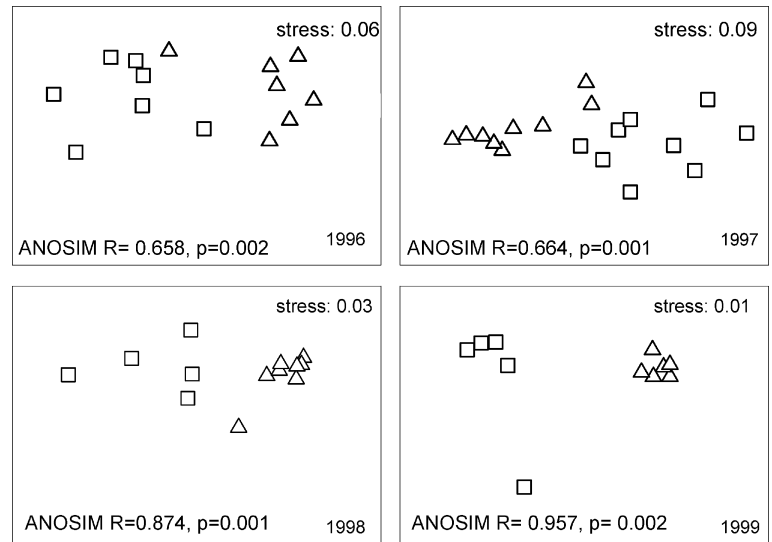
Fig. 4 Mean abundance (A) and relative (% of mean) abundance (B) of meiofauna per sampling quadrat in the different substrata considered (algal fronds, algal holdfasts and adjacent bottom substrate) during the 4 years of study

Discussion

Taxonomic distribution of meiofaunal abundance

The total meiofauna associated with *Laminaria ochroleuca* at Mouro Island shows somewhat lower abundance values per surface unit than those reported from studies on meiofauna associated with other macroalgae (Colman 1940; Hagerman 1966; Gibbons and Griffiths 1986; Johnson and Scheibling 1987). Copepods dominated the fronds and nematodes the holdfasts, which is a pattern similar to that found in other macrophytes (Hagerman 1966; Moore 1972a; Sarma and Ganapati 1972; Pallares and Hall 1974; Hicks 1977a, 1977b; Novak 1982; Jarvis and Seed 1996; De Troch et al. 2001). The meiofauna of *L. ochroleuca* rhizome samples consists of a heterogeneous mix of phytal and psammic organisms, the latter ones favoured by the occurrence of sand grains and debris attached to the algal rhizomes. A mix of phytal and psammic meiofauna has also been described in the basal-most portion of other macroalgae (Hagerman 1966; Moore 1972a, 1972b; Sarma and Ganapati 1972;

Fig. 5 NMDS ordinations of frond (*squares*) and holdfast (*triangles*) samples using the abundance values of major meiofaunal taxa collected in each of the 4 years of study



Hicks 1977b; Novak 1982; De Troch et al. 2001). The meiofauna of fronds appears to be relatively unrelated to that of rhizome and bottom samples. This pattern is also consistent with the results of several studies on algae and seagrasses, in which many of the copepods dominating the fronds were found to possess special adaptations to live on these flat, undulating substrata and cope with the abundant mucilagenous secretions produced by frond cells (Hicks and Grahame 1979; Hicks 1980, 1985; Bell et al. 1987). It is noteworthy that meiobenthic polychaetes were unexpectedly abundant on the fronds (Fig. 4), as this group has usually been described in association with *Laminaria* rhizomes and bottom samples (Colman 1940; Moore 1973). Polychaetes were also very abundant in our holdfast samples.

