

Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada

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ABSTRACT: Abundance and species composition of epifauna on *Ascophyllum nodosum* and *Fucus vesiculosus* on a rocky shore in Nova Scotia show pronounced seasonal variation. Total density of epifauna declined by 2 orders of magnitude between summer and winter. Harpacticoid copepods and their nauplii, nematodes, and halacarid mites were numerically the most important components of the assemblage throughout the 13 mo study (May 1983 to Jun 1984). Density was positively correlated with epiphytic algal biomass for most epifaunal taxa. Cluster analysis and multidimensional scaling also indicate that epifaunal sample groupings were strongly related to epiphyte biomass. There was a greater tendency for samples to cluster according to the 2 macroalgal species during the winter, when epiphyte biomass was low, suggesting that epiphytes obscure differences in morphology and/or microbial surface films between *A. nodosum* and *F. vesiculosus*.

INTRODUCTION

A number of studies have documented seasonal fluctuations in epifaunal assemblages on marine benthic macroalgae (see review in Hicks 1985). In general, these studies have been limited to either meiofaunal or macrofaunal size classes or specific taxa. Few studies have investigated the entire epifaunal assemblage. Temporal and spatial variability in epifaunal assemblages or specific taxa on macroalgae have been attributed to a variety of abiotic and biotic factors, e.g. temperature (Hagerman 1966, Gunnill 1983), desiccation (Colman 1940), tidal exposure (Gunnill 1983), physiological or growth state of the plant (Hagerman 1966, Mukai 1971, Gunnill 1983, Trotter & Webster 1983), abundance of epiphytic algae (Colman 1940, Wieser 1959, Hagerman 1966, Zavodnik 1967, Nagel 1968, Kito 1977, Kangas 1978, Edgar 1983, Gunnill 1983), abundance of specific microorganisms (Trotter & Webster 1983), predation (Hagerman 1966, Edgar 1983), and intra and interspecific competition (Hagerman 1966, Hicks 1977c, Hicks 1980).

Members of the family Fucaceae, including the genera *Ascophyllum* and *Fucus*, are the predominant intertidal macroalgae of the northern hemisphere. These algae are known to support abundant and diverse epifaunal assemblages, but seasonal changes

in these assemblages have been poorly documented (e.g. Colman 1940, Dahl 1948, Ohm 1964, Hagerman 1966, Zavodnik 1967). Most studies have emphasized single taxa, or only the macrofauna, except for those of Colman (1940), Ohm (1964), and Hagerman (1966) which provided detailed taxonomic descriptions of all taxa in both the meiofaunal and macrofaunal size fractions.

This study investigates seasonal changes in the species composition and abundance of epifaunal assemblages (both meiofauna and macrofauna) on 2 common intertidal macroalgae, *Ascophyllum nodosum* and *Fucus vesiculosus*, on a rocky shore in Nova Scotia. Classification and ordination techniques are used to elucidate temporal patterns and to provide insight into the role of epiphytic algae as a determinant of assemblage structure and dynamics.

MATERIALS AND METHODS

Epifauna on *Ascophyllum nodosum* and *Fucus vesiculosus* were sampled monthly between May 1983 and June 1984 on the rocky shore of a moderately exposed bay at Lower Prospect, Nova Scotia (Fig. 1). The bay is shallow (mean depth = 3 m) with a sand and cobble substratum. The shoreline consists of

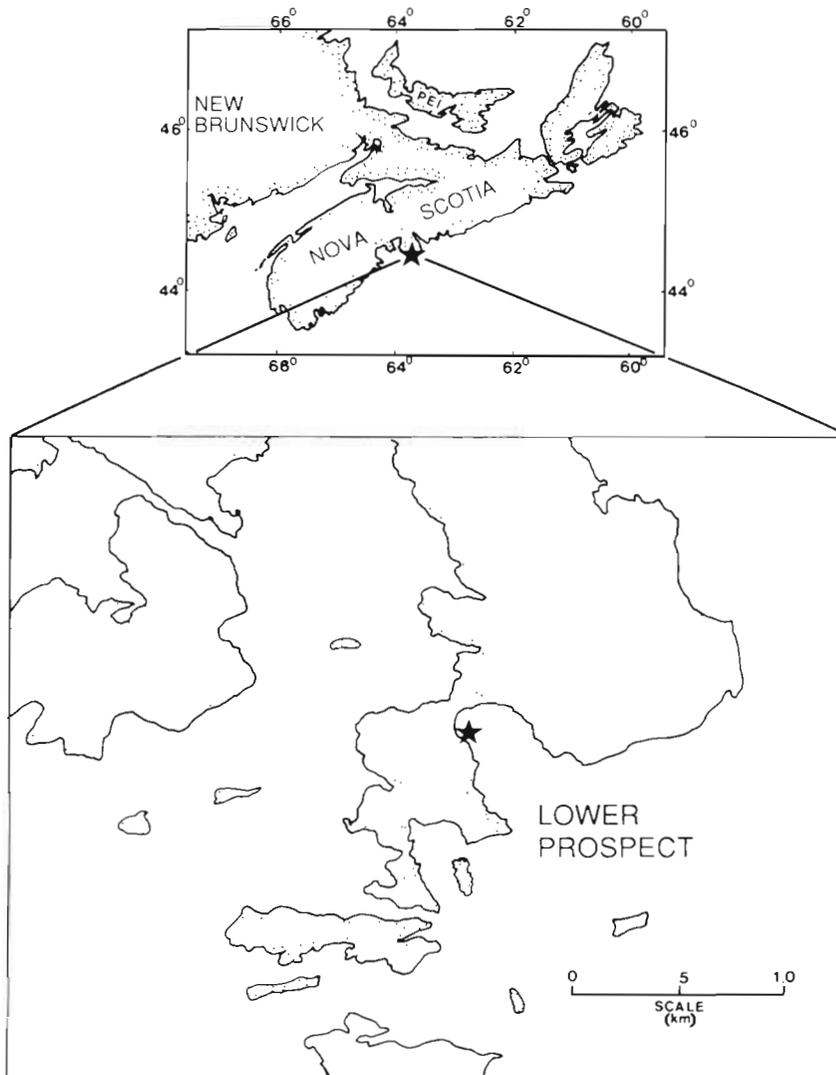


Fig. 1. Map of Nova Scotia, Canada, showing study site (★) at Lower Prospect

gradually sloping bedrock extrusions separated by fine sand beaches. The intertidal macroalgal community is dominated by luxuriant beds of *A. nodosum* and *F. vesiculosus*.

Three specimens each of *Ascophyllum nodosum* and *Fucus vesiculosus* were collected from random locations along a 50 m transect approximately 0.1 m above mean low water shortly after exposure at low tide. Individual specimens were cut from their holdfasts and placed in plastic bags with 5 % formaldehyde solution. Epifauna were washed from each specimen with filtered seawater through 0.50 and 0.063 mm sieves and hand-sorted under a dissecting microscope. The fraction retained on the 0.063 mm sieve was subsampled in May through September 1983, and May through June 1984; the entire fraction was sorted for all other months. Five replicate subsamples (1/20 volume) were taken using a large bore automatic pipette. (Counts were checked for agreement with a Poisson series

indicating random sampling of all taxa.) Between 1 and 5 subsamples were sorted to include at least 200 specimens of the dominant taxa (excluding nematodes and crustacean nauplii which were extremely abundant). Epifauna were identified to species or to higher taxa for some groups (e.g. Foraminifera, Turbellaria, Nematoda, Ostracoda, Halacaridae, Chironomidae).

Filamentous epiphytic algae were scraped from *Ascophyllum nodosum* and *Fucus vesiculosus* with a scalpel and samples retained for identification. Macroalgal specimens were divided into distinct plant regions: blade, eroded blade, or stalk. Five pieces from each region were selected at random and photocopied. The surface area of these pieces was determined by computer-digitizing the photocopy images. Pieces from each region, the remaining portion of the macroalgal specimen, and the epiphytes were dried separately to a constant weight at 60.0 °C. For each region the ratio of surface area to dry weight was calculated as

the average of the 5 pieces. The weight of a given region (weight of the pieces and remaining portion of that region) was then multiplied by the corresponding ratio to give the surface area for that region. Total plant surface area is the sum of the total surface area for each of the regions.

Density of epifauna is expressed as number of individuals m^{-2} of plant surface. The normality of the data was checked and the best transformation for each taxon was estimated using the procedure of Box et al. (1978). For all taxa, logarithmic transformation was indicated; $\log(x+1)$ was used to accommodate rare species. Differences among months and between macroalgal species were investigated by analysis of variance. Residual error terms were tested for normality, independence and noncorrelation using SAS procedures (Ray 1982). Transformation reduced departures from these assumptions, although ANOVA is a relatively robust test procedure especially when applied to balanced designs (Underwood 1981). Relations among samples were examined using the similarity matrix and classification program ORDANA (Bloom et al. 1977) and the non-metric multidimensional scaling program SCALO2 (Maquire 1969). Density data were double root transformed (Field et al. 1982) and a similarity matrix involving all taxa was constructed using the Bray Curtis Index (also known as Czekanowski's Quantitative Index) (Field et al. 1982). This matrix was used to construct classification diagrams of percent similarity using group average sorting (Field et al. 1982). It was also used in non-metric multidimensional scaling analysis (Kruskal 1964a, b, Field et al. 1982).

RESULTS

Habitat description

Surface water temperatures (recorded monthly) ranged from $-1.0^{\circ}C$ (Jan 1984) to $18.7^{\circ}C$ (Jul 1983) and air temperatures ranged from $-4.5^{\circ}C$ (Jan 1984) to $25.0^{\circ}C$ (Jun 1984) (Fig. 2). Temperatures within the macroalgal bed are lower in the summer and higher in the winter than the air temperatures, demonstrating a thermal buffering capacity of the mat. An ice sheet, several centimetres thick, frequently formed during low tide on the surface of the algal mat in January and February. Sea surface salinity ranged from 29.0 to 31.1 ‰.

The abundance of macroalgae did not vary noticeably throughout the year. In September 1983, mean biomass (\pm SE) was 2.7 ± 1.2 kg dry weight m^{-2} rock surface for *Ascophyllum nodosum*, and 0.6 ± 0.2 kg dry weight m^{-2} rock surface for *Fucus vesiculosus*.



Fig. 2. Water (■), air (♦), and algal mat (◊) temperatures (measured with a mercury thermometer) at sampling times between May 1983 and Jun 1984 at Lower Prospect, Nova Scotia

Two-way ANOVA indicates that the biomass of epiphytic algae on *A. nodosum* and *F. vesiculosus* (Fig. 3) varied significantly among months ($p < 0.001$) and between the 2 macroalgal species ($p < 0.001$) with a significant interaction between month and macroalgal species ($p < 0.01$). (A significant difference indicates that the direction of difference between macroalgal species varied among months.) Epiphytes were abundant in the spring and summer and rare to absent through the late fall and winter. *Elachistea fucicola* (Vell.) Aresch. and *Pilaiella littoralis* (L.) Kjellm were the dominant epiphytic species; other species included *Ptilota serrata* Kutz., *Bonnemaisonia hamifera* Hariot., and *Leptonematella fasciculata* (Reinke) Silvia.

Seasonal patterns in density

Fifty-three species or multispecies groupings (Appendices 1 & 2) were identified from *Ascophyllum nodosum* and *Fucus vesiculosus*. The density of the total epifauna shows pronounced seasonal variation (Fig. 4; Appendices 1 & 2). Density on both macroalgal

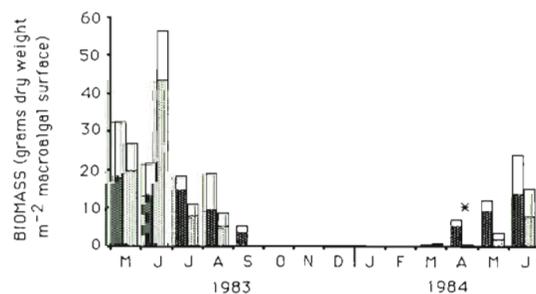


Fig. 3. Biomass of filamentous epiphytic algae on *Ascophyllum nodosum* and *Fucus vesiculosus* at Lower Prospect, Nova Scotia. Dark shading: mean density on *A. nodosum*; light shading: mean density on *F. vesiculosus*; open: 1 standard error of the mean. Sample size is 3 for each macroalgal species. (*) Months with statistically significant differences between macroalgal species (t-test, $p < 0.05$)

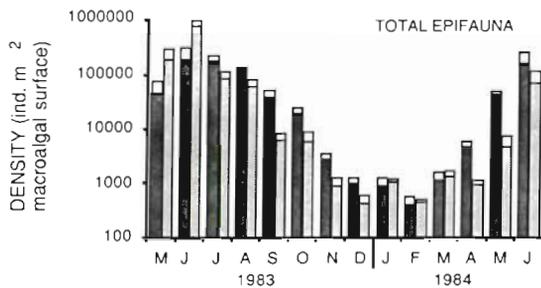


Fig. 4. Density of total epifauna on *Ascophyllum nodosum* and *Fucus vesiculosus* collected at Lower Prospect, Nova Scotia. See Fig. 3 for explanation of shading. Sample size is 3 for each macroalgal species

species was maximal in June 1983 and declined by 2 orders of magnitude to a minimum in mid winter.

