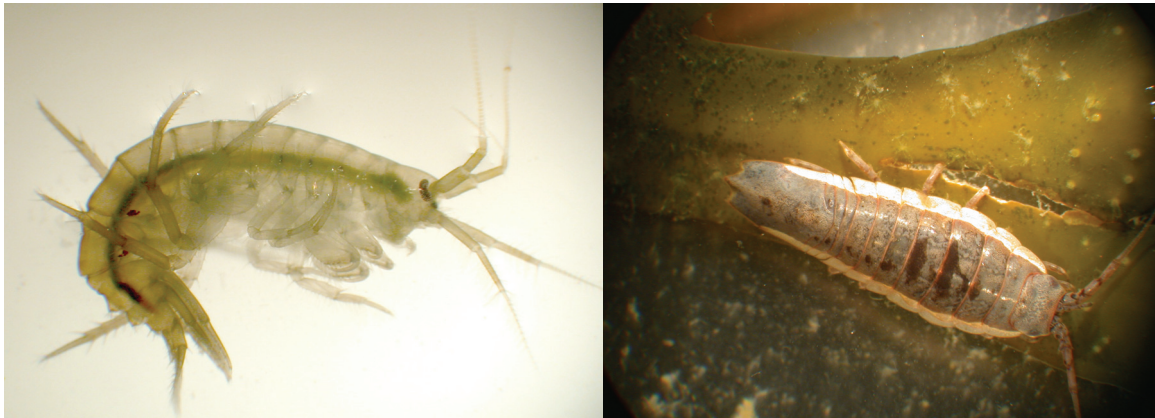# CHAPTER 3

FOOD AND HABITAT CHOICE IN FLOATING SEAWEED CLUMPS: THE OBLIGATE OPPORTUNISTIC NATURE OF THE ASSOCIATED MACROFAUNA

Gammarus sp. – *Idotea baltica*

ABSTRACT

The species composition of macrofauna associated with floating seaweed rafts is highly variable and influenced by many factors like spatial and temporal variation, period since detachment and probably also the seaweed species. The presence of seaweed preferences was assessed by a combination of in situ seaweed samplings and multiple-choice aquarium experiments in a controlled environment, using the seaweed-associated grazing organisms *Idotea baltica* and *Gammarus crinicornis*. Results from the sampling data confirm that the seaweed composition influences macrofaunal species composition and abundance: samples dominated by *Sargassum muticum* displayed higher densities but lower diversities compared to samples dominated by *Ascophyllum nodosum* and *Fucus vesiculosus*. Seaweed preference was also apparent from the multiple-choice experiments, but did not exactly match the results of the community analysis: (1) *I. baltica* had high densities in seaweed samples (SWS) dominated by *F. vesiculosus* and *A. nodosum*, while in the experiments, this isopod was most frequently associated with *Enteromorpha* sp. and *F. vesiculosus*, and fed mostly on *S. muticum, A. nodosum* and *Enteromorpha* sp.; (2) *G. crinicornis* had high densities in SWS dominated by *F. vesiculosus*, while in the experiments, this amphipod was most frequently associated with *S. muticum*, but fed most on *A. nodosum* and *F. vesiculosus*. It is clear from the laboratory experiments that preference for habitat (shelter) and food can differ among seaweed species. However, food and habitat preferences are hard to assess because grazer preference may change if choices are increased or decreased, if different sizes of grazers are used, or if predators or other grazers are added to the experiments. The effects of seaweed composition may also be blurred due to the obligate opportunistic nature of a lot of the associated macrofaunal species.

Keywords: Macrofauna; Floating Seaweed; North Sea; Habitat Preference

1. INTRODUCTION

In recent years, many studies have focused on the fauna associated with floating seaweeds in temperate, (sub)tropical and even polar regions (reviewed by Thiel and Gutow, 2005a, b). Generally, the focal points of these studies are the possibility of rafting as a means of dispersal and the attraction of fish and invertebrates due to the provision of shelter, food and/or a substrate for attachment. Floating seaweeds generally harbour a diverse fauna of grazers that feed on their substrate (Thiel & Gutow, 2005a, b). Both the attractiveness and food value of seaweeds and the presence of pneumatocysts, which increase buoyancy, make them very suitable rafts. The fauna associated with these rafts initially consists of animals originally living on the seaweeds in situ and of a number of mobile species that quickly colonise the seaweeds from the surrounding water column (Ingólfsson, 1995 & 2000, Vandendriessche et al, 2006a). Especially the latter group is very persistent, whereas the number of intertidal species drops with time afloat (Ingólfsson, 1995).

The species composition of macrofauna associated with floating seaweed rafts is shown to be highly variable and influenced by many factors, from which spatial and temporal variations are most intensively studied: densities of associated fauna appear highly seasonal and related to geographic region, distance to shore or the nearest seaweed bank (e.g. Fine, 1970; Stoner & Greening, 1984; Kingsford & Choat, 1985; Tully & O'Ceidigh, 1986; Ingólfsson, 1995). There is, however, little information about the importance of the seaweed species as a structuring factor for the macrofaunal community. As different seaweed species exhibit varying levels of toughness, branching, chemical defenses against grazing, nutritional values and suitability for rafting, it can be expected that some of the seaweed-associated fauna have a preference for a certain seaweed species. As free-swimming associated species are able to move within clumps and between clumps, their seaweed preference (if present) is expected to be expressed in both macrofaunal abundances and seaweed consumption (Thiel & Gutow, 2005b).

