Within- and between-plant distribution of harpacticoid copepods in a North Atlantic bed of *Laminaria ochroleuca*

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The fauna of harpacticoid copepods associated with a North Atlantic sublittoral population of *Laminaria ochroleuca* in Spain was investigated. Copepods belonging to four different orders, i.e. Harpacticoida, Cyclopoida, Poecilostomatoida and Siphonostomatoida, most of which were harpacticoids belonging to 17 different families were collected. Because the family Thalestridae was particularly abundant in the samples, its members were identified down to the species level, totalling 20 species. The copepod fauna was richer and more diverse on holdfasts than on fronds, irrespective of considering the entire harpacticoid assemblage at the family level or just the family Thalestridae at the species level. The effect of these two within-plant microhabitats on the taxonomic composition of the copepod fauna was substantial, with faunal similarity between fronds of plants from different sampling quadrats being usually higher than that between the frond and the holdfast of the same plant. Thalestridae, Harpacticidae and Tisbidae predominated on the fronds, while Diosaccidae, Ameiridae and Ectinosomatidae predominated on the holdfasts. Among the thalestrids, *Parathalestris clausi*, *Paradactylopodia* sp.1, *Dactylopusia tisboides*, and *Dactylopusia vulgaris* were common species, with *Parathalestris clausi* being the most abundant copepod on both fronds and holdfasts. In summary, the fauna of the holdfasts consists mostly of common, eurytopic species, while the fauna of the fronds comprises rare taxa—at least within the scope of the study—with low total abundances and/or usually occurring in few plants.

INTRODUCTION

Marine harpacticoid copepods are common on plants, including sea grass blades, marsh grass stems, macroalgal fronds, and floating algae (for reviews see Hicks & Coull, 1983; Hicks, 1985). Harpacticoids with 'phytal' habits appear to belong to just a few families (Hicks & Coull, 1983; Hicks, 1985). Some studies indicate that the abundance and species richness of copepods on marine plants can be affected by plant surface area (Hicks, 1980), habitat complexity (Gee & Warwick, 1994; Ólafsson et al., 2001; Jenkins et al., 2002), epiphyte biomass (Hall & Bell, 1993), food availability (Hicks, 1980; Webb, 1990), and plant age (Hicks, 1980; Webb, 1990). However, little is known about how the distribution of these animals varies between particular microhabitats in their host plants.

Large and morphologically complex macroalgae, such as many representatives of the order Laminariales, may provide a variety of potential microhabitats for the copepod fauna. Most laminarians have a complex rhizoid system, the holdfast, for attachment to the substratum. The holdfast supports a relatively long, cylindrical stalk that projects into the water column and bears distally a relatively extended, flat frond. The few available studies suggest that the occurrence of harpacticoid copepods on the fronds of laminarians is limited to very few species (Hicks, 1980; Edgar, 1983), while the harpacticoid fauna on the holdfasts is relatively diverse (Moore, 1973; Hicks, 1985). Despite this interesting contrasting pattern, the taxonomic and ecological relationships between the harpacticoid fauna of fronds and holdfasts have not been addressed in detail yet. In this study, we have investigated a North Atlantic population of the kelp *Laminaria ochroleuca* de la Pylaie to characterize taxonomically the harpacticoid fauna associated with the macroalgae and to examine between- and within-plant distribution patterns.

MATERIALS AND METHODS

Location and sampling methods

The study was conducted on a *Laminaria* bed, which extends on the shelf of Mouro Island (Cantabrian Sea, Spain, Bay of Santander; 43°28′24″N 3°45′22″W) to a maximum depth of 25 m. A detailed description of both the sublittoral environments around the island and the kelp bed can be found elsewhere (see Arroyo et al., 2004).

The *Laminaria* bed was sampled using SCUBA divers once a year over a four-year period (1996–1999). We collected plants using 0.5×0.5 m random quadrats during July–August in 1996, May in 1997, July–August in 1998 and May–June in 1999. It is worth noting that the

population of *L. ochroleuca* experienced a progressive dieback with substantial plant mortality and drastic loss of biomass during the years 1998 and 1999. As a consequence, nine samples a year were collected during 1996 and 1997, but only eight quadrats containing plants were sampled in 1998, and six in 1999. Sampling sites were selected at random within the *Laminaria* population and exact locations marked using a portable Magellan Global Positioning System. Further details on sampling and quadrat location can be found in Arroyo et al. (2004).

Taxonomic identification

Immediately after collection, all samples, which included the plants, their associated fauna, and the sediment retained by the rhizoids of the holdfasts, were frozen for later sorting. To process samples, we first picked the macrofauna out under a binocular microscope. Then, samples were sieved through 1 mm and 62 μm meshes and the animals retained by the 62 μm mesh preserved in 4% buffered formalin with rose Bengal. Further details of faunal separation techniques can be found in Arroyo et al. (2004).