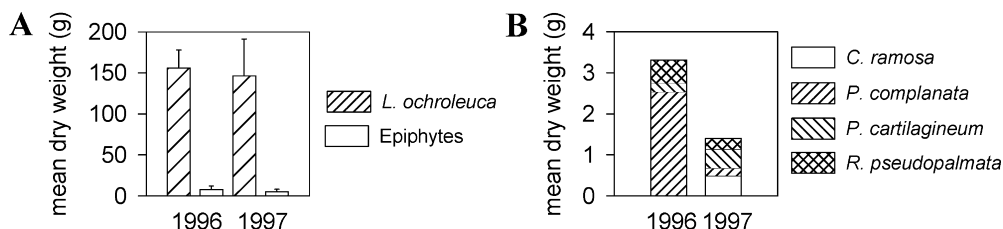
Tanaids and halacarid mites were secondary groups in terms of numerical abundance, usually occurring in holdfast samples. Tanaids have been described in association with the sediment trapped by *L. digitata* tissues (Colman 1940), while mites occur in association with very specific microhabitats within plants (Colman 1940; Pugh and King 1985; Somerfield and Jeal 1996).

A distinctive feature of the meiofauna found on *L. ochroleuca* is the low density of ostracods, a group usually abundant on other macrophytes (Hagerman

1966; Kangas 1978; Hull 1997), including holdfast samples of other *Laminaria* species (Whatley and Wall 1975). A study by Colman (1940) on *L. digitata* also showed an uncommonly low abundance of ostracods. According to some studies, these animals are rare on hydrodynamically exposed shores, where they aggregate on finely branching or filamentous algae (Hagerman 1966; Whatley and Wall 1975; Kangas 1978; Gibbons 1988b; Hull 1997). The absence of these algal morphologies in the studied area and the severe surge around Mouro Island may explain the scarcity of ostracods in our samples.

As part of the temporary meiofauna, the amphipods were one of the most abundant groups. Similarly high abundance has been reported in other phytal studies (Fenwick 1976; Moore 1978), in which benthic amphipods were found in close association with the algal tissue, with sessile invertebrates that colonise the holdfasts, and within tubes built with the sediment attached to the algal rhizomes (Fenwick 1976). Nauplii were also abundant members of the temporary meiofauna. Most collected nauplii belonged to *Verruca stroemia* O.F. Müller, as did the cyprids. Copepod and ostracod nauplii were also collected, but in much lower abundance than nauplii of Cirripedia.

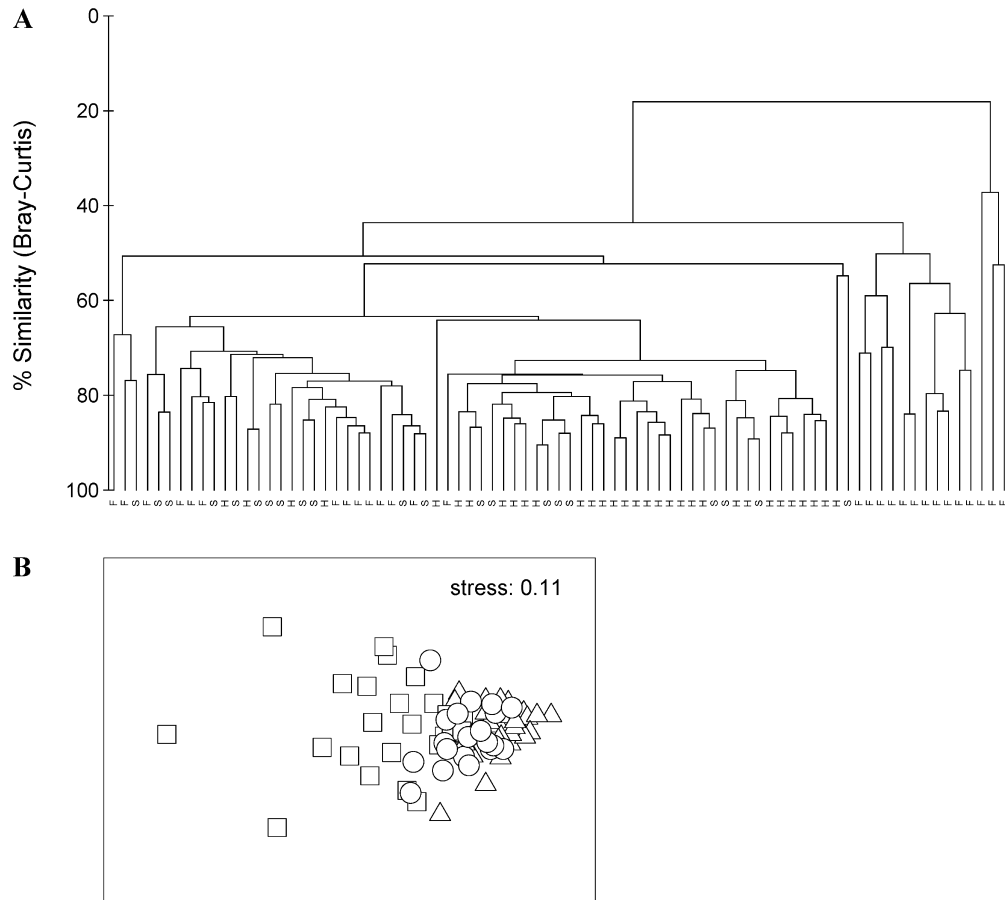
Fig. 6 A Biomass (dry weight) of *Laminaria ochroleuca* and its epiphytes in 1996 and 1997 samples. Values are mean dry weight per sampling quadrat. Error bars: standard error of the mean. **B** Contribution of the most abundant epiphytes (*Cryptopleura ramosa*, *Pterosiphonia complanata*, *Plocamium cartilagineum*, *Rhodymenia pseudopalmata*) to overall epiphyte biomass in 1996 and 1997 samples