Up till now, the relation between macrofaunal abundance and seaweed species composition in floating clumps of seaweed has received little attention. Kingsford & Choat (1985), for example, found significant differences in invertebrate abundances between seaweed species for attached plants, but that pattern was not found for floating seaweeds. They stated that on floating algae, differences between individual plants (e.g. age and origin) are probably a more important source of variation in invertebrate abundances than differences between species. Stoner & Greening (1984) and Ingólfsson (1998) did not find significant correlations between faunal densities and the relative weights of the main constituents (except for the species *Litopia melanostoma*, which was more abundant on *Sargassum natans* than on *S. fluitans* in the Sargasso Sea and the Gulf Stream). Ólafsson et al (2001), however, found significant correlations between diversity and density of harpacticoids and algal diversity, suggesting that the seaweed composition plays an important role in structuring the composition of the associated fauna.

Therefore, the objective of this study is to investigate whether the seaweed species composition of a seaweed clump influences the species composition of the associated macrofauna. The presence of seaweed preferences and the mechanisms by which seaweed species composition influence macrofaunal composition (habitat and food choice) were assessed by a combination of in situ seaweed samplings in the Belgian coastal zone and multiple-choice aquarium experiments in a controlled environment.

2. MATERIALS AND METHODS

2.1 Field data

On 18 May 2004, 23 samples of floating seaweeds were collected at the Belgian continental shelf (BCS), in the southernmost part of the North Sea. On that sampling date, two large seaweed aggregations were encountered, from which the samples were randomly taken. Samples 1-9 were gathered at a distance of 7 km from the coast (51° 11.45N – 2° 36.63E), whereas samples 10-23 were sampled 15 km from the coast (51° 12.87N – 2° 27.59E). The weather conditions were optimal and stable (mean wind speed 7.6 m/s, NW-NE wind, 12.9°C water temperature, humidity 86% and a mean salinity of 33.9 PSU). At the sampling sites, a small assistance boat was lowered from the RV Zeeleeuw to the water surface and the seaweeds were gently approached in order to avoid disturbance. Clumps of floating seaweed were collected using a 300 μm mesh dip net with a ring diameter of 40 cm. Three control samples (i.e. surface water samples without floating seaweed) were taken at each sampling position. After each haul, the net was emptied, rinsed and its contents preserved in an 8% buffered formaldehyde-seawater solution. Each haul was considered as a separate sample and used as such throughout the analyses.

In the laboratory, the preserved samples were rinsed over a 1mm sieve. The seaweeds were sorted and the volume of the algal constituents was recorded to the nearest millilitre, using a graduated cylinder as a measuring device. The macrofauna was identified to species level, wherever possible. For certain taxa, further classification was done based on the life history stage, such as zoea, megalopa or post larval stage of the decapods. Meiofauna and sessile organisms (such as harpacticoid copepods, acarines, nematodes, bryozoans and barnacles) were not counted. The densities were expressed as individuals per litre of seaweed and the diversity was calculated and expressed as expected number of species (per 100 individuals) (Hurlbert, 1971).

Prior to the analyses, the dataset was reduced to the species (1) accounting for > 3% of the total score in any one sample, and (2) found significantly more in seaweed samples compared to control samples. Univariate two-way analysis of variance (ANOVA) was used to test for differences in abundance between seaweed samples and control samples, taking into account the location. If

necessary, a log (x + 1) transformation was performed to meet the required assumptions. In the cases were the assumptions were not met, a non-parametric Mann-Whitney U-test was applied.

Species abundance data of seaweed-associated fauna were subjected to non-metric multidimensional scaling ordination (MDS) using the Bray-Curtis similarity measure. ANalysis Of SIMilarities (ANOSIM) was used to test for significant differences ($p<0.05$) between groups, while the species contributing to dissimilarities between groups were investigated using a similarity-percentages procedure (SIMPER). The relationship between macrofauna densities and variables (sample site, sample volume and relative seaweed species abundance) was analysed using the Spearman rank correlation and the significance was determined using a permutation procedure (RELATE, Clarke & Warwick, 1994). The BIO-ENV procedure was used to define suites of variables that best determine the macrofaunal assemblages. All multivariate community analyses were done using the Primer v5.2.9 software package (Clarke & Gorley, 2001).

2.2 Experimental data

The seaweed preference of two abundant (see Vandendriessche et al, 2006a) floating seaweed-associated organisms from the Belgian coastal waters, *Idotea baltica* and *Gammarus crinicornis* (starved for 48h prior to the start of the experiments)*,* was tested. During the experiments, the organisms were given the choice between five seaweed species that were also sampled on 18th May (see field data) and are commonly encountered in floating seaweed clumps in the English Channel region (Vandendriessche et al, 2006a – *Fucus vesiculosus*, *Himanthalia elongata*, *Enteromorpha* sp., *Ascophyllum nodosum*, *Sargassum muticum*) as well as a plastic aquarium plant as control. Cleaned fragments of the seaweeds of similar size (50 ± 0.5ml; freshly collected from Lake Grevelingen, or from fresh floating seaweed clumps in the case of *H. elongata*) were blotted dry and weighed prior the experiments. The seaweeds were randomly distributed over six compartments in a 1m x 0.3m x 0.4m aquarium and kept in place using nylon string and aquarium suckers. All multiple-choice experiments were conducted at a temperature of 15.5°C (± 1°C) in 34PSU aerated seawater, and the aquarium was provided with removable partitions and equally distributed oxygen sources.