All copepods were sorted under a dissecting microscope and harpacticoids identified to the family level. Given the abundance of the family Thalestridae in the samples, all thalestrids were identified to the species level. Because the thalestrid *Parathalestris clausi* (Norman, 1868) was the dominant harpacticoid species in our samples, we considered it of interest to identify its different life history stages (males, females, ovigerous females and copepodites) and examine their distribution patterns.

Within- and between-plant distribution of harpacticoid copepods

We investigated differences in total number of copepods, number of harpacticoid families, and number of thalestrid species between *Laminaria* fronds and holdfasts. For these analyses, we used samples collected in 1997 and 1999 only, in which *Laminaria* plants within each quadrat were stored separately from each other and their frond and holdfast isolated to prevent faunal mixing. Because each frond is univocally related to a holdfast, differences in total harpacticoid abundance between fronds and holdfasts were analysed using the paired-sample Student's *t*-test on log-transformed data (N=30 plants; 1997 and 1999 samples pooled).

We also investigated differences in numerical abundance between fronds and holdfasts for each of the most common families in the samples (i.e. seven families), as well as for each of the most common thalestrid species (i.e. four species). Finally, we examined differences in the abundance of *P. clausi* life history stages (males, females, ovigerous females and copepodites) between fronds and holdfasts. Differences in mean abundance of each taxon/life stage were analysed using either the paired-sample Student's *t*-test on log-transformed data or its non-parametric equivalent, the Wilcoxon signed-rank test (N=30 plants for families, N=29 plants for species/life stage).

We assessed the contribution of each plant fraction to the total faunal diversity on the plants by calculating the Shannon–Wiener diversity index per plant and per plant fraction for both the total harpacticoid assemblage at the family level (N=30) and the thalestrid assemblage at the species level (N=23).

To assess whether within-plant patterns of faunal similarity prevailed over between-plant patterns or vice versa, we used non-metric multidimensional scaling (nMDS). We performed analyses independently for 1997 and 1999. First, we examined patterns of relationships based on the total harpacticoid fauna (i.e. 17 families) found on a total of 18 and nine plants for 1997 and 1999, respectively. We considered only those plants of each year in which both frond and holdfast contained harpacticoids. We also ran a similar analysis for thalestrid species (i.e. 19 species), involving 15 and seven plants for 1997 and 1999, respectively, in which both frond and holdfast contained thalestrids. Pairwise faunal affinities were estimated using square-root transformed abundances and the Bray–Curtis similarity index, and were then submitted to nMDS, the results being plotted on a bi-dimensional ordination space. Analyses were performed using Primer v5 (Plymouth Routines in Multivariate Ecological Research, PRIMER-E, Plymouth, UK). To make clear global faunal patterns on the ordination space, sampling quadrats were referred to as 'a, b, c, . . . i', so that different plants collected from the various quadrats were labelled as 'a1, a2, . . . an' to 'i1 . . . in'; fronds and holdfasts were discriminated by the letters F and H, respectively. Therefore, the prevalence of between-plant effects over within-plant effects should result in groups of samples containing the same quadrat letter, irrespective of being holdfasts or fronds. In contrast, the prevalence of within-plant effects should yield separate groups of holdfasts and fronds, irrespective of their plant and quadrat allocation.

Effect of algal biomass on harpacticoid fauna

As a simple approach to evaluate the potential effects of habitat complexity on the abundance of harpacticoid fauna, we examined the association between the biomass of each plant (N=29) and total number of copepods, number of harpacticoid families, and number of thalestrid species, respectively.

The association between pairs of variables was estimated by using either Pearson product-moment correlation for normal, log-transformed data sets or Spearman rank correlations for data failing normality after transformation. All analyses were based on pooled samples from 1997 and 1999. Algal biomass was determined as the dry weight (65°C for 48 h) of each plant fraction.

Additionally, we examined the relationship between the biomass of each plant fraction (i.e. frond vs holdfasts) and: (1) the numerical abundance of each of the seven harpacticoid families (N_{fronds}= 31, $N_{holdfasts}$=32); and (2) each of the four thalestrid species (N_{fronds}=29, $N_{holdfasts}$=32) co-occurring in holdfast and frond samples.