Eighteen species or multispecies groupings of harpacticoid copepods from 9 families are identified from both *Ascophyllum nodosum* and *Fucus vesiculosus* (Appendices 1 & 2). Harpacticoids (including nauplii) were the most abundant component of the epifaunal assemblages of both macroalgal species, representing

31 to 82 % of the epifauna of *A. nodosum* and 32 to 70 % of the epifauna of *F. vesiculosus* (Fig. 5). Density of copepod nauplii was comparable to that of adults and copepodites in most months (Fig. 6). Maximum density of harpacticoid copepods and nauplii occurred around June on both macroalgal species although the period of peak abundance was more protracted on *A. nodosum* than on *F. vesiculosus* (Fig. 6).

The density of each of the major harpacticoid species (or multispecies groupings) varied significantly among months and between macroalgal species (with the exception of *Harpacticus* sp. 2, *Parastenhelia spinosa*, and *Heterolaophonte discophora*) (Tables 1 & 2). Except for *Harpacticus* sp. 2, *Tisbe* spp., *Mesochra* sp. 1, and *H. discophora* the interactions between month and macroalgal species were significant. Density of most species was highest between June and August and declined throughout the fall and winter. During the period of maximum abundance, the genus *Heterolaophonte* was dominant (Fig. 7). Other numerically important species at this time include *Harpacticus* sp. 2, *P. spinosa*, *Amphiascopsis* sp., *Mesochra* sp. 2, and *Nitocra typica* (on *Fucus vesiculosus* only).

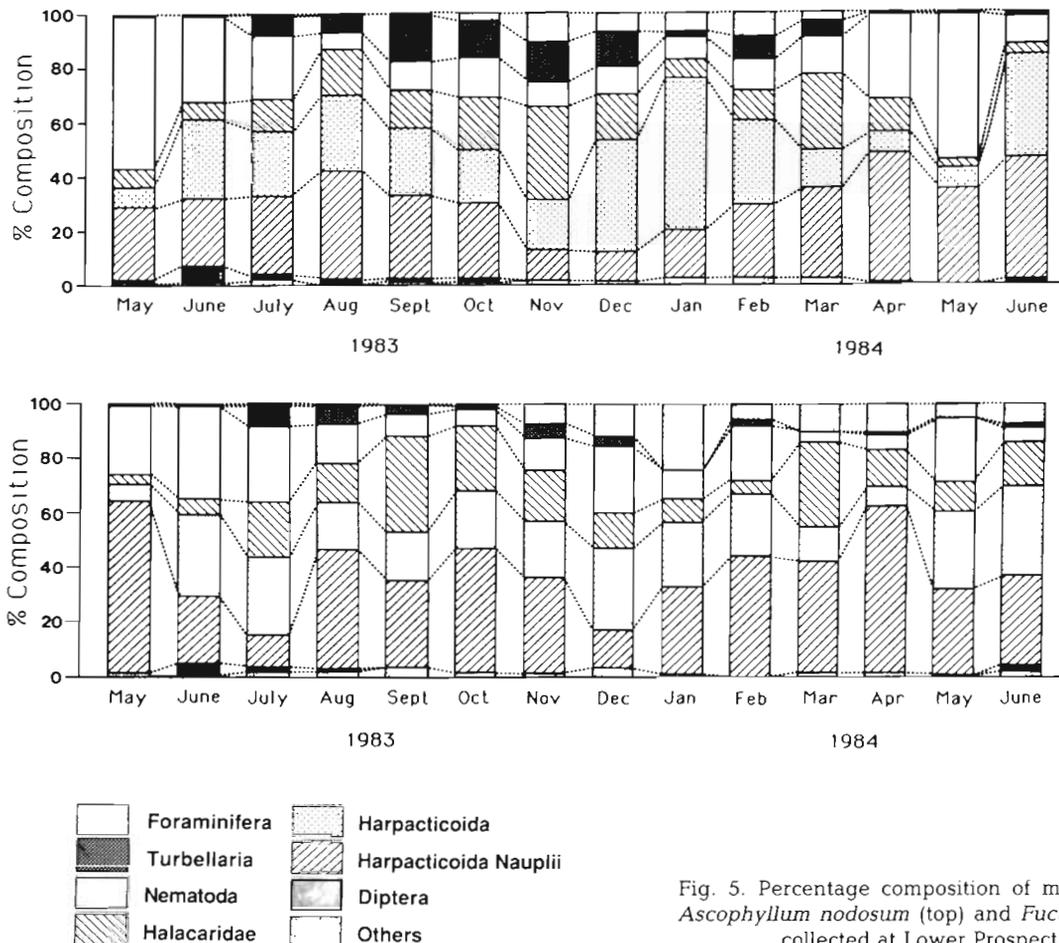


Fig. 5. Percentage composition of major epifaunal taxa on *Ascophyllum nodosum* (top) and *Fucus vesiculosus* (bottom) collected at Lower Prospect, Nova Scotia

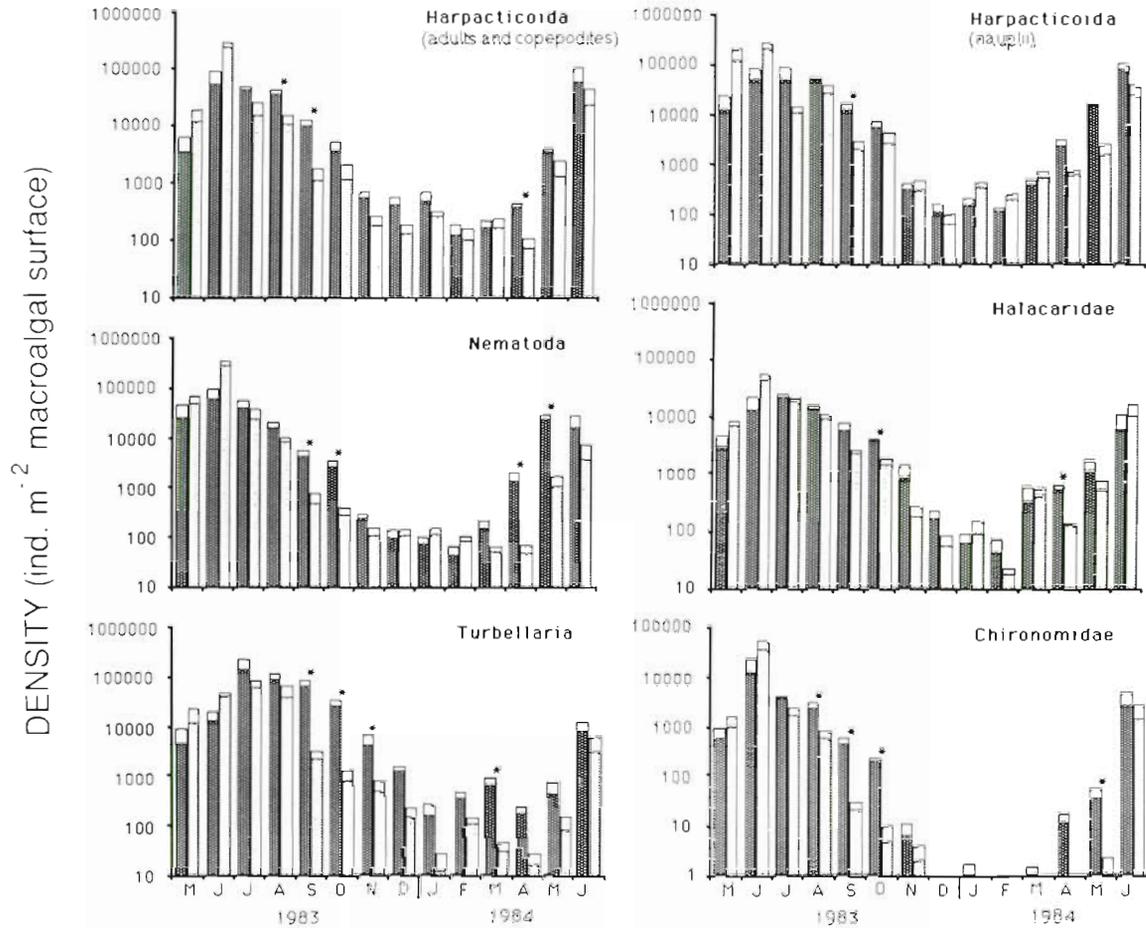


Fig. 6. Density of major taxa on *Ascophyllum nodosum* and *Fucus vesiculosus* collected at Lower Prospect, Nova Scotia. See Fig. 3 for explanation of shading. Sample size is 3 for each macroalgal species. (*) Months with statistically significant differences between macroalgal species (t-test, $p < 0.05$)

Mesochra sp. 1 and *N. typica* (on *Ascophyllum nodosum*) were most abundant in the fall and early winter (Fig. 7). *Tisbe* spp. showed little seasonal fluctuation in density (Fig. 7).

Nematodes were the second most abundant taxon, representing 8 to 56 % of the epifauna on *Ascophyllum nodosum* and 5 to 34 % of the epifauna on *Fucus vesiculosus* (Fig. 5). Nematode density varied significantly between macroalgal species and among months with a significant interaction between month and macroalgal species (Table 1). Maximum density on both macroalgal species occurred in June 1983; density declined by 3 orders of magnitude during the fall and remained low throughout the winter (Fig. 6).

Halacarid mites represented about 3 to 35 % of the epifauna on both macroalgal species (Fig. 5). Density of halacaridae varied significantly among months but not between macroalgal species with a significant interaction between month and macroalgal species (Table 1). Density was maximum around June and July 1983 on both macroalgal species respectively, and

declined by 2 to 3 orders of magnitude by February 1984 (Fig. 6). Members of the genus *Rhombognathides* accounted for >90 % of the total mite density on both macroalgal species throughout the year.

Turbellarians represented < 1 to 16 % of the epifauna on *Ascophyllum nodosum* and < 1 to 8 % of the epifauna on *Fucus vesiculosus* (Fig. 5). Pronounced seasonal changes in density of turbellaria occurred on both macroalgal species (Fig. 6). Turbellarian density varied significantly between macroalgal species and among months (Table 1). Maximum density on both macroalgal species occurred in July 1983; density declined during the fall and remained low throughout the winter. One species, *Notoplana atomata*, and a multispecies grouping were identified. Density of *N. atomata* reached a maximum in September 1983 on both macroalgal species (*N. atomata* accounted < 18 and < 9 % of all turbellarians present on *A. nodosum* and *F. vesiculosus* respectively in any month).