Factors affecting distribution of meiofauna

The spatial distribution of the studied meiofauna seems to be affected by microhabitat factors, such as type of substratum (holdfast, frond, bottom), rather than by

Fig. 7 Classification analysis (A) and NMDS ordination (B) of fronds, holdfasts and bottom samples from the 4 years of study, using presence-absence of major meiofaunal taxa (in the dendrogram: *F*, *H* and *S*; in the ordination: squares, triangles and circles indicate frond, holdfast and bottom samples, respectively)



meso-scale factors, such as depth and exposure to surge. Neither depth differences (within the 5–25 m sampled range) nor differences in surge (exposed vs. semi-exposed quadrats) had any apparent effect on the abundance and gross taxonomic composition of the meiofauna. Nevertheless, we realise that such a conclusion is only moderately supported by our observational data, as the number of samples taken from the semi-exposed side ($N=4$) was relatively low compared with that from the exposed side ($N=14$). On the other hand, the idea that the distribution of sublittoral meiofauna is more dependent on microhabitat conditions than on general environmental features, whenever changes in the latter features have no substantial repercussion at the microhabitat level, is consistent with the results of several other studies (Gibbons and Griffiths 1986; Gibbons 1988a; Somerfield and Jeal 1996; De Troch et al. 2001; Prathep et al. 2003). Abundance and diversity of macroinvertebrates have generally been found to be positively correlated with plant biomass (Heck and Wetstone 1977; Gunnill 1982b). In our study, both diversity of total meiofauna on fronds and abundance of several taxa in frond samples were also positively correlated with the dry-weight biomass of this algal fraction. A slightly different pattern characterised the meiofauna of holdfasts, in which meiofaunal diversity positively correlated with holdfast biomass, but the abundances of meiofaunal organisms did not. Indeed, the numerical abun-

dances of meiofauna are unlikely to be linearly correlated with rhizome weight (Moore 1972a; Preston and Moore 1988; Edgar 1990). Whereas the surface provided by the fronds is directly dependent on their biomass, this is not the case for the holdfasts. Rather, the intricate structure of the holdfast provides a multiplicity of microhabitats for meiofauna and favours occurrence of dense faunal aggregations. By contrast, the comparative structural simplicity of the *L. ochroleuca* fronds, along with the mucous exudation characterising the frond surface, make them a generally unsuitable habitat.