RESULTS

Within- and between-plant distribution of harpacticoid copepods

The four-year sampling rendered a total of ∼37,000 copepods belonging to four different orders, i.e. Harpacticoida, Cyclopoida, Poecilostomatoida and

Table 1. *Harpacticoid families collected from* Laminaria ochroleuca *at Mouro Island. Values are mean numerical abundance (±SD) per plant fraction, year, and sampling quadrat (N). Data of abundance of non-harpacticoid copepods (i.e. orders Cyclopoida, Poecilostomatoida and Siphonostomatida) found in the samples are also given (upper case).*

| Taxa	1996		1997		1998		1999	
	Frond	Holdfast	Frond	Holdfast	Frond	Holdfast	Frond	Holdfast
Ambunguipedidae	0	0	1 ±2	0.75 ±096	0	0	0	10 ±11
Ameiridae	2 ±1	40 ±8	0	352 ±249	0	108 ±80	0	119 ±68
Ancorabolidae	0	6 ±9	0	10 ±12	0	3 ±0.58	0	2 ±2
Canthocamptidae	1 ±2	1	0	11 ±9	0	6 ±5	0.2 ±0.5	3 ±3
Diosaccidae	11 ±7	308 ±173	11 ±8	438 ±283	0.2 ±0.5	139 ±96	0.7 ±0.5	143 ±59
Ectinosomatidae	16 ±9	224 ±1	6 ±5	287 ±165	4 ±4	93 ±72	1 ±1	49 ±15
Harpacticidae	2 ±3	6 ±8	25 ±21	69 ±55	0.5 ±1	5 ±7	3 ±3	16 ±14
Laophontidae	11 ±12	128 ±13	0	179 ±129	0.2 ±0.5	70 ±54	0	47 ±14
Longipediidae	0	0	0	0	0	13 ±21	0	2 ±3
Normanellidae	0	10 ±15	0	12 ±12	0	5 ±5	0	0
Orthopsyllidae	0	10 ±15	0	6 ±5	0	3 ±4	0	5 ±2
Paramesochridae	0	0	0	0.7 ±1	0	0	0	1 ±2
Peltidiidae	0	1 ±1	0	3 ±3	0	1 ±2	0	2 ±1
Porcellidiidae	3 ±3	2 ±1	0	2 ±3	0	2 ±3	0	2 ±3
Tegastidae	0.5 ±1	11 ±6	0.2 ±0.5	14 ±16	0	7 ±6	0	11 ±9
Thalestridae	27 ±38	59 ±14	0.7 ±0.5	109 ±88	13 ±9	41 ±26	8 ±8	52 ±41
Tisbidae	7 ±6	10 ±4	47 ±48	31 ±26	6 ±4	16 ±12	11 ±8	21 ±6
CYCLOPOIDA	0	0	0	2 ±3	0	0.7 ±1.15	0	2 ±3
POECILOSTOMATOIDA	0	10 ±5	3 ±2	9 ±13	0	2 ±2	0.5 ±0.6	14 ±7
SIPHONOSTOMATOIDA	2 ±2	23 ±13	0	27 ±21	0	18 ±18	0.2 ±0.5	24 ±10
N	4	2	4	4	4	3	4	4

Table 2. *Harpacticoid families collected from* Laminaria ochroleuca *at Mouro Island in 1997 and 1999. Values are mean (±SD) numerical abundance per year and plant (N). Data on unidentified copepodites are also given (upper case).*

Taxa	1997		1999		
	Frond	Holdfast	Frond	Holdfast	Total
Ameiridae	2 ±2	70 ±69	0	53 ±35	60 ±58
Ancorabolidae	0	3 ±4	0	4 ±2	4 ±3
Canthocamptidae	0	4 ±2	1	3 ±1	3 ±2
Diosaccidae	4 ±3	88 ±90	1 ±0	69 ±50	57 ±72
Ectinosomatidae	3 ±1	57 ±45	1 ±1	29 ±22	33 ±39
Hamondidae	0	1 ±0	0	6 ±7	5 ±7
Harpacticidae	8 ±6	15 ±22	2 ±1	8 ±8	10 ±15
Laophontidae	2 ±1	36 ±43	1	30 ±28	29 ±36
Longipediidae	0	0	0	2 ±1	2 ±1
Normanellidae	0	4 ±3	0	0	4 ±3
Orthopsyllidae	0	3 ±3	0	2 ±1	3 ±2
Paramesochridae	0	1 ±1	0	2 ±0.5	2 ±0.5
Peltidiidae	0	2 ±1	0	2 ±1	2 ±1
Porcellidiidae	1 ±0.5	2 ±1	0	2 ±1	2 ±1
Tegastidae	1 ±0	4 ±4	0	5 ±6	4 ±4
Thalestridae	10 ±10	14 ±22	4 ±4	16 ±19	12 ±18
Tisbidae	7 ±6	6 ±10	4 ±3	63 ±135	18 ±63
COPEPODITES	2 ±2	34 ±28	9 ±11	81 ±100	41 ±65
N	21	20	11	12	

Siphonostomatoida (Table 1). Within the Harpacticoida, 17 families were represented (Table 1, Figure 1A).