Three types of experiment were carried out; each replicated three times and lasting for 12h (constant light): (1) seaweed preference of *Idotea baltica*, (2) seaweed preference of *Gammarus crinicornis*, and (3) seaweed preference of the two species put together, with possible preference shifts due to competition. The numbers of individuals used for the experiments were based on actual densities on floating seaweeds (83 Ind/l seaweed for *I. baltica* and 67 Ind/l seaweed for *G. crinicornis* on 18th May). Only adult individuals were used with mean lengths of 9 mm for *G. crinicornis* and 25 mm for *I. baltica.* In each experiment, the isopods and/or amphipods could graze and swim freely between the different algal species. Every 2 h, the number of swimming individuals was recorded. At the end of the experiment, the number of swimming and grazing individuals was recorded, the

partitions were put in place and the number of individuals on each seaweed fragment was counted. Afterwards, the seaweeds were blotted dry and weighed again. Three control treatments (to check for autogenic weight loss of the algae) contained the same algae (except *Himanthalia elongata* due to a shortage of fresh material) but no isopods or amphipods. Wet weight of the control algae was determined before and after each experiment.

Differences between initial and final wet weight of the algae were used to calculate the percentage of algae consumed (± SD). Any negative weights were considered as non-grazing events and analysed as zero values (Goecker and Kåll, 2003). The presence of significant autogenic changes in the control treatments was tested with Wilcoxon matched pairs tests, taking into account the variation in initial weight.

All percentage data were arcsin transformed prior to the analyses. Variations in percent weight loss due to grazing, association frequencies of isopods and amphipods, and shifts in preferences of the grazers in the combined experiment compared to the experiments with one single grazer were investigated using Log-Linear Analysis of Frequency Tables, with seaweed species, treatment (single species or combined), and test (three replicates) as factors and association frequencies or weight loss as dependent variables.

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3. RESULTS

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3.1 Field data

The 22 analysed seaweed samples had an average seaweed volume of 327 ml, ranging from 30 ml to 7513 ml. Some SWS also contained floating debris other than seaweed (mean 22 ml - 6% of total volume) like nylon, feathers, plastic and oil. Three seaweed species predominated and were found on both sampling sites (Fig. 1): *Ascophyllum nodosum* (32% of total volume), *Fucus vesiculosus* (31%) and *Sargassum muticum* (22%). The species *Himanthalia elongata* (7%), *Fucus spiralis* (2%), *Cystoseira baccata* (0.3%), *Halidrys siliquosa* (0.1%) and *Enteromorpha* sp. (0.2%) were less common. All SWS, except two, consisted of more than one species, from which *F. vesiculosus* and *A. nodosum* were most frequently encountered (in 18 and 16 samples out of 22, respectively).
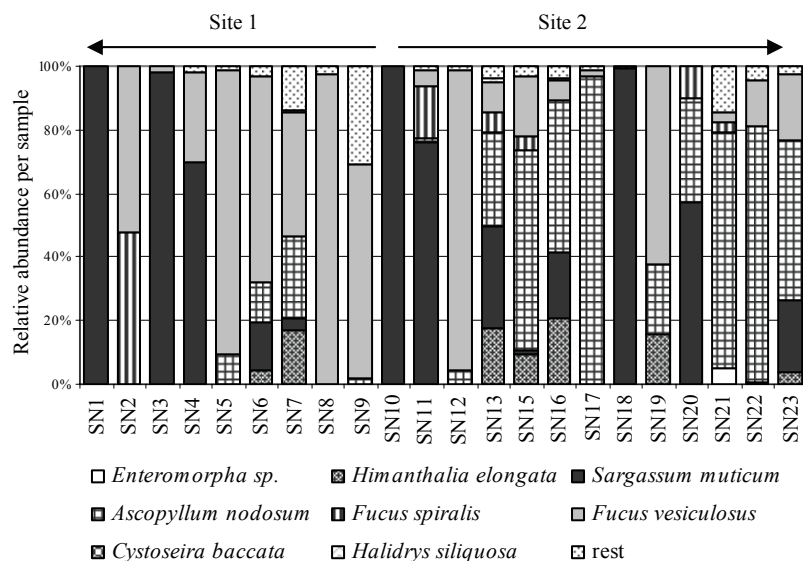
Fig. 1. Column chart showing relative abundances (%) of seaweed species per sample (SN$_x$), with indication of the sample site.

A total of 17148 organisms were identified, belonging to 78 taxa. From the 14 abundantly encountered taxa (> 3% of the total score in any one sample), ten were found significantly more in seaweed samples (SWS) compared to the surrounding water column (CS) (table 1).