Chironomid larvae and pupae represented from 0 to 7 % of the epifauna on *Ascophyllum nodosum* and 0 to

Table 1. *Ascophyllum nodosum* and *Fucus vesiculosus*. Two-way ANOVA of the density of major epifaunal taxa between 2 macroalgal species and among 14 mo. Data are F-values with corresponding probability levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns, not significant

Taxon	Month	Algal species	Interaction
Foraminifera	7.17***	0.01 ns	2.91**
Turbellaria	25.33***	36.80***	1.82 ns
Nemertinea	18.06***	4.00*	1.58 ns
Nematoda	39.72***	16.92***	4.36***
Annelida	31.38***	12.52***	3.27***
Gastropoda	19.47***	1.05 ns	0.47 ns
Bivalvia	15.65***	5.74*	2.04*
Halacaridae	37.61***	0.88 ns	2.38*
Ostracoda	0.89 ns	1.56 ns	0.83 ns
Harpacticoida (adults and copepodites)	27.93***	15.09***	2.15*
Harpacticoida (nauplii)	33.28***	3.84 ns	3.18**
Calanoida	37.34***	1.78 ns	1.07 ns
Isopoda	11.60***	1.17 ns	0.71 ns
Amphipoda	29.19***	0.09 ns	1.39 ns
Diptera	48.86***	20.42***	2.80**

Table 2. *Ascophyllum nodosum* and *Fucus vesiculosus*. Two-way ANOVA of the density of major harpacticoid species between 2 macroalgal species and among 14 mo. Data are F-values with corresponding probability levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns, not significant

Species	Month	Algal species	Interaction
<i>Harpacticus</i> sp. 2	8.80***	3.58 ns	0.60 ns
<i>Tisbe</i> spp.	4.82***	4.44*	0.63 ns
<i>Thalestris purpurea</i>	5.36***	10.14**	2.44*
<i>Parastenhelia spinosa</i>	5.54***	1.55 ns	3.12**
<i>Amphiascopsis</i> sp.	10.09***	9.53**	3.14**
<i>Nitocra typica</i>	10.40***	18.21***	2.27**
<i>Mesochra</i> sp. 1	4.82***	44.62***	1.29 ns
<i>Mesochra</i> sp. 2	28.49***	41.81***	2.94**
<i>Heterolophonte discophora</i> (adults)	16.65***	3.98 ns	1.53 ns
<i>Heterolophonte</i> spp. (adults)	50.85***	16.46***	2.69**
<i>Heterolophonte</i> spp. (juveniles)	52.27***	8.84**	3.86***

4 % of the epifauna on *Fucus vesiculosus* (Fig. 5). Chironomid density varied significantly among months and between macroalgal species with a significant interaction between month and macroalgal species (Table 1). Densities increased markedly from May 1983 to a maximum in June 1983 on both macroalgal species (Fig. 6), then declined rapidly during the summer and fall. The marked decline in density is in part due to the emergence of adults from pupae over

this time. Chironomids were rare or absent throughout the winter and spring.

Other less abundant taxa included Foraminifera, Nemertinea, Annelida, Gastropoda, Bivalvia, Ostracoda, Calanoida, Isopoda, and Amphipoda (Fig. 8; Appendices 1 & 2). With the exception of Ostracoda, the density of these minor taxa varied significantly among months (Table 1). Seasonal fluctuations in density were similar among all these taxa with the exception of Foraminifera on *Ascophyllum nodosum*, and Ostracoda and Calanoida on both macroalgal species. Densities generally increased during the spring reaching maxima between June and August 1983. Densities generally declined rapidly throughout the summer and early fall, although some taxa (e.g. Isopoda) had a more protracted period of maximal density. Nemertinea, Gastropoda, Isopoda and Amphipoda were rare or absent throughout the winter, while other minor taxa occurred at low densities. The densities of Nemertinea, Annelida, and Bivalvia varied significantly between macroalgal species (Table 1). The interaction between month and macroalgal species was significant for Annelida and Bivalvia.

The density of most major harpacticoid species, total harpacticoid density (including nauplii) and the total density of most other major (nematodes, halacarid mites, tubellarians and chironomids) and minor taxa were positively correlated with epiphyte biomass on both macroalgal species (Tables 3 & 4).

Classification and ordination

Bray-Curtis similarity coefficients were calculated between macroalgal samples for both *Ascophyllum nodosum* and *Fucus vesiculosus*. Dendrograms produced by group average clustering of these values show 2 distinct clusters separating at approximately 42 and 35 % similarity for *A. nodosum* (Fig. 9) and *F. vesiculosus* (Fig. 10) respectively. These clusters correspond closely to the periods May through October, and November through April. For *A. nodosum*, these clusters subdivide into 4 clusters at approximately 60 % similarity, generally corresponding to the periods: (A) June through October; (B) May; (C) November, March, April; (D) December through February. For *F. vesiculosus* 4 clusters at approximately 52 % similarity corresponded closely to the periods: (A) September, May, June, October; (B) June through August; (C) October, November, March, April; (D) December through February. Samples collected within months were generally most similar to each other.

Ordination by multidimensional scaling (MDS) of macroalgal samples yielded results similar to those of

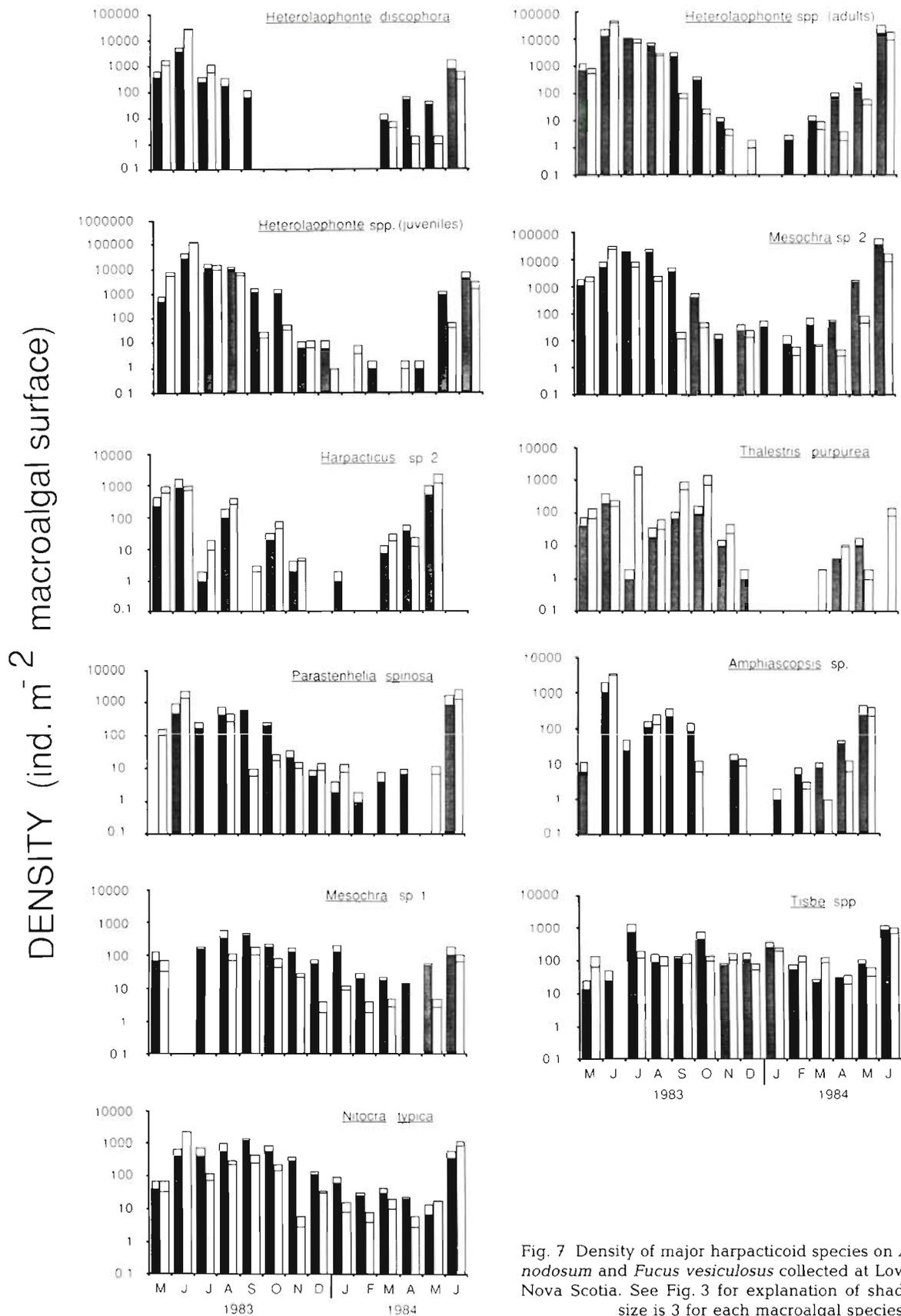


Fig. 7 Density of major harpacticoid species on *Ascophyllum nodosum* and *Fucus vesiculosus* collected at Lower Prospect, Nova Scotia. See Fig. 3 for explanation of shading. Sample size is 3 for each macroalgal species

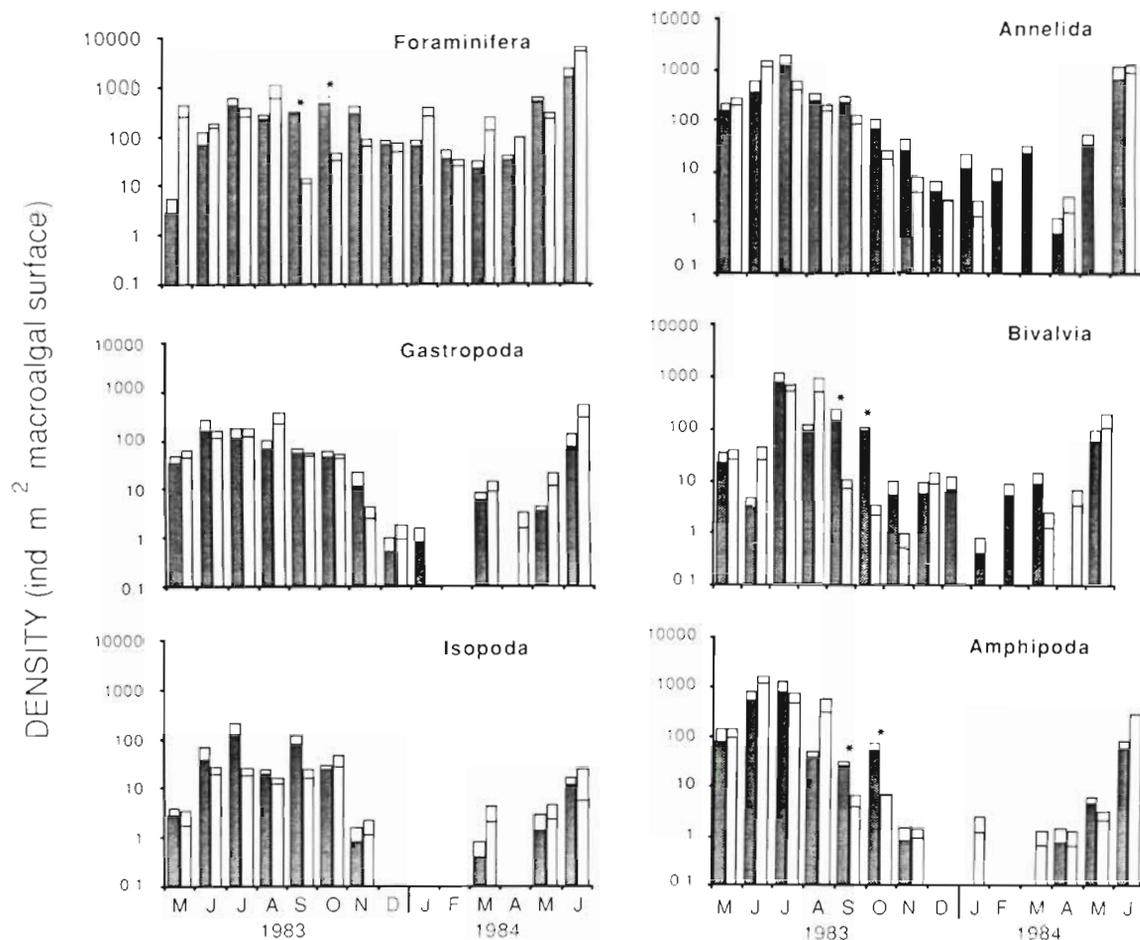


Fig. 8. Density of minor taxa on *Ascophyllum nodosum* and *Fucus vesiculosus* collected at Lower Prospect, Nova Scotia. See Fig. 3 for explanation of shading. Sample size is 3 for each macroalgal species. (*) Months with statistically significant differences between macroalgal species (t-test, $p < 0.05$)

Table 3. *Ascophyllum nodosum* and *Fucus vesiculosus*. Relationship of density of major epifaunal taxa and epiphyte biomass for months where macroscopic epiphytic algae were present. Data are Spearman rank correlation coefficients and corresponding probability levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns, not significant. Sample size is 36 for *A. nodosum* and 30 for *F. vesiculosus*.

Taxon	<i>A. nodosum</i>	<i>F. vesiculosus</i>
Turbellaria	0.308 ns	0.561***
Nematoda	0.842***	0.853***
Annelida	0.541***	0.538**
Gastropoda	0.409*	0.491**
Bivalvia	0.177 ns	0.449*
Halacaridae	0.630***	0.824***
Harpacticoida (adult and copepodites)	0.723***	0.774***
Harpacticoida (nauplii)	0.767***	0.756***
Isopoda	0.276 ns	0.171 ns
Amphipoda	0.576***	0.769***
Diptera	0.688***	0.799***
Total fauna	0.809***	0.789***

Table 4. *Ascophyllum nodosum* and *Fucus vesiculosus*. Relationship of density of harpacticoid copepods and epiphyte biomass for months where macroscopic epiphytic algae were present. Data are Spearman rank correlation coefficients and corresponding probability levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns, not significant. Sample size is 36 for *A. nodosum* and 30 for *F. vesiculosus*.