By analysing pooled samples from 1997 and 1999, we found that average abundance of harpacticoids was significantly higher (paired *t*-test: *P* < 0.001; Figure 2A, last column) on holdfasts (mean ±SD: 343 ±337 individuals) than on fronds (21 ±20 individuals). The average number of families was also significantly higher (paired
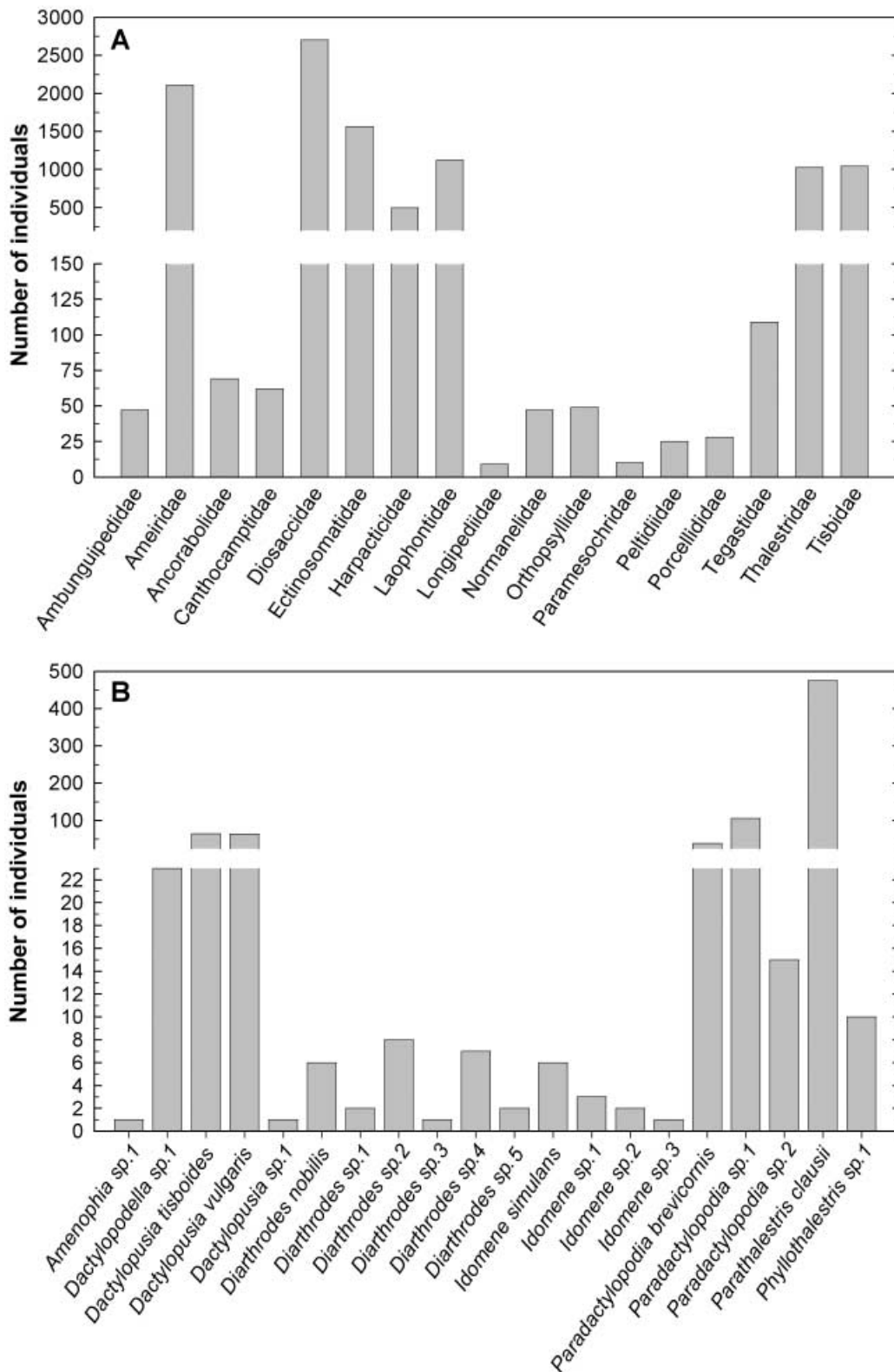
Figure 1. (A) Family distribution of the harpacticoids collected in the four-year sampling; and (B) species distribution of individuals belonging to the family Thalestridae.

t-test, $P < 0.001$) on holdfasts (11 ±2 families) than on fronds (4 ±2 families), with seven families occurring exclusively on holdfasts, ten on both holdfasts and fronds, and none exclusively on fronds (Table 2). Six of the seven families co-occurring in holdfasts and fronds had significantly higher numbers of individuals on holdfasts than on fronds (Figure 2A). Only the family Tisbidae

showed no significant difference in abundance between fronds and holdfasts.