Table 1. Univariate analyses p-values (effect of sample type: SWS vs. CS) concerning macrofaunal abundance (significant values: p<0.05 – italic) per species, with their mean association degree (percent of the total number of individuals found in seaweed samples) – designation to groups: bg = background fauna, sw = seaweed-associated fauna – mean density (individuals per liter of seaweed) of seaweed fauna

Group	Species (and stage)	effect SWS/CS p-value	mean association %	group	Mean density Ind/l seaweed
Polychaeta	*Autolytus prolifer* (polybostrichus)	0,214	73,7	bg	-
Insecta	Aphididae sp.	*0,001*	73,1	sw	35.86
Insecta	Formicidae sp.	0,194	75,0	bg	-
Insecta	Chironomidae sp.	*0,000*	75,0	sw	10.62
Crustacea	Calanoida sp.	0,157	29,3	bg	-
Crustacea / Decapoda	*Liocarcinus holsatus* zoea	0,935	45,0	bg	-
Crustacea / Decapoda	*Liocarcinus holsatus* megalopa	*0,000*	73,7	sw	345.74
Crustacea / Decapoda	*Liocarcinus holsatus* juv.	*0,001*	75,0	sw	15.60
Crustacea / Isopoda	*Idotea baltica*	*0,000*	75,0	sw	69.50
Crustacea / Isopoda	*Idotea* sp.	*0,039*	74,9	sw	21.95
Crustacea / Amphipoda	*Stenothoe marina*	*0,000*	75,0	sw	36.13
Crustacea / Amphipoda	*Gammarus crinicornis*	*0,000*	74,8	sw	40.01
Ascidiacea	Larvacea sp.	*0,001*	0,0	bg	-
Osteichthyes / Gadiformes	*Ciliata mustela*	*0,010*	75,0	sw	7.69

When only considering the seaweed-associated fauna, density of the SWS averaged 583 Ind/l (range 136-1609 Ind/l), while the ES (100) averaged 7.2 (range 5-9). Significant correlations were found between volume of the clumps and density of the associated macrofauna (R: -0.55, p: 0.008); and between volume of the clumps and diversity of the associated macrofauna (R: 0.49, p: 0.02). The effect of clump volume was not the same for all the species: some species exhibit a positive relation

with clump volume (*Idotea baltica, Idotea* juveniles*, *Ciliata mustela*) while others show a negative relation (Aphididae sp., Chironomidae sp., *Stenothoe marina*, *Liocarcinus holsatus* megalopae* and juveniles*, *Gammarus crinicornis*) (asterisks indicate significant correlations at the level p<0.05).

MDS and ANOSIM (p= 0.146) analyses based on densities (Ind/l) of the seaweed-associated fauna (Bray-Curtis similarity) indicated no differences between the two sampling points (samples 1-9 and 10-23). Groups defined according to the dominant seaweed species in the samples (highest relative abundance – all seaweed species and fraction of debris considered) do show differences in macrofaunal species composition (Fig. 2; Table 2).
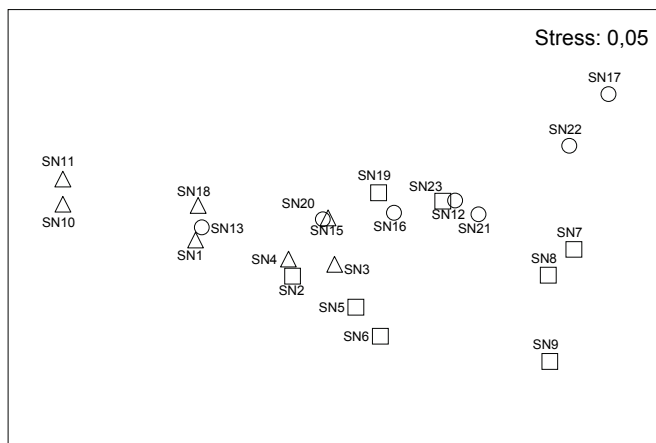

Fig. 2. MDS plot (Bray-Curtis similarities) of samples based on species densities, with indication of dominant seaweed species (highest relative abundance in each sample). *Sargassum muticum* = triangle, *Fucus vesiculosus* = square, *Ascophyllum nodosum* = circle

Results of pair-wise tests reveal significant differences between the *S. muticum* dominated group and the groups dominated by *F. vesiculosus* and *A. nodosum* (dissimilarities of 61% and 53%, respectively - Table 2). The SIMPER-analysis indicated that the dissimilarity between the *S. muticum* dominated group and the *F. vesiculosus* dominated group is mainly due to the abundant presence of *Liocarcinus holsatus* megalopae (percentage contribution: 63%) and *Stenothoe marina* (8%) in the first group and of *Gammarus crinicornis* (9%), *Idotea baltica* (5%) and *Idotea* juveniles (4%) in the second group. Similarly, the differences between the *S. muticum* dominated group and the *A. nodosum* dominated group are caused by the higher abundances of *L. holsatus* megalopae and juveniles (66% and 5%) and *S. marina* (8%) in the first group and of *I. baltica* (5%) and Aphididae sp. (5%) in the second group. Densities of the discussed macrofaunal species per seaweed group are displayed in Fig. 3.

Table 2. Results of ANOSIM and pair-wise tests for differences in macrofaunal community structure depending on the dominant seaweed species in a sample. R-values and p-values are reported.