The affinity in meiofaunal community structure between holdfast and bottom samples, along with the dissimilarity between those and that from the frond, suggests that only the meiofauna associated with the *L. ochroleuca* frond can be considered as strictly phytal. The variation in abundance between fractions (Fig. 4) indicates that most groups found in holdfast samples also occur with similar abundances in bottom samples. Only cirripedes were absent from bottom samples, despite the fact that barnacle nauplii and cyprids were found in this fraction.

Holdfast meiofauna is not strictly phytal, but a mixture of inhabitants from phytal, epibenthic and interstitial rocky-bottom habitats, associated mainly with the sediment retained by the holdfast structure and the variety of niches and refuge provided by them. This is

bound to result in much higher abundances of the meiofauna associated with this fraction compared to the fronds of the plant, particularly considering that meiofauna is a typically benthic taxon. Further, it may also explain the apparent lack of “response” of the meiofauna associated with the holdfasts to *L. ochroleuca*—die-back during the last 2 years of the study. Contrary to the fronds, the holdfasts maintained a relatively “healthy” structure until the last year of the study, with similar sediment-retention capabilities, and remained available as attachment surface for macroepifauna and other epiphytic algae. Hence, the associated meiofauna may not necessarily not be affected by a global loss in biomass, which was mainly due to frond deterioration (Arroyo 2002). This hypothesis is consistent with other data from the literature, in which several epiphytic animals have been found to respond more to the physical structure of the algae they inhabit than to biological aspects such as primary production, growth, or reproduction. In general, an indirect relationship between the animals and their host plant has been pointed out, often mediated by the presence of other epiphytic algae (Edgar 1983a; Johnson and Scheibling 1987; Hall and Bell 1988; Viejo 1999).

In our study, the presence of epiphytes on *L. ochroleuca* had a negligible effect on the abundance of the associated meiofauna, except for the epiphytic alga *C. ramosa*. The increasing abundance of this species was weakly associated with a decrease in abundance of copepods and ostracods. Sulphated galactans with high cytotoxic concentrations have been isolated from this alga (Carlucci et al. 1997), which may be of detriment to some meiofaunal taxa. Several authors have suggested the occurrence of slimes or the exudation of particular metabolites as factors determining the suitability of a substratum to host epifauna (Hornsey and Hide 1976; Lippert et al. 2001). Because the biomass of the epiphytes on *L. ochroleuca* was just moderate to low, the lack of correlation between epiphytic biomass and abundance of meiofauna was not surprising (Hicks 1977b; Edgar 1983a, 1983c; Hall and Bell 1988).

Other studies analysing the importance of habitat complexity in macrophytic communities have found that the total number of individuals was not affected directly by this factor, but taxonomical changes at species levels occurred (e.g. Young and Young 1977; Sánchez-Jerez et al. 1999), and this may have been the case in our study. Similarly, specific differences in depth distribution or in tolerance to exposure (regardless of complexity differences at the microhabitat level), undetectable by an analysis at the high taxonomic level, may have occurred at Mouro Island, and should not be discounted. Indeed, because our study deals with meiofauna at high taxonomic levels, the interpretation of most of the results is limited and should be considered a preliminary examination of the meiofauna associated with *L. ochroleuca*, which is to be complemented with further studies focussed on the most relevant groups (Arroyo et al., in preparation). Nevertheless, despite limitations, some general trends emerge clearly. The distribution of the

meiofauna associated with the population of *L. ochroleuca* appears to be affected mainly by within-plant factors. The holdfasts of *L. ochroleuca* host a substantially higher abundance of meiofauna than both fronds and the adjacent bottom. The holdfasts appear to be an ecotone for meiofauna, because they transiently contain organisms from the fronds and the adjacent bottoms, in addition to their “own” particular fauna.

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