A total of 20 thalestrid species were found on the plants belonging to 1997 and 1999 samples (Figure 2, Table 3). The average number of thalestrid species was significantly (paired *t*-test, $P < 0.001$) higher on the holdfasts (4 ±3) than on fronds (1 ±1), with seven species occurring
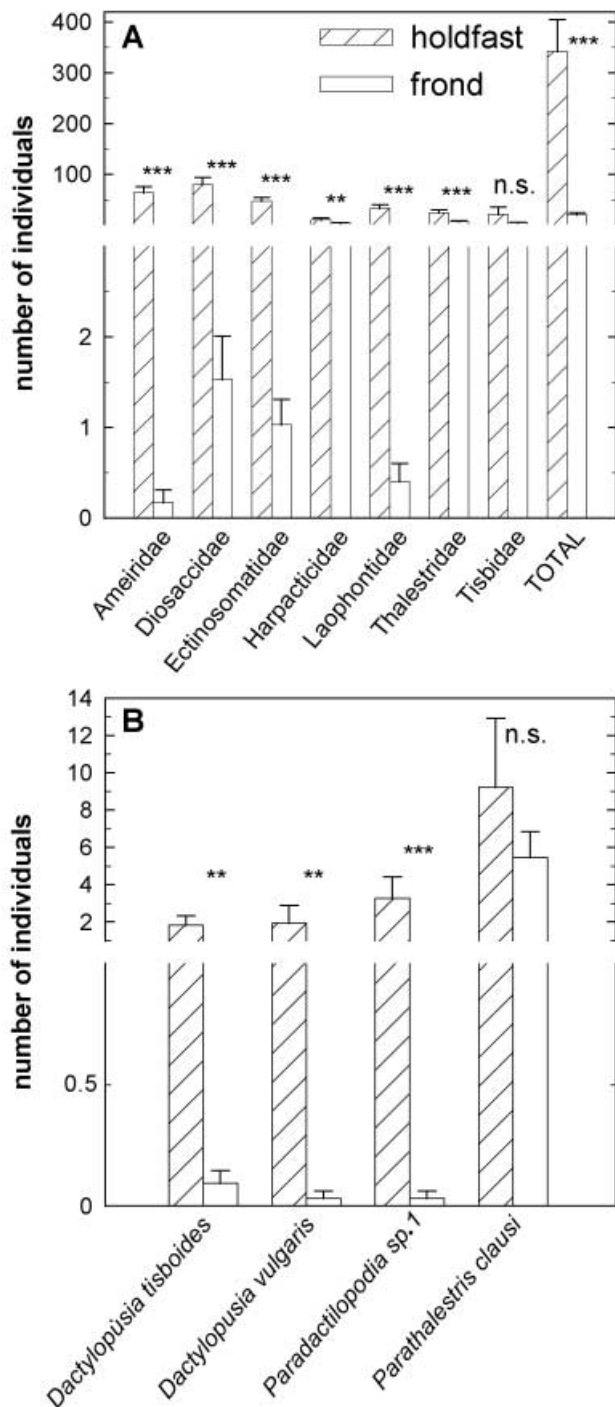
Figure 2. (A) Abundance (mean ±SD) of the predominant harpacticoid families; and (B) thalestrid species on fronds and holdfasts of plants collected in 1997 and 1999. A comparison of total harpacticoid fauna on fronds and holdfasts is also represented by the pair of columns to the right in Figure 2A (i.e. TOTAL). The statistical significance of the results of paired *t*-tests for mean comparison is referred to as '***' for $P < 0.001$, '**' for $P < 0.01$, and 'n.s.' for non-significant differences.

Table 3. *Numerical abundance (±SD) of thalestrid species on* Laminaria ochroleuca *at Mouro Island per year and plant fraction (N).*

Species	1997		1999	
	Frond	Holdfast	Frond	Holdfast
Amenophia sp.1	0	0	0	1
Dactylopodella sp.1	0	1 ±0.6	0	5 ±4
Dactylopusia tisboides	1	4 ±3	1	3 ±3
Dactylopusia vulgaris	1	5 ±9	0	3 ±2
Dactylopusia sp.1	0	1	0	0
Diarthrodes nobilis	0	0	1	2 ±0.6
Diarthrodes sp.1	0	1	0	0
Diarthrodes sp.2	0	1	0	2 ±1
Diarthrodes sp.3	0	0	0	1
Diarthrodes sp.4	0	1	0	1 ±1
Diarthrodes sp.5	0	0	0	2
Idomene simulans	0	1	0	3
Idomene sp.1	1 ±1	0	0	0
Idomene sp.2	0	1	0	0
Idomene sp.3	0	1	0	0
Paradactylopodia brevicornis	1	3 ±0.6	0	2 ±1
Paradactylopodia sp.1	0	3 ±2	0	9 ±9
Paradactylopodia sp.2	0	6	1	2 ±1
Parathalestris clausi	9 ±9	15 ±26	5 ±3	11 ±22
Phyllothalestris sp.1	0	0	0	1 ±1
N	21	20	12	13

Three of these species, i.e. *Dactylopusia tisboides* (Claus, 1863), *D. vulgaris* Sars, 1905, and *Paradactylopodia* sp.1, were significantly (paired *t*-test, $P > 0.05$) more abundant on holdfasts than on fronds (Figure 2B). A fourth species, *Parathalestris clausi*, which reached the highest abundance values, in both fractions, showed no difference in abundance between fronds and holdfasts (paired *t*-test, $P > 0.05$; Figure 2B). Similarly, the various life stages of *P. clausi* (i.e. males, non-ovigerous females, ovigerous females and copepodites) showed non-significant (Wilcoxon signed-rank test, $P > 0.05$) within-plant differences in abundance distribution (data not shown).