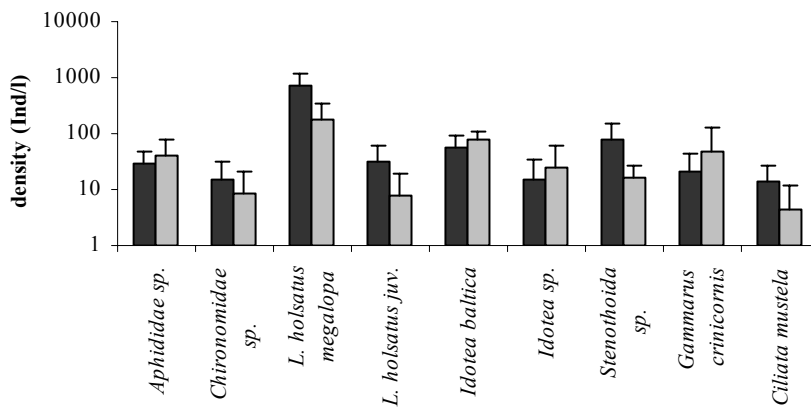| Community structure of seaweed-associated fauna		
	R-value	p-value
Global test	0.277	*0.004*
Groups compared		
S. muticum – F. vesiculosus	0.414	*0.003*
S. muticum – A. nodosum	0.349	*0.021*
F. vesiculosus – A. nodosum	0.076	0.175

Fig. 3. Column chart showing mean densities (Ind/l - indication of SD – logarithmic scale) of the discussed macrofaunal species for the *Sargassum muticum* group (black) and the *Fucus vesiculosus / Ascophyllum nodosum* group (grey)
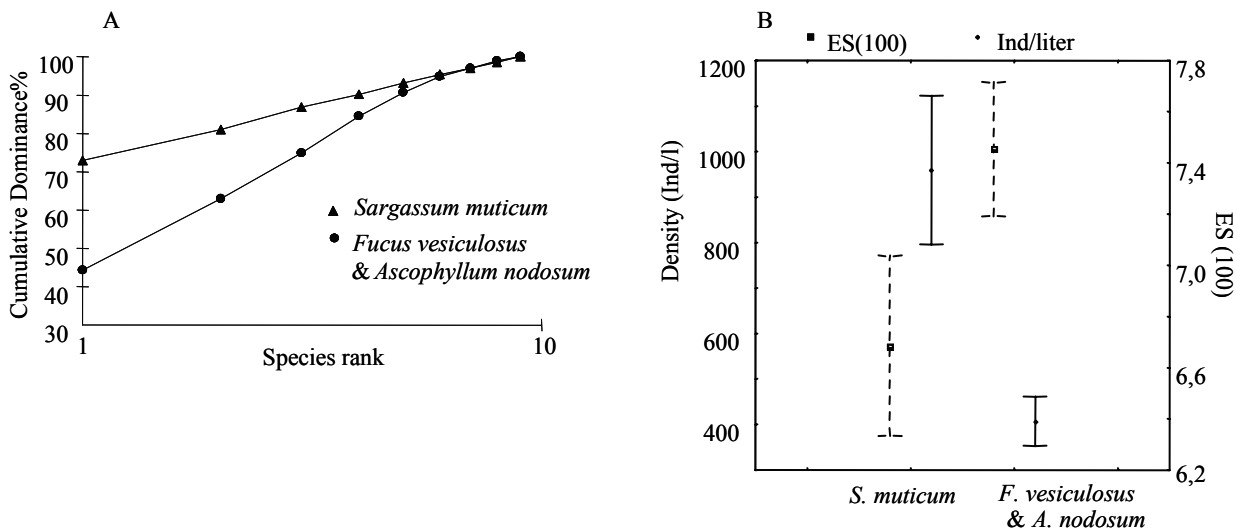

Fig. 4. A. K-dominance curves for the two significantly different sample groups (*S. muticum* and *Fucus vesiculosus/Ascophyllum nodosum*) – B. Whisker plots of density (Ind/l – left Y) and diversity (ES(100) – right Y), with indication of mean and standard error.

As multivariate analysis only indicates differences between *S. muticum* dominated samples and samples dominated by other seaweeds, density and diversity are discussed for two groups. When comparing density and diversity data of *S. muticum* dominated samples with samples dominated by *F. vesiculosus* or *A. nodosum*, we found that: (1) density was significantly higher (MWU p= 0.001) in *S. muticum* dominated samples (mean 960 Ind/l) compared to *F. vesiculosus/A. nodosum* dominated samples (mean 407 Ind/l); (2) the Expected Number of Species was higher in *F. vesiculosus / A. nodosum* dominated samples (mean 7.5 vs. 6.7), however not significantly (MWU p= 0.18); (3) next to a higher diversity, *F. vesiculosus / A. nodosum* dominated samples also exhibited a much higher evenness (Fig. 4a).

Results from the RELATE and BIO-ENV analyses confirmed the influences of seaweed species and volume on the macrofaunal assemblages. RELATE indicated a significant correlation between the standardised Euclidian distance matrix of the variables (sample site, sample volume and relative seaweed species abundance) and the similarity matrix of macrofaunal data ($p < 0.005$). The draftsman plot and the associated correlation matrix showed no evidence of collinearity, so all variables were used in the BIO-ENV analysis. Within the analysed SWS, a combination of five variables (volume and relative abundances of *S. muticum, A. nodosum, F. vesiculosus* and the debris fraction) best explained the macrofaunal assemblages ($\sigma = 0.557$). Correlation analyses between the five selected variables, density and diversity reflect the results discussed in previous sections and in Fig 4b: volume has a negative effect on density and a positive effect on diversity; increasing relative abundances of *F. vesiculosus* and *A. nodosum* have a positive effect on diversity and a negative effect on density, while it is the other way round for *S. muticum*. The effect of an increasing rest fraction (positive for diversity, negative for density) is similar to the effect of *F. vesiculosus* and *A. nodosum*.