Species	<i>A. nodosum</i>	<i>F. vesiculosus</i>
<i>Harpacticus</i> sp. 2	0.357*	0.471***
<i>Tisbe</i> spp.	0.125 ns	0.413*
<i>Thalestris purpurea</i>	0.062 ns	0.113 ns
<i>Parastenhelia spinosa</i>	0.128 ns	0.507**
<i>Amphiascopsis</i> sp.	0.290 ns	0.281 ns
<i>Nitocra typica</i>	0.042 ns	0.302 ns
<i>Mesochra</i> sp. 1	0.193 ns	0.284 ns
<i>Mesochra</i> sp. 2	0.760***	0.826***
<i>Heterolaophonte discophora</i>	0.757***	0.711***
<i>Heterolaophonte</i> spp. (adult)	0.734***	0.775***
<i>Heterolaophonte</i> spp. (juvenile)	0.654***	0.813***

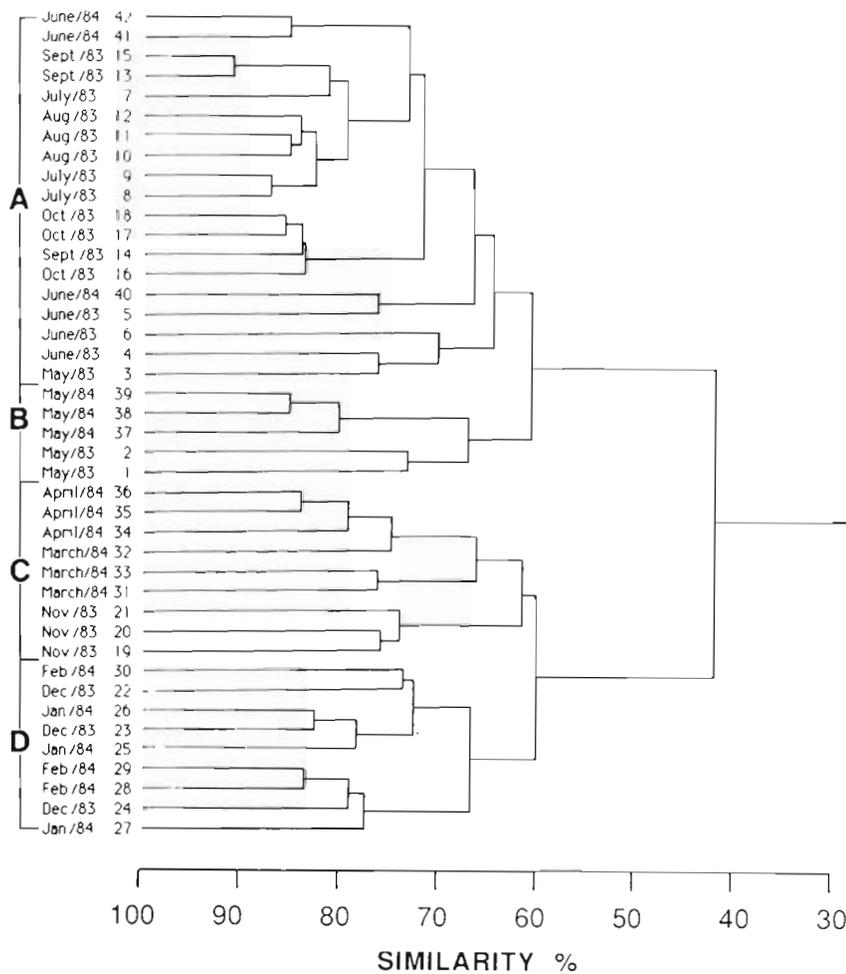


Fig. 9. *Ascophyllum nodosum*. Dendrogram of percentage similarity (Bray-Curtis measure) of faunal composition among 42 samples collected over 14 mo at Lower Prospect, Nova Scotia. Four main clusters (A, B, C, D) are delineated at approximately the 60 % similarity level

cluster analysis for both *Ascophyllum nodosum* (Fig. 11) and *Fucus vesiculosus* (Fig. 12). Clusters of samples from the corresponding classification dendrograms have been delineated on these plots. Samples within months generally show the closest proximity (similarity). The distribution of samples shows a clear relation with epiphytic algal biomass. For both *A. nodosum* and *F. vesiculosus*, epiphyte density generally decreases from the lower left to the upper right of these figures. In general, where samples within months did not group well, between-sample variability in epiphytic algal biomass is high. Stress values (relating to the effectiveness of MDS in representing actual similarities between samples) for the 2-dimensional solutions are 0.102 and 0.087 for *A. nodosum* and *F. vesiculosus* respectively, indicating a satisfactory representation of similarities between samples (Kruskal 1964a).

The program ORDANA is limited to < 51 samples. To enable comparisons of faunal similarity between macroalgal species, the samples were split into 2 groups: May through October, and November through April based on the above clustering and ordination

results (Fig. 9 & 10). Samples from May through October separate at 56 % similarity into 2 major clusters (Fig. 13). These clusters show no clear trends with respect to month or macroalgal species. Both macroalgal species and all months except July, August, and October are common to both clusters (Fig. 13). (Samples from October occur only in Cluster A; samples from July and August occur only in Cluster B.) Ordination by multidimensional scaling of these samples for both macroalgal species supports these results (Fig. 14). Clusters of samples from the corresponding dendrogram are delineated on this plot. Epiphyte biomass decreases from the lower left to upper right of this plot. Samples in Cluster A have lowest epiphyte biomass (Fig. 14). The stress of this 2-dimensional solution is 0.132, indicating a satisfactory representation of similarities between samples (Kruskal 1964a).

Samples from November through April separate at 57 % similarity into 2 clusters closely corresponding to the periods: (A) November, March, April; (B) December through February (Fig. 15). The 2 macroalgal species tend to cluster separately at approximately

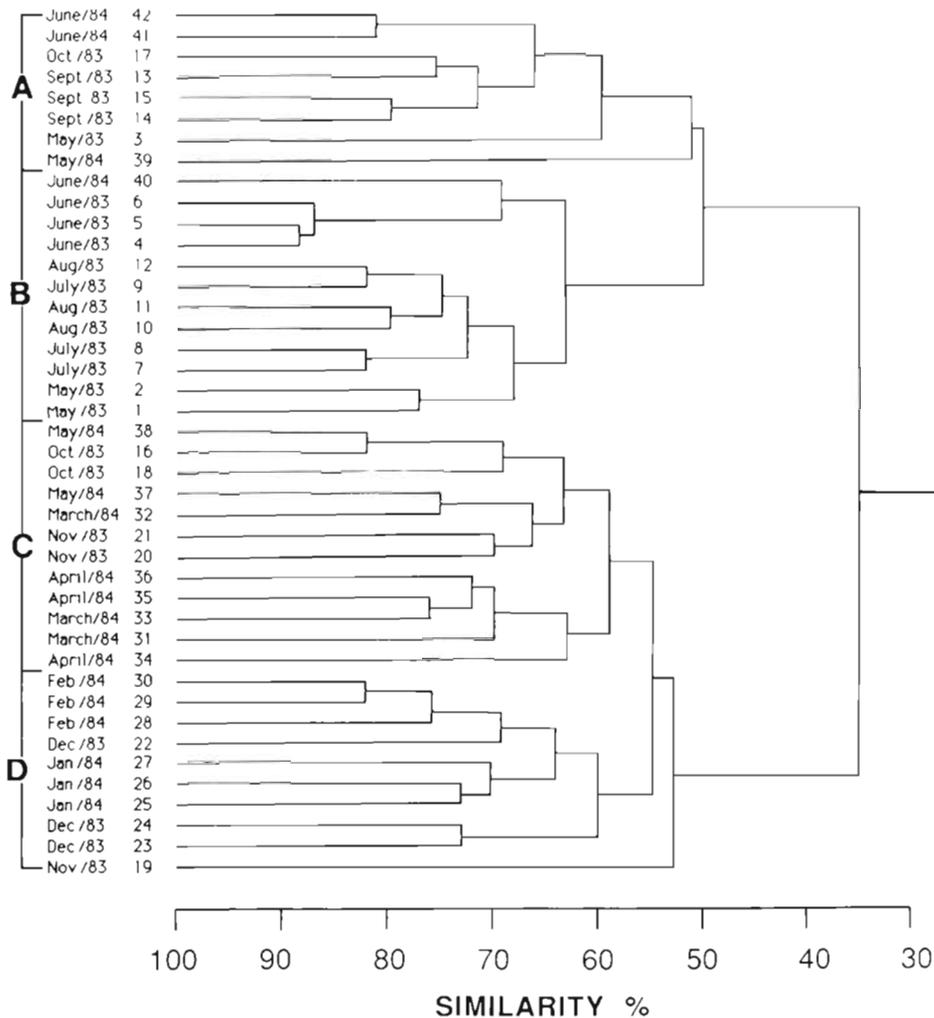


Fig. 10. *Fucus vesiculosus*. Dendrogram of percentage similarity (Bray-Curtis measure) of faunal composition among 42 samples collected over 14 mo at Lower Prospect, Nova Scotia. Four main clusters (A, B, C, D) are delineated at approximately the 52 % similarity level

58 and 62 % similarity within Clusters A and B respectively. Separation of samples by macroalgal species is particularly apparent in samples from December through February (Cluster B). Ordination by multidimensional scaling supports these results (Fig. 16). The stress of this representation is 0.200 indicating a poor representation of actual similarities between samples (Kruskal 1964a).

DISCUSSION

The composition of the epifaunal assemblages of *Ascophyllum nodosum* and *Fucus vesiculosus* in this study is similar to that reported for intertidal *A. nodosum* and *F. vesiculosus* in England (Colman 1940), subtidal *F. vesiculosus* and *F. serratus* in Germany (Ohm 1964), and subtidal *F. serratus* in Denmark (Hagerman 1966). These assemblages are dominated by harpacticoid copepods and their nauplii, and contain many of the meiofaunal families and genera which

constitute the 'typical' phytal fauna (see reviews by Coull et al. 1983, Hicks 1985). The composition of the harpacticoid epifauna corresponds closely to that previously reported for macroalgae (Colman 1940, Ohm 1964, Hagerman 1966, Hicks 1980, 1985) or macroalgal debris (Marcotte 1977). The harpacticoid families Harpacticidae, Tisbidae, and Diosaccidae are typically phytal dwelling (Hicks 1977b). The families Laophontidae and Canthocamptidae are more characteristic of sediment biotopes (Hicks 1977b), although several species of these families are also abundant on *A. nodosum*, *F. vesiculosus*, and *F. serratus* (Colman 1940, Ohm 1964, Hagerman 1966, Hicks 1980).