The analysis of harpacticoid diversity at the family level indicated that holdfasts show an average value of family diversity as high as that of the entire plants and nearly twice more diverse values than that of fronds (Figure 3A). These within-plant differences in faunal diversity are greater for the group of thalestrid species, which is more than three times more diverse on holdfasts than on fronds (Figure 3B).

The nMDS representation considering the abundance of 17 harpacticoid families in fronds and holdfasts clearly separates holdfast samples from frond samples, both in 1997 and in 1999 (Figure 4). Such a clear separation indicates major differences between plant fractions in assemblage structure. Table 1 indicates that most of the taxa which appear in the holdfasts also occur on the fronds, though with much lower abundances. In the nMDSs, frond samples do not make a cohesive group, indicating a high heterogeneity in harpacticoid family composition. The nMDSs also show that the magnitude of between-plant distance appears to have a weaker effect on the

exclusively on the holdfasts, 12 on both holdfasts and fronds, and one species on just fronds. Nevertheless, the latter species, i.e. *Idomene* sp.1, is represented in the study by just two individuals. Only four thalestrid species out of the 12 co-occurring in holdfasts and fronds occurred in a sufficient number of plants to support statistical analysis.
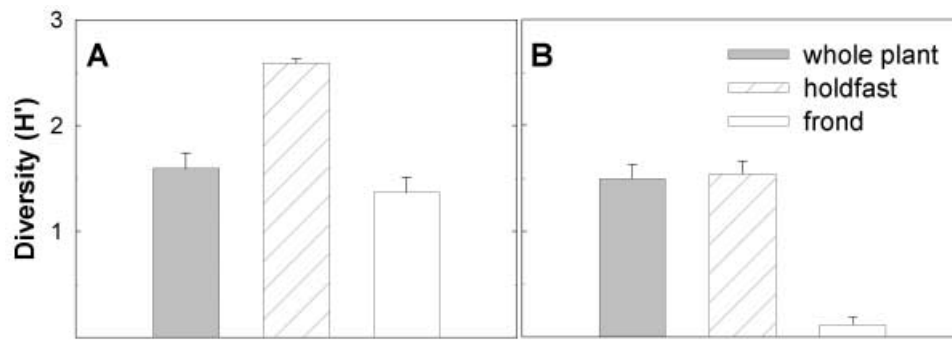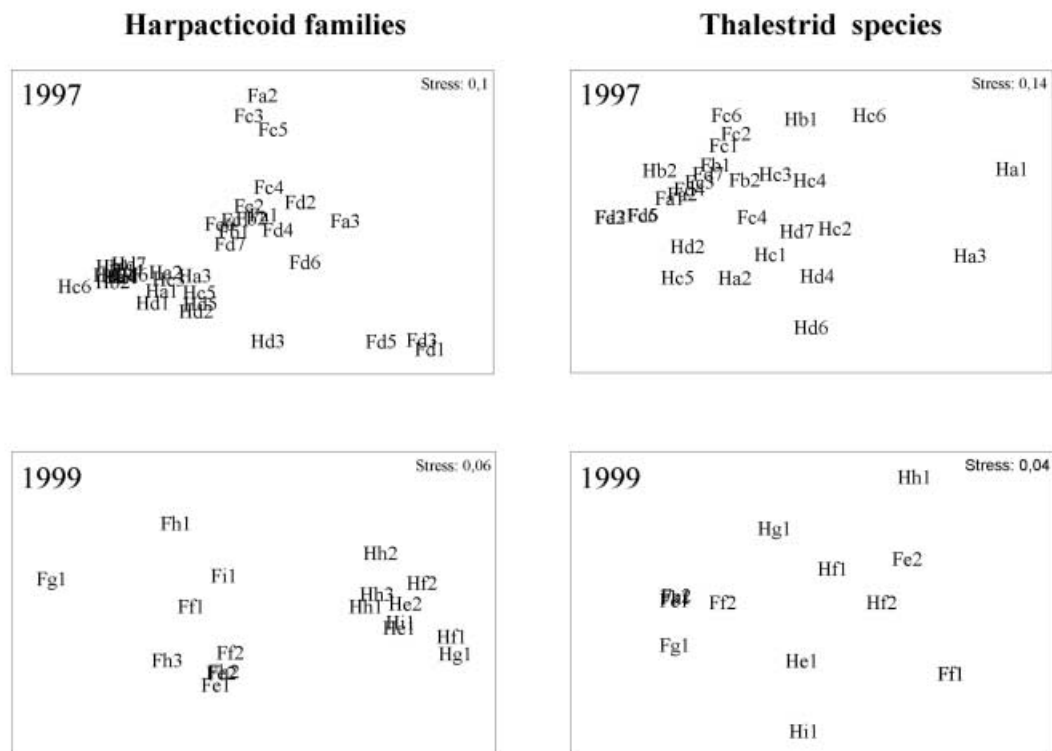
Figure 3. Mean (±SD) Shannon–Wiener diversity (H′) calculated for (A) the harpacticoid fauna considered at the family level; and (B) the set of thalestrid species on plants, holdfasts, and fronds, respectively.