3.2 Experiments

Control samples showed no significant weight loss (*Enteromorpha* sp. $p = 0.14$; *Sargassum muticum* $p = 0.07$; *Fucus vesiculosus* $p = 0.7$; *Ascophyllum nodosum* $p = 0.14$) for the examined seaweed species. Therefore, a correction factor for autogenic changes of the seaweeds during the experiments was not used (Petersen & Renaud, 1989).

The preference order of *Idotea baltica* based on the association percentage was: *Enteromorpha* sp. (27%), *F. vesiculosus* (26%), *S. muticum* (9%), plastic (8%), *H. elongata* (7%) and *A. nodosum* (7%). An average of 5% of the population was swimming at the end of the experiments. Although a preference (effect seaweed Chi-sqr.: 52.6; $p < 0.001$) was shown for some seaweed species, this preference was not reflected in the weight loss due to grazing (Fig. 5). As a food choice, *S. muticum* (14% weight loss), *A. nodosum* (13% weight loss) and *Enteromorpha* sp. (11% weight loss) seem to be more attractive (effect seaweed: Chi-sqr.: 167.9; $p < 0.001$).

The weight loss effect due to the grazing activity of *Gammarus crinicornis* was smaller (mean weight loss: 2%) compared to the one of *I. baltica* (mean weight loss: 7%). *G. crinicornis* showed a clear preference for *S. muticum* with 44% of the population found on this seaweed species (effect seaweed Chi-sqr.: 68.3; $p < 0.001$). In spite of this high association percentage, the mean weight loss (2.8%) is slightly lower compared to the ones found for *A. nodosum* (3.8%) and *F. vesiculosus* (2.9%) (effect seaweed Chi-sqr.: 158.2; $p < 0.001$).

The experiments in which both species were used (Fig. 6), show moderate shifts in association percentages of both species, compared to the experiments concerning a single grazer (Fig. 5) (Log-Linear Analysis *Idotea baltica* (a) effect seaweed $p < 0.001$, (b) effect test $p = 0.5$ (c) effect treatment $p = 0.29$, (c) all combined effects $p > 0.05$ – *Gammarus crinicornis* (a) effect seaweed $p < 0.001$, (b) effect test $p = 97$, (c) effect treatment $p = 0.15$, (d) combined effects $p > 0.05$). For both species, there are no significant changes due to the presence of another grazer. As no distinction could be made between the grazing marks of both species in the combined experiment, no conclusions can be made about shifts in grazing effects on the different seaweed species.
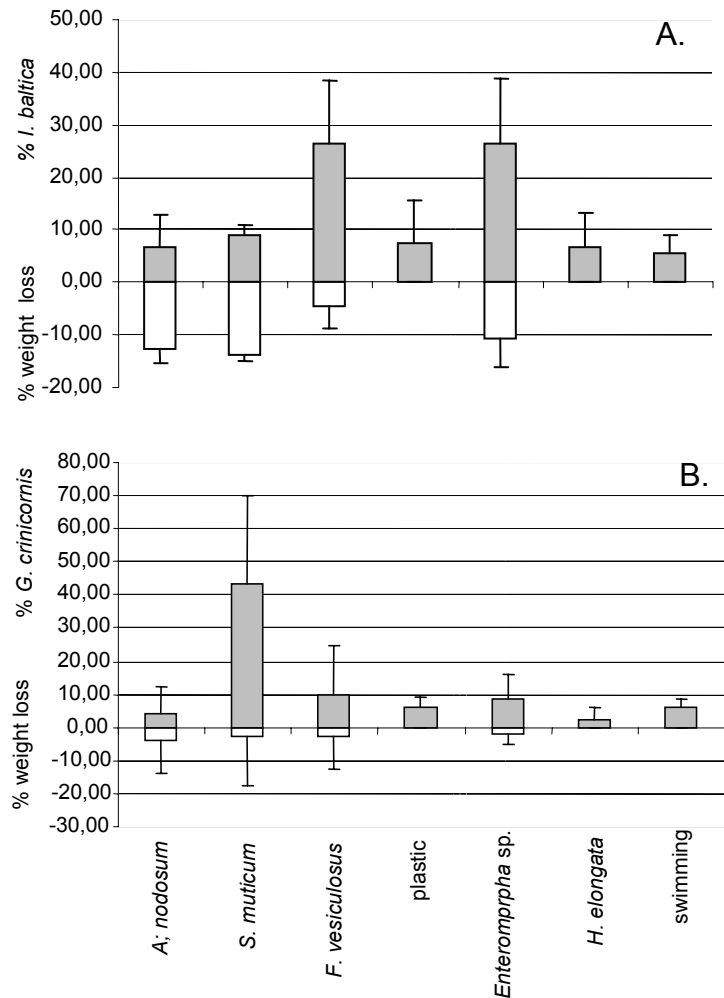