Pronounced seasonal changes in density and species composition are evident for most components of the epifaunal assemblage of both *Ascophyllum nodosum* and *Fucus vesiculosus* in this study. Seasonal variation in epifauna has been documented previously for intertidal macroalgae (Gunnill 1983) and subtidal macroalgae (Ohm 1964, Hagerman 1966, Mukai 1971, Haage 1975, Edgar 1983). Variations in density reflect popula-

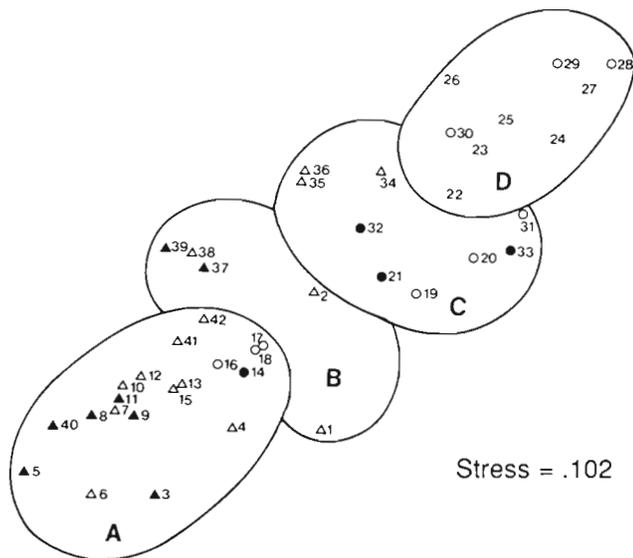


Fig. 11. *Ascophyllum nodosum*. Ordination by multidimensional scaling of 42 samples collected over 14 mo at Lower Prospect, Nova Scotia. Four clusters (A, B, C, D) of samples are delineated visually based on the dendrogram in Fig. 9. Symbols indicate different levels of epiphytic algal biomass (g dry weight m^{-2} macroalgal surface) in samples: no symbol, $0 g m^{-2}$; (○) $< 0.1 g m^{-2}$; (●) $\geq 0.1, < 1.0 g m^{-2}$; (Δ) $\geq 1.0, < 10.0 g m^{-2}$; (▲) $\geq 10.0, < 100.0 g m^{-2}$

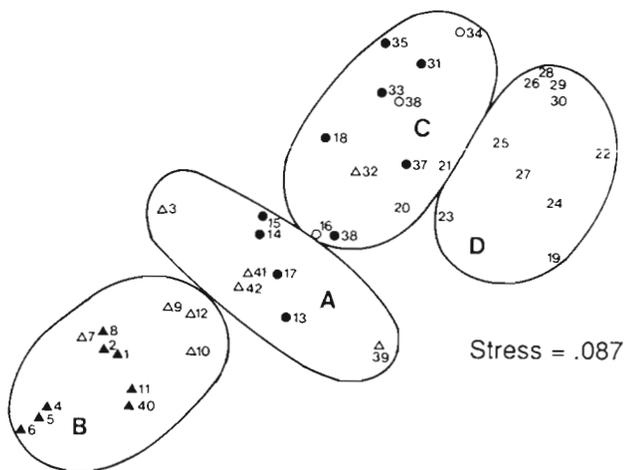


Fig. 12. *Fucus vesiculosus*. Ordination by multidimensional scaling of 42 samples collected over 14 mo at Lower Prospect, Nova Scotia. Four clusters (A, B, C, D) of samples are delineated visually based on the dendrogram in Fig. 10. Symbols indicate different levels of epiphytic algal biomass (g dry weight m^{-2} macroalgal surface) in samples: no symbol, $0 g m^{-2}$; (○) $< 0.1 g m^{-2}$; (●) $\geq 0.1, < 1.0 g m^{-2}$; (Δ) $\geq 1.0, < 10.0 g m^{-2}$; (▲) $\geq 10.0, < 100.0 g m^{-2}$

tion dynamics, which are controlled by a complex interplay of physical and biological factors. Fluctuations in the density of epifaunal taxa in this study generally exceed those previously reported. This may be due in part to the relatively harsh physical environment at Lower Prospect. Low epifaunal densities on

subtidal *F. serratus* in the Oresund have been related to low water temperatures (Hagerman 1966). However, most seasonal studies of macroalgal epifauna have been limited to more temperate regions where water temperatures do not fall below $7.0^{\circ}C$.

Epiphytic algae appear to have a pronounced effect on the abundance and species composition of the epifauna of *Ascophyllum nodosum* and *Fucus vesiculosus*. The density of most major taxa was positively correlated with epiphyte biomass, and cluster analysis and multidimensional scaling indicated that sample groupings were strongly related to epiphytic algal biomass. A similar relation has been reported previously for various macroalgal species (Colman 1940, Hagerman 1966, Zavodnick 1967, Nagel 1968, Kangas 1978, Gunnill 1982, 1983, Edgar 1983). Epiphytic algae and associated microflora (bacteria, diatoms, fungi) represent abundant and diverse food resources. Amphipods (Hagerman 1966, McBane & Croker 1983, Pederson & Capuzzo 1984, D'Antonio 1985), gastropods (Hagerman 1966, D'Antonio 1985) and chironomid larvae (Hagerman 1966, Morley & Ring 1972) are known to graze epiphytic algae. Harpacticoid copepods and nematodes consume microbial films and may exhibit very specific food preferences (Lee et al. 1976, Hicks 1977a, Trotter & Webster 1984). Highly selective feeding by members of the epifaunal community may allow for the coexistence of a wide variety of morphologically similar species.

The presence of epiphytic algae increases microhabitat complexity providing spatial refuges which may reduce predation on the epifauna (Coull & Wells 1983). Conversely, the presence of epiphytic algae may enhance predation rates on some species by attracting predators. Pederson & Capuzzo (1984) showed that the amphipod *Calliopius laevisculus* is attracted to the epiphytes of *Fucus* which it consumes along with associated harpacticoid copepods. Increased structural complexity afforded by epiphytic algae also increases opportunities for attachment, enabling species to become established or to maintain their position on macroalgae when subjected to wave action or currents. Microhabitat structure is especially important for those species or life history stages which are poor swimmers. Populations may spread from refuge areas (e.g. the subtidal or areas of low wave exposure) to take advantage of seasonal increases in epiphyte abundance (Edgar 1983).

Dessication is another important factor controlling the distribution and abundance of epifaunal species on intertidal macroalgae (Gunnill 1983). Due to the thickness of the macroalgal mat at Lower Prospect, only the surface layer dried at low tide while the inner fronds remained wet. The algal mat also provides some thermal buffering: temperatures within the mat were up to

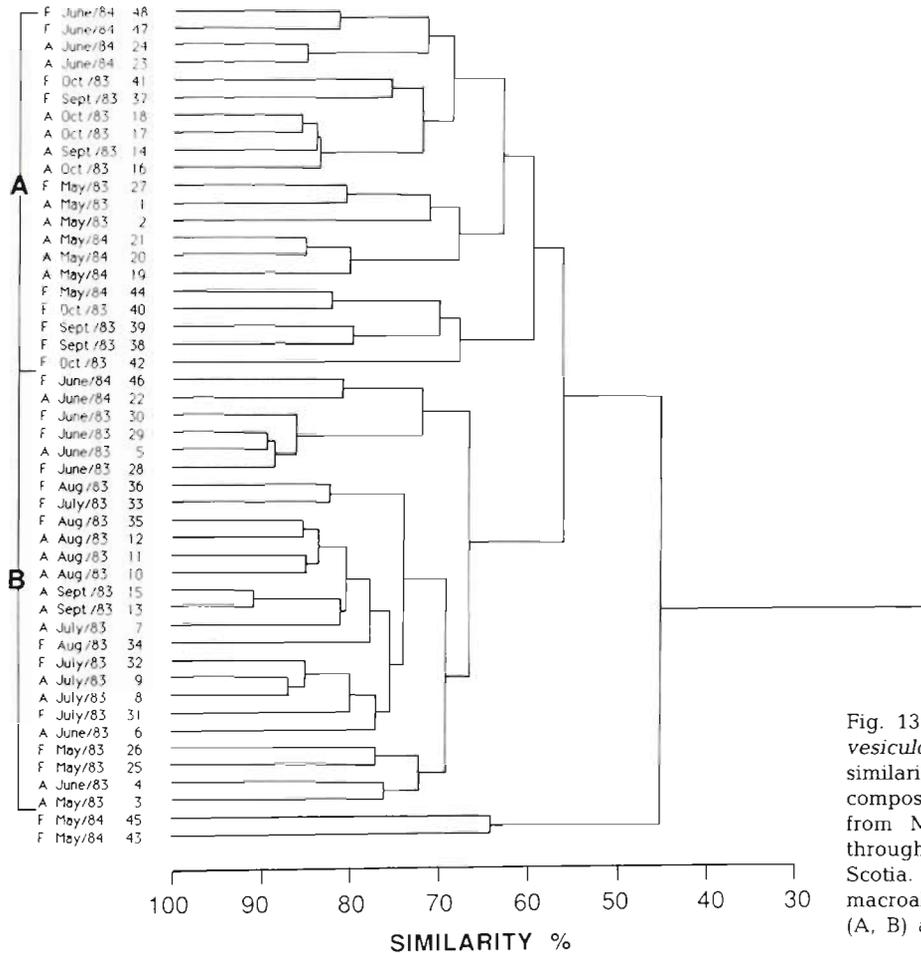


Fig. 13. *Ascophyllum nodosum* and *Fucus vesiculosus*. Dendrogram of percentage similarity (Bray-Curtis measure) of faunal composition among 48 samples collected from May through Oct 1983, and May through Jun 1984 at Lower Prospect, Nova Scotia. Total number of samples for each macroalgal species is 24. Two main clusters (A, B) are delineated at approximately the 56% similarity level

3.0°C cooler in the summer and up to 2.0°C warmer in the winter than air temperatures. Epifaunal species such as the amphipod *Hyale nilssoni* may migrate into the mat when exposed at low tide (McBane & Croker 1983). Smaller, less motile taxa generally are associated with epiphytic algae which retain large amounts of water when exposed at low tide.

Retention of sediments by macroalgae may also influence species composition and abundance of epifauna in some areas (Dahl 1948, Wieser 1959, Hicks 1977b, Warwick 1977). Epiphytic algae and surface mucus secretions of macroalgae may trap sediment and detritus (Dahl 1948, Hicks 1980). However, sediment retention on plants in this study was low, presumably because of the low turbidity of the embayment and the coarseness of its sediments (pers. obs.). Small quantities of coarse grain sediments occasionally were present on *Ascophyllum nodosum* and *Fucus vesiculosus* after storms.

Seasonal changes in the physiological state of the macroalgae may influence the epifaunal assemblage directly or indirectly by affecting the microbial surface film. Increased phenolic release or sloughing of outer

cell layers by *Ascophyllum nodosum* may limit or reduce certain microflora (Filion-Myklebust & Norton 1981). Increased mucus secretion during reproductive periods may affect phytal epifauna by trapping sediments or rendering the surface uninhabitable (Hagerman 1966). Abundance and species composition of the epifauna on the subtidal macroalga *Sargassum seratifolium* in the Sea of Japan was related to growth and annual senescence of the plant fronds (Mukai 1971, Kito 1977). Gunnill (1983) reports that epifauna are in low abundance on *Pelvetia fastigiata* during the winter reproductive period of the alga, although this may be due to environmental factors rather than algal physiological state. In Nova Scotia, epifaunal abundance increases during the reproductive period of *A. nodosum* (Apr to Jun) but decreases during the reproductive period of *Fucus vesiculosus* (Sep). Changes in the reproductive condition of macroalgae may affect only those epifauna which dwell on the surfaces of the macroalgae.

Comparisons of Bray-Curtis similarities between samples of *Ascophyllum nodosum* and *Fucus vesiculosus* indicate a stronger tendency for samples to

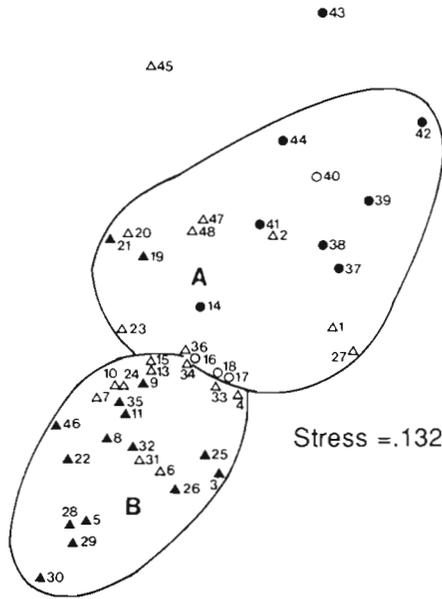


Fig. 14. *Ascophyllum nodosum* and *Fucus vesiculosus*. Ordination by multidimensional scaling of 48 samples collected from May through Oct 1983, and May through Jun 1984 at Lower Prospect, Nova Scotia. Total number of samples for each macroalgal species is 24. Two clusters (A, B) of samples are delineated visually based on the dendrogram in Fig. 13. Symbols indicate different levels of epiphytic algal biomass (g dry weight m⁻² macroalgal surface) in samples: no symbol, 0 g m⁻²; (○) <0.1 g m⁻²; (●) ≥0.1, <1.0 g m⁻²; (△) ≥1.0, <10.0 g m⁻²; (▲) ≥10.0, <100.0 g m⁻²

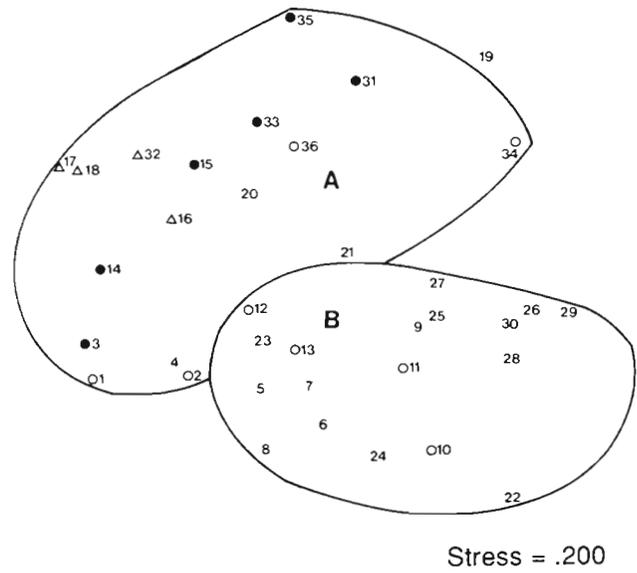


Fig. 16. *Ascophyllum nodosum* and *Fucus vesiculosus*. Ordination by multidimensional scaling of 36 samples collected from Nov 1983 to Apr 1984 at Lower Prospect, Nova Scotia. Total number of samples for each macroalgal species is 18. Two clusters (A, B) of samples are delineated visually based on the dendrogram in Fig. 14. Symbols indicate different levels of epiphytic algal biomass (g dry weight m⁻² macroalgal surface) in samples: no symbol, 0 g m⁻²; (○) <0.1 g m⁻²; (●) ≥0.1, <1.0 g m⁻²; (△) ≥1.0, <10.0 g m⁻²; (▲) ≥10.0, <100.0 g m⁻²