Figure 4. Non-metric multidimensional scaling ordination based on the abundance of harpacticoid families and thalestrids species of frond and holdfast samples in 1997 and 1999. Figures show the relative positions of holdfasts (H) and fronds (F). Letters 'a' to 'i' in labels indicate quadrats and numbers '1' to '7' refer to different plants within a given quadrat. Here, quadrat labels 'a, b, c and d' correspond to samples '976, 971, 978 and 972', respectively, while quadrat labels 'e, f, g, h and i' correspond to samples '992, 993, 994, 995 and 996', respectively as shown in the map represented in Arroyo et al. (2004).

pattern of faunal relationships, faunal similarity between two fronds from different sampling quadrats being usually higher than between the frond and the holdfast of a plant. Therefore, it can be deduced that between-plant differences in microhabitat have less effect than within-plant differences on faunal patterns. On the other hand, when considering fractions independently, it does seem that holdfasts or fronds that were collected in the same quadrat (that is, that show the same letter 'a' to 'i' in the nMDS) show higher similarities among them than with those of other quadrats.

The pattern of faunal relationships is less clear when based on just the set of thalestrid species. In the 1997 nMDS representation, most frond samples are clumped (Figure 4), while holdfast samples appear scattered. The

spreading of holdfasts on the ordination space indicates that they do not share much of the thalestrid fauna with each other, even if they belonged to the same sampling quadrat. Again, the thalestrid fauna on the holdfasts were somewhat richer than that occurring in most frond samples, which were characterized by sporadic appearances of most taxa (Table 2). In 1999 (Figure 4), both fronds and holdfasts appear scattered in the ordination plot, no clear separation between fractions being noticeable. The *Laminaria* plants were in a severe declining state, which may have affected particularly phytal taxa such as thalestrids, rendering communities in the fronds and the holdfasts less stable. As regards between-plant differences, and proximity of plants in space, again the pattern is less clear, especially in 1999, when the low

Table 4. *Results of Pearson product-moment correlation between the abundance of the seven predominant harpacticoid families and holdfast and frond biomass (as dry weight), respectively. 'N' refers to number of plants submitted to analyses.*

Families	Frond	Holdfast
Ameiridae	$r^2=0.19; P>0.050$	$r^2=0.49; P<0.001$
Diosaccidae	$r^2=0.27; P<0.010$	$r^2=0.48; P<0.001$
Ectinosomatidae	$r^2=0.16; P<0.050$	$r^2=0.38; P<0.001$
Harpacticidae	$r^2=0.42; P<0.001$	$r^2=0.25; P<0.010$
Laophontidae	$r^2=0.04; P>0.050$	$r^2=0.22; P<0.010$
Thalestridae	$r^2=0.45; P<0.001$	$r^2=0.35; P<0.001$
Tisbidae	$r^2=0.30; P<0.010$	$r^2=0.08; P>0.050$
N	31	32

number of plants of a same quadrat containing thalestrids makes it difficult to establish these comparisons.

Effect of algal biomass on harpacticoid fauna

Total plant biomass correlated neither total abundance of harpacticoids (Pearson product-moment, $P>0.05$) nor number of harpacticoid families (Spearman correlation, $P>0.05$). Nevertheless, the number of thalestrid species showed a weak positive relationship with plant biomass (Spearman $R=0.369$, $P<0.05$). Total abundances of the families Diosaccidae, Ectinosomatidae, Harpacticidae and Thalestridae on fronds and holdfasts showed weak positive correlation with both frond and holdfast biomass, respectively (Table 4). In contrast, frond biomass was unrelated to the abundance of Ameiridae and Laophontidae, while holdfast biomass was unrelated to abundance of Tisbidae (Table 4).

Only two thalestrid species (i.e. *P. clausi* and *D. vulgaris*) had their abundance associated with plant biomass. Abundance of *P. clausi* was positively correlated with both frond ($r^2=0.63$, $P<0.001$) and holdfast ($r^2=0.4l7$, $P<0.05$) biomass. Abundance of *D. vulgaris* on holdfasts correlated positively to holdfast biomass ($r^2=0.29$, $P<0.01$).