Fig. 5. Seaweed choice of *Idotea baltica* (A) and *Gammarus crinicornis* (B), expressed as the mean percentage (± SD) of the population per seaweed species, and the mean percentage of each seaweed species grazed (± SD)
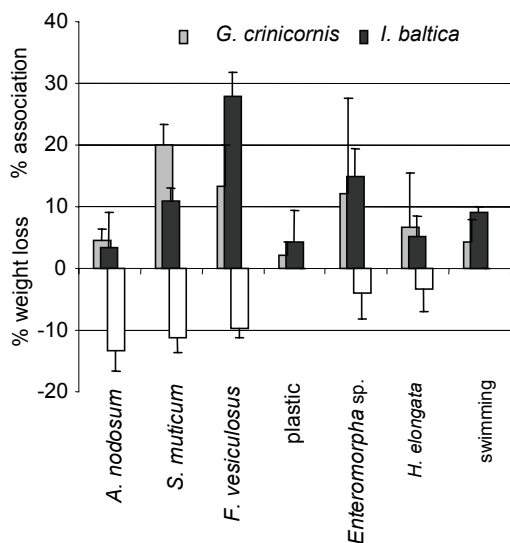

Fig. 6. Seaweed choice of *Idotea baltica* and *Gammarus crinicornis* in a combined multiple-choice aquarium experiment, expressed as the mean percentage (± SD) of the population per seaweed species, and the mean percentage of each seaweed species grazed (± SD)

The main objective of this study was to assess the importance of the seaweed species in structuring the species composition, density and diversity of the seaweed-associated macrofauna. Therefore, an attempt was made to minimise spatial and temporal variation in the field study. A factor that could not be eliminated from this study, however, was the variation in clump size. Some authors have found positive relationships between the abundance of associated fauna and clump size (Fine, 1970; Stoner & Greening, 1984; Kingsford & Choat, 1985; Safran & Omori, 1990; Kingsford 1992; Druce & Kingsford, 1995; Ingólfsson, 1995 & 1998; Ólafsson et al, 2001, Thiel & Gutow, 2005a,b), which may be due to greater protection from predators in larger clumps, reduced danger of dropping off the clumps, a higher food supply compared to the surrounding water column and more surface for attachment. In this study, only few species were found to show such a correlation and therefore it is likely that correlations vary greatly depending on the origin of the seaweeds and the association degree and behaviour of the associated species. A positive correlation between species richness and clump size was not found in Fine (1970), but was found to be significant in Ingólfsson (1995 & 1998), Ólafsson *et al* (2001) and the present study. Thiel and Gutow (2005a) mention a positive correlation between the surface area and the species richness, for at least some floating items. Surface area can be substantially higher for seaweeds with a complex 3D structure. The higher structural complexity of *Sargassum muticum*, compared to *Fucus vesiculosus* and *Ascophyllum nodosum*, may be responsible for differences in density and diversity of the associated macrofauna. The amphipod *Stenothoe marina*, for example, is known to associate with highly branched structures such as seaweeds and hydroids (Bradshaw et al, 2003) and may therefore display higher densities in *S. muticum*. Furthermore, varying levels of toughness, chemical defenses against grazing, nutritional values, value as a refuge and suitability for rafting of different seaweed species (Ragan & Jensen, 1977; Salemaa, 1987; Hay et al, 1988; Tuomi et al, 1988; Denton & Chapman, 1991; Hemmi & Jomalainen, 2004; Thiel & Gutow, 2005a) are expected to result in preferences of macrofaunal species for certain seaweed species in clumps of floating seaweeds. In literature, however, little evidence can be found for the confirmation of this hypothesis (Stoner & Greening, 1984; Kingsford & Choat, 1985; Ingólfsson, 1998; Ólafsson et al, 2001). However, interesting results were obtained when reducing the number of variables in a study. Ingólfsson & Ólafsson (1997) focused on only one species, the harpacticoid *Parathalestris croni*, and found a clear preference for floating thalli of *A. nodosum* and its epiphyte *Polysiphonia lanosa*, to which the copepods can easily cling. In the present study, reduction of macrofaunal data to the clearly associated organisms (see table 1) and minimisation of spatial and temporal variation resulted in clear patterns of seaweed preference. Seaweed preference was also apparent from the results of the multiple choice experiments, but did not exactly match the results of the community analysis: (1) *Idotea baltica* had high densities in seaweed samples dominated by *Fucus vesiculosus* and *Ascophyllum nodosum*, while in the experiments this isopod was most frequently