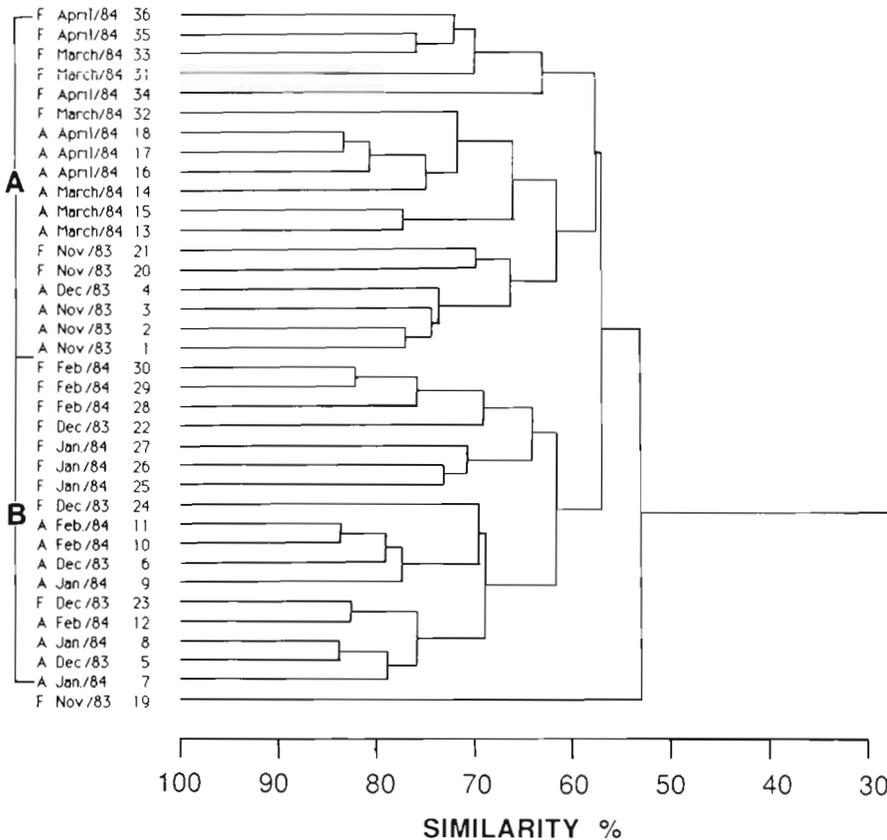


Fig. 15. *Ascophyllum nodosum* and *Fucus vesiculosus*. Dendrogram of percentage similarity (Bray-Curtis measure) of faunal composition among 36 samples collected from Nov 1983 to Apr 1984 at Lower Prospect, Nova Scotia. Total number of samples for each macroalgal species is 18. Two main clusters (A, B) are delineated at approximately the 57% similarity level

Appendix 1. *Ascophyllum nodosum*. Mean density and standard error (in parentheses) of epifauna (individuals m⁻² of macroalgal surface) at Lower Prospect, Nova Scotia. Sample size is 3

Taxa	May	June	July	August	September	October	November
Foraminifera	3 (3)	69 (57)	454 (170)	239 (37)	308 (19)	429 (192)	298 (110)
Turbellaria	476 (424)	1325 (724)	14 877 (8918)	9056 (2787)	6662 (2115)	2673 (854)	413 (239)
Unidentified	468 (428)	1311 (727)	14 848 (8898)	8965 (2742)	6553 (2139)	2649 (851)	340 (183)
<i>Notoplana atomata</i>	8 (4)	14 (4)	29 (21)	91 (46)	109 (24)	25 (10)	74 (57)
Nemertinea	1 (1)	1 (1)	15 (3)	50 (5)	14 (4)	6 (1)	0
Nematoda	25 773 (21 603)	62 465 (36 674)	41 772 (16 011)	16 371 (5738)	4339 (1454)	2784 (920)	247 (70)
Annelida	166 (70)	366 (283)	1257 (650)	261 (81)	242 (58)	70 (38)	26 (17)
<i>Lumbricillus lineatus</i>	166 (70)	296 (245)	1205 (619)	229 (64)	212 (70)	57 (38)	20 (15)
<i>Fabricia sabella</i>	0	71 (43)	47 (29)	31 (16)	35 (29)	11 (6)	3 (3)
<i>Spirorbis borealis</i>	0	0	4 (4)	0	0	2 (2)	2 (2)
<i>Streptosyllis varians</i>	0	0	1 (1)	1 (1)	1 (1)	0	0
Unidentified polychaete	0	0	0	0	0	0	0
Gastropoda	35 (20)	164 (120)	120 (74)	69 (37)	58 (12)	47 (13)	12 (11)
<i>Skeneopsis planorbis</i>	0	103 (103)	9 (9)	1 (1)	11 (7)	3 (2)	0
<i>Lacuna vineta</i>	0	2 (1)	3 (2)	4 (2)	0	5 (3)	1 (1)
<i>Littorina littorea</i>	0	0	0	0	0	0	0
<i>Littorina obtusata</i>	35 (20)	59 (25)	108 (66)	64 (35)	48 (14)	39 (9)	11 (11)
Misc. gastropod	0	0	0	0	0	0	0
Bivalvia	22 (16)	87 (82)	862 (309)	98 (31)	153 (95)	94 (14)	6 (5)
<i>Mytilus edulis</i>	22 (16)	87 (82)	862 (309)	97 (31)	151 (96)	55 (21)	6 (5)
Unidentified spat	0	0	0	0	2 (1)	39 (30)	0
Halacaridae	3020 (1395)	12 540 (9484)	21 191 (3188)	14 145 (1976)	5573 (1902)	3797 (197)	897 (518)
<i>Rhombognathides seahami</i>	2958 (1357)	11 461 (8474)	21 039 (3154)	13 935 (1908)	5465 (1912)	3780 (195)	896 (518)
<i>Halacarellus</i> spp.	61 (40)	1079 (1014)	152 (43)	210 (81)	108 (12)	16 (4)	2 (2)
Ostracoda	3 (3)	0	0	0	6 (6)	6 (3)	0
Harpacticoida	3533 (2669)	55 173 (34 969)	43 919 (5552)	37 114 (4674)	9827 (2881)	3743 (1580)	567 (142)
Family Ectinosomatidae	65 (51)	77 (54)	0	0	0	30 (4)	0
<i>Microsetella norvegica</i>	65 (51)	77 (54)	0	0	0	30 (4)	0
Family Harpacticidae	297 (290)	837 (824)	13 (12)	115 (89)	0	27 (7)	2 (1)
<i>Harpacticus</i> sp. 1	41 (41)	0	12 (12)	11 (11)	0	7 (5)	1 (1)
<i>Harpacticus</i> sp. 2	223 (217)	837 (824)	1 (1)	104 (78)	0	20 (11)	2 (2)
<i>Harpacticus</i> sp. 3	19 (17)	0	0	0	0	0	0
<i>Zaus abbreviatus</i>	14 (14)	0	0	0	0	0	0
Family Tisbidae	14 (14)	25 (25)	778 (536)	97 (66)	124 (20)	490 (286)	72 (12)
<i>Tisbe</i> spp.	14 (14)	25 (25)	788 (536)	97 (66)	124 (20)	490 (286)	72 (12)
Family Thalestridae	180 (179)	1081 (705)	26 (26)	18 (18)	67 (39)	92 (69)	10 (5)
<i>Thalestris purpurea</i>	41 (41)	202 (202)	1 (1)	18 (18)	67 (39)	92 (69)	10 (5)
<i>Thalestris gibba</i>	0	0	0	0	0	0	0
<i>Parathalestris</i> sp.	1 (1)	0	0	0	0	0	0
<i>Diarthrodes major</i>	138 (138)	879 (503)	25 (25)	0	0	0	0
Family Parastenheliidae	0	485 (485)	169 (93)	445 (351)	583 (54)	212 (46)	22 (14)
<i>Parastenhelia spinosa</i>	0	485 (485)	169 (93)	445 (351)	583 (54)	212 (46)	22 (14)
Family Diosaccidae	6 (6)	1051 (1020)	25 (25)	111 (47)	220 (141)	89 (50)	0
<i>Amphiascopsis</i> sp.	6 (6)	1051 (1020)	25 (25)	111 (47)	220 (141)	89 (50)	0
Family Ameiridae	43 (34)	416 (277)	410 (300)	615 (393)	1234 (223)	589 (333)	295 (111)
<i>Nitocra typica</i>	43 (34)	416 (277)	410 (300)	615 (393)	1234 (223)	589 (333)	295 (111)
Family Canthocamptidae	1264 (795)	5448 (2771)	19 785 (1448)	18 929 (6699)	4110 (1523)	598 (175)	141 (36)
<i>Mesochra</i> sp. 1	72 (72)	0	159 (32)	346 (260)	427 (69)	189 (48)	129 (41)
<i>Mesochra</i> sp. 2	1193 (833)	5448 (2771)	19 625 (1462)	18 583 (6490)	3686 (1567)	408 (156)	12 (6)
Family Laophontidae	1163 (1387)	45 710 (28 974)	22 713 (5398)	16 784 (4738)	3462 (1483)	1521 (534)	25 (13)
<i>Pseudonochocamptus koreni</i>	3 (3)	0	0	11 (11)	0	53 (53)	9 (9)
<i>Heterolaophonte discophora</i>	373 (316)	3755 (1713)	241 (134)	171 (170)	62 (61)	0	0
<i>Heterolaophonte</i> spp. (adults only)	743 (650)	12 756 (9040)	10 066 (871)	5635 (1624)	2188 (2188)	325 (72)	9 (4)
<i>Heterolaophonte</i> spp. (juveniles only)	545 (423)	29 199 (18 275)	12 407 (4973)	10 966 (3098)	1213 (484)	1143 (411)	7 (4)
Other harpacticoids	0	42 (42)	0	0	25 (14)	96 (85)	2 (2)
Harpacticoid nauplii	12 394 (10 599)	51 195 (33 020)	51 421 (35 789)	53 102 (31 07)	12 417 (3700)	5496 (2139)	305 (99)
<i>Centropages typicus</i>	0	0	0	0	20 (8)	3 (1)	0
Isopoda	3 (1)	38 (34)	118 (104)	20 (4)	81 (37)	24 (5)	1 (1)
<i>Jaera marina</i>	1 (1)	19 (15)	110 (103)	13 (6)	72 (36)	16 (4)	0
<i>Idotea baltica</i>	2 (2)	7 (7)	8 (3)	7 (4)	9 (2)	9 (1)	1 (1)
<i>Idotea phosphorea</i>	0	12 (12)	0	0	0	0	0
Amphipoda	84 (76)	567 (291)	843 (431)	39 (12)	28 (6)	55 (24)	1 (1)
<i>Amphitoe rubncata</i>	1 (1)	14 (11)	22 (8)	4 (2)	24 (7)	48 (25)	1 (1)
<i>Calliopius laeviusculus</i>	0	0	3 (3)	8 (4)	0	0	0
<i>Chaetogammarus finmarchicus</i>	0	1 (1)	0	0	1 (1)	0	0
<i>Gammarellus angulosus</i>	0	0	0	0	0	0	0
<i>Gammarus oceanicus</i>	1 (1)	1 (1)	10 (9)	2 (1)	0	0	0
<i>Hyale nüssoni</i>	82 (75)	547 (277)	805 (413)	25 (9)	1 (1)	1 (1)	0
<i>Jassa falcata</i>	0	40 (3)	3 (2)	0	2 (2)	6 (4)	0
Diptera (larvae)	563 (417)	13 285 (9830)	3725 (315)	2392 (635)	427 (157)	198 (30)	6 (4)
Total	46 076 (37 233)	197 190 (125 342)	180 574 (53 308)	132 957 (73 81)	40 154 (11 001)	19 481 (4804)	2779 (688)