DISCUSSION

Our study indicates that fronds and holdfasts of *Laminaria ochroleuca* strongly differ in both the taxonomic composition and the abundance of the harpacticoid fauna that they harbour. These results are consistent with reported differences in total meiofaunal abundance between fronds and holdfasts of *L. ochroleuca* (Arroyo et al., 2004). Similar patterns of within-plant faunal differences have also been reported for phytal harpacticoids on sea grasses (De Troch et al., 2001) and total meiofauna associated with seaweed beds (e.g. Colman, 1940; Hicks, 1985).

The harpacticoid fauna associated with the fronds of *L. ochroleuca* at Mouro Island was mainly composed of families often regarded as plant specialists (Hicks & Coull, 1983; Hicks, 1985), while the holdfasts were dominated by taxa also found among sediment and other epibenthic microhabitats (e.g. Dahl, 1948; Hicks & Coull, 1983). Surprisingly, Porcellididae, Peltidiidae or

Tegastidae, which are traditionally regarded as typically phytal families, were mostly found on holdfasts in our study. Porcellidids and peltidids typically have dorsoventrally flattened bodies and mouthparts adapted to facilitate adhesion to flat thalloid algal surfaces and cope with turbulence and currents (Hicks, 1985). Nevertheless, given that *L. ochroleuca* holdfasts showed abundant epiphytic algae characterized by a flat morphology, we cannot discard the idea that the epiphytes favoured occurrence of porcellidids and peltidids on holdfasts. It is also possible that the slimy surface of the *Laminaria* fronds may somehow hinder the ventral structures of peltidids and porcellidids from adhering properly. If so, robust prehensile maxillipeds and hooked swimming legs, such as those of thalestrids and harpacticids, may result in more efficient clinging to the fronds. Indeed, thalestrids appear to be a group particularly associated with macroalgae (Hicks & Coull, 1983), showing not only specific morphological adaptations to facilitate life on plants (Bell et al., 1987), but being also able to feed on macroalgal tissues (e.g. Hicks, 1985; Ho & Hong, 1988).

Most of the thalestrid species identified on *L. ochroleuca* can be regarded as either eurytopic or phytal euryoic species, occurring in a panoply of phytal microhabitats (Lang, 1948; Hicks, 1980), ranging from red algae (e.g. Lang, 1948; Hicks, 1985) to various kelp species (Moore, 1973; Pallares & Hall, 1977). The fact that many thalestrids are phytal eurioic organisms may explain why differences between fronds and holdfasts in the abundance of thalestrid fauna were smaller than those found for the total harpacticoid assemblage.

Among the thalestrids, *Parathalestris clausi* was the only species with really high abundance on fronds. This species is known to 'manipulate' the mucilage secreted by *Fucus* with the antennae and other secondary mouthparts to form a 'feeding bolus', in which cyanobacteria, bacteria, diatoms, and fungal cells are aggregated for subsequent ingestion (Hicks, 1980). Abundant production of mucus by *L. ochroleuca* probably favours abundance of *P. clausi* on the fronds. Other thalestrids, such as *Diarthrodes* sp. 1 and *Idomene* sp.1, were particularly associated with fronds in our study (Figure 5B). The members of the genus *Diarthrodes* are known to attach to macroalgae by means of self-secreted mucous, which they may also use for feeding (Hicks & Grahame, 1979). The genus *Idomene* is characterized by a flattened morphology, which appears well suited for life on laminarian blades. Nevertheless, given that the total abundance of these species in our samples was low, we cannot decide whether they are frond specialists or casual visitors. Several of the remaining thalestrids species found in our study—i.e. *Paradactylopodia brevicornis* (Claus, 1866), *Dactylopodella flava* (Claus, 1866), and *Dactylopusia tisboides*—are known to have strong preference for red algae (Lang, 1948; Hicks, 1980), which may explain why they showed higher abundances on holdfasts than on fronds.

The multivariate analyses revealed that within-plant differences in microhabitat (i.e. differences in spatial complexity between frond and holdfast) have stronger effects than between-plant differences on faunal abundance and taxonomic composition. The fact that algal biomass and more specifically holdfast biomass correlated positively with family and species abundance in many

cases suggests again that the abundance of the harpacticoid fauna is affected by the level of complexity of the microhabitat. The biomass effect was particularly relevant for holdfasts, since variation in holdfast size involves changes in not only the spatial complexity of the available microhabitat for phytal harpacticoids, but also in the amount of sediment retained between the rhizoids and, therefore, in the chances of attracting psammic harpacticoids from the adjacent sea-floor.

Altogether our results indicate that fronds and holdfasts provide clearly different microhabitats that are exploited differentially by the harpacticoid fauna.

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