associated with *Enteromorpha* sp. and *F. vesiculosus*, and fed mostly on *S. muticum, A. nodosum* and *Enteromorpha* sp.; (2) *Gammarus crinicornis* had high densities in seaweed samples dominated by *F. vesiculosus*, while in the experiments this amphipod was most frequently associated with *S. muticum*, but fed most on *A. nodosum* and *F. vesiculosus*. Neither the present study, nor literature provides a definite answer about the preference of these species. It is clear from the laboratory experiments, however, that preference for habitat (shelter) and food can differ among seaweed species. Orav-Kotta and Kotta (2004), for example, found a significant correlation between distributions of *I. baltica* and *F. vesiculosus* in the Baltic Sea, but a shift towards filamentous macro-algae in case of eutrophication. In multiple-choice experiments, it seemed that *F. vesiculosus* was selected as shelter, while filamentous algae were preferred as food when both seaweed species were offered. A similar food preference for filamentous algae was found by Goecker and Kåll (2003) for *I. baltica* and *Gammarus oceanicus*, while Jormalainen et al (2001) and Schaffelke et al (1995) found that *I. baltica* preferred *F. vesiculosus* over other algae, including *Enteromorpha* sp. In a host plant preference experiment including *Fucus serratus* and the red alga *Polysiphonia fucoides*, *I. baltica* was evenly distributed between the host plants, but grazed more on *F. serratus* (Svensson et al, 2004). Pavia et al (1999) performed multiple-choice experiments on *Idotea granulosa* and *Gammarus locusta* and found that the isopods grazed heavily on apices of *A. nodosum*, while the amphipods preferred macro-epiphytes.

Previous studies have suggested that habitat choice of grazers is mainly a function of algal morphology (e.g. Nicotri, 1980) and colour (Salemaa, 1987), while they prefer to feed on filamentous algae due to a higher nutritional value (Boström & Mattila, 1999; Pavia et al, 1999). However, food and habitat preferences are hard to assess because grazer preference may change if choices are increased or decreased, if different sizes of grazers are used, or if predators or other grazers are added to the experiments (Hay et al, 1988; Arrontes, 1990; Schaffelke et al, 1995; Pavia et al, 1999; Boström & Mattila, 1999). The effect of the presence of a second grazer was not significant in the present study, although Pavia et al (1999) and Viejo and Åberg (2003) already suggested that superficial wounds inflicted by isopods could facilitate the feeding of gammarid amphipods. Salemaa (1987), on the other hand, only found negligible competitive effects when using three *Idotea* congeners in different microhabitats.

Although seaweed preference of the associated macrofauna appears highly variable, it is clear that the macrofaunal species composition is strongly influenced by the size and seaweed composition of the clumps. However, these factors do not explain all the variation in species associations, densities and species richness, so it is very likely that, next to spatial and temporal variation (minimised in the present study), the period since detachment (Stoner & Greening, 1984; Edgar, 1987; Ingólfsson, 1995 & 1998; Ingólfsson & Ólafsson, 1997; Ólafsson *et al*, 2001; Thiel, 2003) or the event of washing onto a beach and refloating (Kingsford & Choat, 1985) may also be major structuring factors. The discrepancies between habitat choices found in floating seaweeds and laboratory experiments may, in part, be due to the history of the seaweeds: the stress of floating at the surface (higher temperatures

and UV radiation compared to attached algae) can have a significant effect on the palatability of the algae (Cronin & Hay, 1996) and therefore also on the food choice of the species. Effects of seaweed composition may also be blurred due to the obligate opportunistic nature of a lot of the associated macrofaunal species. The survival of some of these species (e.g. flying insects that were blown offshore and land on floating seaweeds – juvenile fish that need shelter from larger predators) depends on the food, shelter and attachment space offered by the seaweeds. The seaweed-associated fauna therefore takes advantage of the presence of all alternative habitats in the neustonic environment, regardless of the seaweed composition. Eventually, only species/individuals with a good swimming ability (e.g. *I. baltica, G. crinicornis*) can move to a clump with more favourable conditions (higher nutritional value or more shelter) whenever such clumps are available. The availability of the preferred seaweeds is in turn highly dependent on seasonal factors, such as fragmentation at the end of the growing season, variation in the amount of grazing damage and the occurrence of storms (Thiel & Gutow, 2005a). In short, the transient and unpredictable nature of floating seaweed clumps (and their constituent species) is believed to induce an opportunistic behaviour in the associated fauna ensuring their survival but obscuring their food and/or habitat preferences.

In the case of floating seaweeds off the Belgian coast, where few seaweed species (mostly *F. vesiculosus* and *Enteromorpha* sp.) are encountered on the artificial hard substrates, the input of several seaweed species from neighbouring coastlines results in an increased structural complexity of the neustonic layer in the Belgian coastal zone and consequently in higher faunal densities and diversities. Especially the presence of the invading seaweed species *S. muticum* seems to have a significant effect on the encountered species assemblages. The growing importance of this structurally complex seaweed species may enhance the rafting opportunities of high densities of several macrofaunal species that are not commonly encountered in other seaweed clumps.

5. CONCLUSION

In this study, it is clearly shown that the macrofaunal species composition was influenced by the species composition of the seaweeds; and that in some cases the effect of seaweed species may be stronger than competition and spatial distribution. Food and habitat choice are the main mechanisms influencing the seaweed preference of associated macrofauna. However, interpretation of the sample data and experimental outcome, in the light of seaweed preferences, should be done with care. Food and habitat preferences are highly dependent on the offered choices. Preference sequences may alter completely when omitting one or more seaweed species in the experiments, or by changing seaweed abundance. The same is true if the abundance and number of seaweed species to choose from is lower in one seaweed clump compared to another. Another factor to consider, when studying effects of seaweed preference in the field, is the obligate opportunistic nature of some of the associated species:

due to the transient nature of floating seaweed clumps, associated fauna have to be able to survive in sub-optimal conditions concerning food and/or habitat.