Appendix 1 (continued)

Taxa	December	January	February	March	April	May	June
Foraminifera	72 (12)	66 (21)	36 (16)	23 (9)	33 (8)	506 (139)	624 (778)
Turbellaria	128 (23)	15 (11)	35 (12)	68 (28)	18 (7)	45 (31)	850 (423)
Unidentified	127 (22)	15 (11)	35 (12)	65 (28)	17 (6)	42 (32)	833 (427)
<i>Notoplana atomata</i>	1 (1)	0	1 (1)	3 (1)	1 (1)	3 (2)	17 (9)
Nemertinea	0	0	0	1 (1)	0	0	16 (3)
Nematoda	100 (35)	77 (26)	46 (20)	157 (61)	1425 (632)	23 925 (5775)	17 117 (12 069)
Annelida	4 (3)	12 (10)	7 (5)	22 (9)	1 (1)	34 (19)	658 (525)
<i>Lumbricillus lineatus</i>	3 (2)	1 (1)	0	21 (8)	1 (1)	34 (19)	226 (131)
<i>Fabricia sabella</i>	0	10 (10)	6 (5)	2 (2)	0	0	418 (407)
<i>Spirorbis borealis</i>	0	0	0	0	0	0	1 (1)
<i>Streptosyllis varians</i>	1 (1)	1 (1)	1 (1)	0	0	0	0
Unidentified polychaete	0	0	0	0	0	0	0
Gastropoda	1 (1)	1 (1)	0	6 (2)	0	4 (1)	76 (62)
<i>Skeneopsis planorbis</i>	0	0	0	0	0	0	1 (1)
<i>Lacuna vincta</i>	1 (1)	0	0	0	0	1 (1)	0
<i>Littorina littorea</i>	0	0	0	0	0	0	0
<i>Littorina obtusata</i>	0	1 (1)	0	6 (3)	0	2 (1)	74 (61)
Misc. gastropod	0	0	0	0	0	0	0
Bivalvia	7 (3)	7 (5)	1 (1)	6 (4)	9 (7)	0	58 (36)
<i>Mytilus edulis</i>	7 (3)	7 (5)	1 (1)	6 (4)	8 (7)	0	15 (12)
Unidentified spat	0	0	0	0	1 (1)	0	43 (41)
Halacandae	166 (52)	61 (27)	45 (29)	327 (266)	556 (129)	1107 (603)	6057 (5333)
<i>Rhombognathides seahamii</i>	166 (52)	61 (27)	44 (28)	324 (263)	547 (125)	1090 (592)	5810 (5107)
<i>Halacarellus</i> spp.	0	0	1 (1)	3 (3)	9 (5)	17 (12)	247 (226)
Ostracoda	2 (1)	2 (0)	3 (1)	1 (1)	4 (2)	7 (7)	0
Harpacticoida	411 (141)	511 (209)	127 (58)	162 (64)	371 (62)	3502 (539)	58 734 (44 027)
Family Ectinosomatidae	5 (3)	5 (2)	2 (1)	6 (3)	7 (1)	29 (15)	0
<i>Microsetella norvegica</i>	5 (3)	5 (2)	2 (1)	6 (3)	7 (1)	29 (15)	0
Family Harpacticidae	7 (5)	4 (1)	10 (7)	11 (7)	73 (33)	502 (408)	0
<i>Harpacticus</i> sp. 1	1 (1)	2 (0)	2 (1)	0	0	0	0
<i>Harpacticus</i> sp. 2	0	1 (1)	0	7 (6)	36 (17)	494 (401)	0
<i>Harpacticus</i> sp. 3	0	0	0	0	4 (1)	1 (1)	0
<i>Zaus abbreviatus</i>	6 (6)	1 (1)	8 (8)	4 (1)	33 (21)	7 (7)	0
Family Tisbidae	111 (59)	261 (97)	53 (23)	22 (6)	29 (3)	85 (23)	886 (304)
<i>Tisbe</i> spp.	111 (59)	261 (97)	53 (23)	22 (6)	29 (3)	85 (23)	886 (304)
Family Thalestridae	2 (1)	4 (3)	1 (1)	3 (2)	12 (7)	52 (27)	0
<i>Thalestris purpurea</i>	1 (1)	0	0	0	4 (0)	11 (6)	0
<i>Thalestris gibba</i>	1 (1)	0	0	0	3 (3)	42 (31)	0
<i>Parathalestris</i> sp.	0	4 (3)	1 (1)	0	1 (1)	0	0
<i>Diarthrodes major</i>	0	0	0	3 (2)	6 (3)	0	0
Family Parastheneludae	6 (3)	2 (2)	1 (1)	4 (4)	7 (3)	0	908 (878)
<i>Parasthenelia spinosa</i>	6 (3)	2 (2)	1 (1)	4 (4)	7 (3)	0	908 (878)
Family Diosaccidae	13 (6)	0	1 (1)	5 (3)	8 (3)	38 (8)	237 (217)
<i>Amphiascopsis</i> sp.	13 (6)	0	1 (1)	5 (3)	8 (3)	38 (8)	237 (217)
Family Ameiridae	117 (26)	62 (33)	25 (7)	31 (14)	21 (3)	7 (7)	380 (229)
<i>Nitocra typica</i>	117 (26)	62 (33)	25 (7)	31 (14)	21 (3)	7 (7)	380 (229)
Family Canthocamptidae	85 (30)	168 (74)	29 (16)	59 (33)	65 (7)	1601 (263)	35 062 (24 876)
<i>Mesochra</i> sp. 1	60 (18)	134 (75)	21 (8)	18 (5)	14 (1)	50 (7)	110 (83)
<i>Mesochra</i> sp. 2	25 (17)	34 (23)	8 (8)	41 (32)	51 (8)	1551 (262)	34 952 (24 932)
Family Laophontidae	63 (57)	5 (5)	4 (1)	20 (11)	131 (44)	1181 (268)	21 291 (18 091)
<i>Pseudonchocamptus koreni</i>	57 (52)	5 (5)	1 (0)	2 (2)	1 (1)	0	13 (7)
<i>Heterolaophonte discophora</i> (adults only)	0	0	0	8 (6)	49 (12)	31 (9)	801 (763)
<i>Heterolaophonte</i> spp. (adults only)	0	0	2 (1)	10 (5)	80 (33)	159 (93)	16 297 (13 785)
<i>Heterolaophonte</i> spp. (juveniles only)	6 (6)	0	1 (1)	0	1 (1)	991 (211)	4180 (3552)
Other harpacticoids	2 (2)	1 (1)	3 (2)	1 (1)	19 (7)	7 (7)	42 (42)
Harpacticoid nauplii	111 (47)	159 (45)	110 (22)	390 (99)	2230 (733)	15 671 (1086)	76 074 (25 806)
<i>Centropages typicus</i>	0	1 (1)	0	0	1 (1)	0	0
Isopoda	0	0	0	0	0	2 (2)	11 (5)
<i>Jaera marina</i>	0	0	0	0	0	1 (1)	9 (6)
<i>Idotea baltica</i>	0	0	0	0	0	1 (1)	1 (1)
<i>Idotea phosphorea</i>	0	0	0	0	0	0	1 (1)
Amphipoda	0	0	0	0	1 (1)	5 (2)	65 (24)
<i>Amphitoe rubricata</i>	0	0	0	0	0	3 (1)	1 (1)
<i>Calliopius laeviusculus</i>	0	0	0	0	0	0	0
<i>Chaetogammarus finmarchicus</i>	0	0	0	0	1 (1)	0	0
<i>Gammarellus angulosus</i>	0	0	0	0	0	0	0
<i>Gammarus oceanicus</i>	0	0	0	0	0	2 (1)	36 (26)
<i>Hyale nilssonii</i>	0	0	0	0	0	0	27 (24)
<i>Jassa falcata</i>	0	0	0	0	0	0	1 (1)
Diptera (larvae)	0	1 (1)	0	1 (1)	12 (6)	35 (20)	2561 (2374)
Total	1000 (261)	913 (329)	409 (148)	1165 (439)	4659 (1424)	44 870 (5574)	163 900 (90 467)

Appendix 2. *Fucus vesiculosus*. Mean density and standard error (in parentheses) of epifauna (individuals m⁻² of macroalgal surface) at Lower Prospect, Nova Scotia. Sample size is 3

Taxa	May	June	July	August	September	October	November
Foraminifera	257 (179)	159 (27)	262 (122)	635 (491)	12 (2)	34 (12)	66 (23)
Turbellaria	1250 (1111)	4177 (741)	6381 (2432)	3954 (2815)	232 (81)	85 (45)	48 (30)
Unidentified	1248 (1110)	4176 (742)	6380 (2433)	3943 (2815)	211 (68)	79 (45)	47 (30)
<i>Notoplana atomata</i>	3 (2)	1 (1)	2 (2)	11 (4)	20 (16)	6 (3)	1 (1)
Nemertinea	2 (2)	2 (2)	4 (4)	30 (17)	19 (17)	1 (1)	0
Nematoda	50 624 (22 875)	280 672 (73 785)	25 198 (13 048)	8794 (1565)	504 (299)	284 (125)	107 (46)
Annelida	212 (73)	1205 (245)	428 (207)	157 (50)	91 (43)	18 (8)	4 (4)
<i>Lumbricillus lineatus</i>	144 (38)	861 (347)	404 (209)	126 (20)	76 (48)	5 (2)	4 (4)
<i>Fabricia sabella</i>	62 (50)	343 (133)	24 (3)	30 (30)	0	3 (2)	0
<i>Spirorbis borealis</i>	4 (2)	0	0	0	15 (11)	10 (8)	0
<i>Streptosyllis varians</i>	0	0	0	0	0	0	0
Unidentified polychaete	2 (2)	0	0	0	0	0	0
Gastropoda	48 (16)	123 (39)	124 (67)	239 (144)	49 (8)	43 (11)	2 (2)
<i>Skeneopsis planorbis</i>	12 (12)	52 (45)	2 (2)	7 (4)	4 (2)	1 (1)	0
<i>Lacuna vincta</i>	7 (5)	0	2 (2)	71 (58)	0	14 (9)	0
<i>Littorina littorea</i>	0	4 (2)	3 (2)	0	1 (1)	0	0
<i>Littorina obtusata</i>	27 (2)	67 (39)	116 (70)	162 (87)	45 (8)	27 (11)	2 (2)
Misc. gastropod	0	0	0	0	0	0	0
Bivalvia	25 (14)	26 (18)	572 (193)	549 (480)	10 (2)	2 (1)	1 (1)
<i>Mytilus edulis</i>	25 (14)	26 (18)	572 (193)	549 (480)	10 (2)	2 (1)	1 (1)
Unidentified spat	0	0	0	0	0	1 (1)	0
Halacaridae	6601 (1336)	44 681 (9376)	18 258 (2752)	9071 (1547)	2206 (314)	1440 (370)	171 (100)
<i>Rhombognathides seahami</i>	6135 (1066)	41 127 (8947)	17 993 (2748)	8969 (1492)	2200 (313)	1438 (368)	169 (98)
<i>Halacarellus</i> spp.	463 (297)	3554 (585)	267 (45)	102 (62)	6 (2)	2 (2)	3 (2)
Ostracoda	80 (74)	53 (53)	0	0	2 (1)	5 (5)	5 (4)
Harpacticoida	12 032 (6597)	244 402 (37 502)	25 392 (8749)	10 726 (4340)	1129 (612)	1199 (892)	190 (81)
Family Ectinosomatidae	471 (225)	37 (37)	0	0	39 (12)	12 (7)	0
<i>Microsetella norvegica</i>	471 (225)	37 (37)	0	0	39 (19)	12 (7)	0
Family Harpacticidae	669 (323)	715 (212)	108 (94)	256 (138)	2 (1)	51 (24)	9 (2)
<i>Harpacticus</i> sp. 1	0	54 (52)	0	0	0	2 (2)	5 (3)
<i>Harpacticus</i> sp. 2	610 (330)	662 (237)	10 (10)	256 (138)	2 (1)	44 (28)	4 (1)
<i>Harpacticus</i> sp. 3	52 (47)	0	98 (98)	0	0	0	0
<i>Zaus abbreviatus</i>	7 (4)	0	0	0	0	4 (3)	0
Family Tisbidae	69 (69)	0	128 (79)	73 (73)	87 (74)	99 (44)	110 (52)
<i>Tisbe</i> spp.	69 (69)	0	128 (79)	73 (73)	87 (74)	99 (44)	110 (52)
Family Thalestridae	1278 (1250)	26 066 (7149)	1558 (1084)	31 (31)	517 (362)	711 (694)	24 (22)
<i>Thalestris purpurea</i>	73 (67)	165 (76)	1509 (1100)	31 (31)	517 (362)	710 (694)	24 (22)
<i>Thalestris gibba</i>	0	3 (3)	0	0	0	0	0
<i>Parathalestris</i> sp.	38 (33)	0	0	0	0	0	0
<i>Diarthrodes major</i>	167 (1150)	25 897 (7181)	49 (49)	0	0	1 (1)	0
Family Parastenheliidae	105 (61)	1458 (940)	0	288 (209)	6 (4)	18 (9)	11 (5)
<i>Parastenhelia spinosa</i>	105 (61)	1458 (940)	0	288 (209)	6 (4)	18 (9)	11 (5)
Family Diosaccidae	0	3106 (351)	0	138 (108)	0	6 (6)	0
<i>Amphiascopsis</i> sp.	0	3106 (351)	0	138 (108)	0	6 (6)	0
Family Ameiridae	35 (35)	2325 (579)	79 (43)	223 (74)	268 (192)	148 (81)	3 (3)
<i>Nitocra typica</i>	35 (35)	2325 (579)	79 (43)	223 (74)	268 (192)	148 (81)	3 (3)
Family Canthocamptidae	1642 (778)	23 737 (7949)	5454 (3019)	1696 (875)	119 (72)	76 (58)	22 (7)
<i>Mesochra</i> sp. 1	35 (35)	0	0	72 (41)	107 (79)	44 (41)	22 (7)
<i>Mesochra</i> sp. 2	1607 (775)	23 737 (7949)	5454 (3019)	1624 (840)	12 (9)	32 (17)	0
Family Laophontidae	7484 (4110)	186 959 (31 785)	18 065 (8223)	8010 (3170)	82 (43)	74 (46)	10 (7)
<i>Pseudonychocamptus koreni</i>	189 (139)	0	0	0	0	21 (21)	0
<i>Heterolaophonte discophora</i> (adults only)	1143 (560)	25 553 (2809)	627 (572)	0	0	0	0
<i>Heterolaophonte</i> spp. (adults only)	558 (252)	38 226 (7576)	6857 (3069)	2384 (508)	65 (32)	18 (9)	3 (2)
<i>Heterolaophonte</i> spp. (juveniles only)	5594 (3460)	123 180 (25 290)	10 580 (5980)	5626 (2663)	18 (13)	36 (19)	7 (6)
Other harpacticoids	279 (151)	53 (53)	0	10 (10)	10 (9)	4 (3)	1 (1)
Harpacticoid nauplii	125 146 (77 434)	205 587 (60 013)	10 375 (2974)	27 172 (9821)	1983 (869)	2650 (1608)	315 (157)
<i>Centropages typicus</i>	0	0	0	0	23 (9)	1 (1)	0
Isopoda	2 (2)	20 (7)	18 (8)	12 (5)	16 (8)	27 (19)	1 (1)
<i>Jaera marina</i>	0	2 (2)	9 (3)	3 (2)	11 (7)	22 (18)	1 (1)
<i>Idotea baltica</i>	2 (2)	6 (3)	9 (9)	9 (4)	6 (6)	5 (2)	0
<i>Idotea phosphorea</i>	0	12 (7)	0	0	0	0	0
Amphipoda	100 (48)	1174 (469)	479 (283)	341 (272)	4 (3)	7 (1)	1 (1)
<i>Amphitoe rubricata</i>	47 (24)	109 (80)	32 (19)	10 (4)	2 (1)	0	0
<i>Calliopius laevisculus</i>	0	0	0	56 (30)	0	0	0
<i>Chaetogammarus finmarchicus</i>	2 (2)	0	0	0	0	0	0
<i>Gammarus oceanicus</i>	1 (1)	0	4 (4)	2 (2)	0	0	0
<i>Hyale nilssoni</i>	49 (26)	1055 (489)	443 (260)	272 (263)	2 (2)	4 (2)	0
<i>Jassa falcata</i>	3 (2)	10 (7)	0	1 (1)	0	3 (2)	1 (1)
Diptera (larvae)	1064 (485)	35 473 (16 180)	1703 (585)	565 (212)	21 (7)	5 (5)	2 (2)
Total	197 386 (107 762)	817 753 (190 676)	89 195 (25 315)	62 246 (20 028)	6302 (2091)	5799 (2981)	913 (383)

Appendix 2 (continued)

Taxa	December	January	February	March	April	May	June
Foraminifera	52 (24)	263 (118)	25 (8)	135 (116)	100 (56)	233 (67)	5337 (1286)
Turbellana	14 (8)	1 (1)	10 (4)	3 (2)	2 (1)	8 (7)	324 (277)
Unidentified	14 (8)	1 (1)	10 (4)	2 (1)	2 (1)	7 (5)	313 (282)
<i>Notoplana atomata</i>	0	0	0	1 (1)	0	1 (1)	11 (6)
Nemertinea	0	0	0	0	0	1 (1)	28 (11)
Nematoda	107 (28)	114 (34)	87 (22)	50 (11)	49 (20)	1117 (641)	3931 (3534)
Annelida	3 (0)	1 (1)	0	0	2 (2)	0	937 (368)
<i>Lumbricillus lineatus</i>	1 (1)	0	0	0	2 (2)	0	404 (171)
<i>Fabrcia sabella</i>	1 (1)	1 (1)	0	0	0	0	6 (6)
<i>Spirorbis borealis</i>	1 (1)	0	0	0	0	0	526 (502)
<i>Streptosyllis varians</i>	0	0	0	0	0	0	0
Unidentified polychaete	0	0	0	0	0	0	0
Gastropoda	1 (1)	0	0	9 (6)	2 (2)	12 (10)	296 (249)
<i>Skeneopsis planorbis</i>	0	0	0	0	0	0	0
<i>Lacuna vincta</i>	0	0	0	2 (2)	0	2 (2)	0
<i>Littorina littorea</i>	0	0	0	1 (1)	0	0	2 (2)
<i>Littorina obtusata</i>	1 (1)	0	0	6 (4)	2 (2)	9 (8)	293 (249)
Misc. gastropod	0	0	0	0	0	0	1 (1)
Bivalvia	9 (5)	0	0	0	1 (1)	4 (4)	110 (93)
<i>Mytilus edulis</i>	9 (5)	0	0	0	1 (1)	3 (3)	12 (7)
Unidentified spat	0	0	0	0	0	1 (1)	98 (98)
Halacaridae	56 (28)	94 (50)	19 (5)	416 (159)	126 (7)	535 (257)	10593 (6631)
<i>Rhombognathides seahami</i>	56 (28)	93 (50)	19 (5)	415 (159)	126 (7)	525 (257)	10493 (6578)
<i>Halacarellus</i> spp.	0	1 (1)	0	1 (1)	0	10 (2)	100 (53)
Ostracoda	2 (1)	3 (3)	0	1 (1)	14 (12)	4 (4)	16 (16)
Harpacticoida	132 (57)	258 (58)	107 (47)	169 (70)	72 (31)	1351 (1093)	22525 (20096)
Family Ectinosomatidae	1 (1)	0	0	3 (2)	2 (1)	1 (1)	0
<i>Microsetella norvegica</i>	1 (1)	0	0	3 (2)	2 (1)	1 (1)	0
Family Harpacticidae	1 (1)	20 (15)	1 (1)	26 (8)	29 (14)	1146 (1023)	513 (499)
<i>Harpacticus</i> sp. 1	1 (1)	4 (4)	0	0	1 (1)	0	33 (33)
<i>Harpacticus</i> sp. 2	0	0	0	18 (12)	12 (10)	1146 (1023)	0
<i>Harpacticus</i> sp. 3	0	0	0	0	2 (1)	0	0
<i>Zaus abbreviatus</i>	0	19 (10)	1 (1)	9 (4)	15 (9)	0	481 (467)
Family Tisbidae	53 (28)	204 (49)	96 (42)	87 (39)	20 (16)	34 (29)	681 (372)
<i>Tisbe</i> spp.	53 (28)	204 (49)	96 (42)	87 (39)	20 (16)	34 (29)	681 (372)
Family Thalestridae	7 (2)	1 (1)	0	5 (2)	10 (2)	2 (1)	97 (75)
<i>Thalestris purpurea</i>	0	0	0	2 (0)	9 (2)	1 (1)	81 (59)
<i>Thalestris gibba</i>	0	0	0	0	1 (1)	0	0
<i>Parathalestris</i> sp.	7 (2)	1 (1)	0	0	0	0	0
<i>Diarthrodes major</i>	0	0	0	3 (2)	0	1 (1)	16 (16)
Family Parastenheiididae	9 (6)	8 (6)	0	0	0	7 (5)	1319 (1316)
<i>Parasthenelia spinosa</i>	9 (6)	8 (6)	0	0	0	7 (5)	1319 (1316)
Family Diosaccidae	9 (5)	0	0	2 (1)	1 (1)	6 (6)	223 (181)
<i>Amphiascopsis</i> sp.	9 (5)	0	0	2 (1)	1 (1)	6 (6)	223 (181)
Family Ameiridae	32 (5)	8 (8)	4 (4)	11 (10)	3 (3)	18 (1)	878 (413)
<i>Nitocra typica</i>	32 (5)	8 (8)	4 (4)	11 (10)	3 (3)	18 (1)	878 (413)
Family Canthocamptidae	16 (15)	9 (3)	5 (5)	10 (3)	3 (2)	52 (33)	8124 (7984)
<i>Mesochra</i> sp. 1	2 (2)	9 (3)	2 (2)	3 (2)	0	3 (2)	68 (40)
<i>Mesochra</i> sp. 2	14 (12)	0	3 (3)	7 (1)	3 (2)	49 (35)	8056 (8018)
Family Laophontidae	2 (1)	4 (4)	1 (1)	24 (21)	3 (3)	85 (43)	10605 (10109)
<i>Pseudonychocamptus koreni</i>	0	0	1 (1)	15 (13)	0	0	40 (28)
<i>Heterolaophonte discophora</i>	0	0	0	4 (3)	1 (1)	1 (1)	285 (282)
(adults only)							
<i>Heterolaophonte</i> spp.	1 (1)	0	0	5 (4)	2 (2)	41 (22)	8720 (8382)
(adults only)							
<i>Heterolaophonte</i> spp.	1 (1)	4 (4)	0	1 (1)	0	43 (23)	1561 (1465)
(juveniles only)							
Other harpacticoids	2 (0)	1 (1)	1 (1)	1 (1)	2 (0)	0	85 (79)
Harpacticoid nauplii	61 (26)	358 (69)	196 (55)	558 (142)	583 (156)	1560 (880)	22764 (14426)
<i>Centropages typicus</i>	0	0	0	0	2 (1)	0	0
Isopoda	0	0	0	2 (2)	0	2 (2)	19 (6)
<i>Jaera marna</i>	0	0	0	2 (2)	0	0	19 (6)
<i>Idotea baluca</i>	0	0	0	0	0	2 (2)	0
<i>Idotea phosphorea</i>	0	0	0	0	0	0	0
Amphipoda	0	1 (1)	0	1 (1)	1 (1)	2 (1)	310 (291)
<i>Amphitoe rubricata</i>	0	0	0	0	0	0	2 (1)
<i>Calliopius laeviusculus</i>	0	0	0	0	0	0	0
<i>Chaetogammarus finmarchicus</i>	0	0	0	0	1 (1)	0	0
<i>Gammarus oceanicus</i>	0	0	0	0	0	0	12 (8)
<i>Hyale nilssoni</i>	0	1 (1)	0	0	0	0	296 (296)
<i>Jassa falcata</i>	0	0	0	1 (1)	0	1 (1)	0
Diptera (larvae)	0	0	0	0	0	1 (1)	1368 (1349)
Total	436 (166)	1095 (92)	445 (54)	1345 (398)	951 (195)	4829 (2479)	86560 (47118)

separate according to macroalgal species from November to April, when epiphytic biomass was low, than from May to October, when epiphytic algal biomass was high. *A. nodosum* and *F. vesiculosus* have different phenologies (*A. nodosum* consists of numerous slender elliptical stalks, while *F. vesiculosus* has numerous broad thin thalli). These differences may be obscured by epiphytic algae when they are abundant. Since *A. nodosum* and *F. vesiculosus* have a similar epiphytic flora (Sieburth & Tootle 1981), differences in the composition of epifauna between *A. nodosum* and *F. vesiculosus* may only become apparent when epiphytic algae are sparse or absent.

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