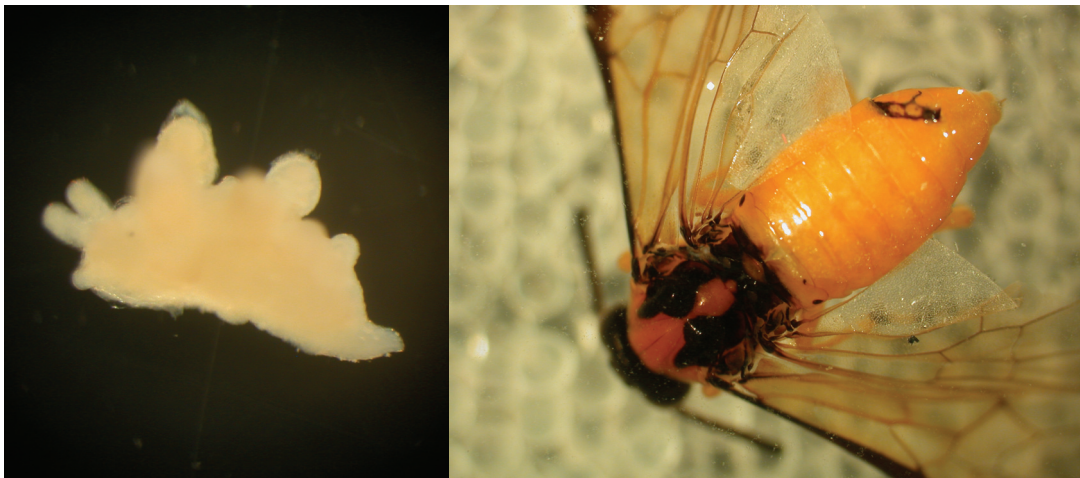# CHAPTER 4

SOURCES OF VARIATION IN FLOATING SEAWEED-ASSOCIATED MACRO-INVERTEBRATES

Tergipes tergipes and Tenthredinidae sp.

ABSTRACT

The species composition and density of fauna associated with floating seaweeds is highly variable and influenced by many factors such as spatial and temporal variation, period since detachment and seaweed species composition. Based on data from floating seaweeds in the Belgian coastal zone, the present study aimed to determine what the driving forces of variation are within the invertebrate community associated with floating seaweeds, and what their relative importance is. Additionally, the temporal variation within the populations of *Gammarus* sp. and *Idotea* sp. was analysed on the levels of size distribution and sexual maturity. The results of the multivariate analysis indicated that spatial and especially seasonal variation are important factors, next to the seaweed species composition of the clumps: the combination of the volume percentages of *Fucus vesiculosus* and *Fucus spiralis*, sea surface temperature and depth resulted in the highest matching coefficient in the BIO-ENV procedure (Rho = 0.26). This coefficient, however, was still rather low, implying that other factors like seaweed age and travelling history strongly structure the assemblage. A large part of the seasonal variation was determined by the timing of the reproduction periods of the associated invertebrates. Both *Gammarus* sp. and *Idotea* sp., for example, reproduced all year round, with the highest intensity in spring. Next to predictable and measurable factors like sea surface temperature, clump volume and seaweed species composition, there are a lot of factors that are hard (e.g. clump age) or even impossible (e.g. occurrence of storms, exchanges between clumps) to quantify. Consequently, the composition and density of floating seaweed-associated macro-invertebrates can only partially be predicted or explained.

Keywords: Macrofauna; Floating Seaweed; North Sea; Spatial and Temporal Variation

1. INTRODUCTION

The presence of floating seaweeds on the sea surface has an important impact on the species composition and diversity of the neustonic fauna. Not only do floating seaweeds carry littoral fauna that stayed associated after detachment, they also attract fauna from the surrounding and underlying water column due to the provision of shelter, a food source, surface for attachment and a means of passive long distance dispersal (Tully & O'Ceidigh, 1986; Ingólfsson, 1995, 1998, 2000; Ólafsson et al, 2001; Thiel & Gutow, 2005a). This process of continuous colonisation results in substantial increases in diversity, density and biomass of the surface layer fauna (Kingsford & Choat, 1985; Druce & Kingsford, 1995; Vandendriessche et al, 2006a). However, floating seaweed clumps are complex systems, in which the species assemblages are influenced by a wide range of factors. The effects of raft age, origin and distance travelled reflect the process of succession during the voyage of floating seaweed clumps after the event of detachment (Stoner & Greening, 1984; Ólafsson et al, 2001, Thiel & Gutow, 2005a). During the drift, the seaweeds and their associated epiphytes and fauna change markedly, altering the living conditions for other colonisers (Edgar, 1987; Ingólfsson & Ólafsson, 1997, Thiel, 2003). The effects of variation linked to the size of the clumps were not straightforward throughout the different studies in the past: 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), 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 Highsmith (1985) and Vandendriessche et al (2006b), only few macrofaunal 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), Hobday (2000b), Ólafsson et al (2001) and Vandendriessche et al (2006b). The effects of seaweed species composition have already been confirmed in Iceland (Ingólfsson & Ólafsson, 1997; Ólafsson et al, 2001) and in the southern part of the North Sea (Vandendriessche et al, 2006b), where some invertebrates show a preference for a certain seaweed species as habitat or food source. However, due to the ephemeral status of floating seaweed patches and the opportunistic nature of the associated fauna, seaweed preference is often not expressed. Influences of spatial and temporal variation on the associated fauna have already been established in studies throughout the world: densities of associated fauna appear highly seasonal and related to geographic region, distance to shore or the nearest seaweed bank (Fine, 1970; Stoner & Greening, 1984; Kingsford, 1992; Kingsford & Choat, 1985; Tully & O'Ceidigh, 1986; Ingólfsson, 1995;

Ingólfsson & Ólafsson, 1997, Dempster & Kingsford, 2004; Ohta & Tachihara, 2004; Wells & Rooker, 2004; Salovius et al, 2005).

Most studies about fauna associated with floating seaweeds focus on a limited number of variation sources: Wells and Rooker (2004), for example, only discussed spatial and temporal variation, while Thiel (2003) focused on the age of seaweed rafts and temporal succession, and Vandendriessche et al (2006b) dealt with the impact of variations in seaweed species composition. The aim of the present study is to synthesise and quantify the combined effects of different sources of variation (depth, temperature, salinity, sample site and date, sample volume, relative seaweed species abundance, clump age), based on data of ephemeral floating seaweed patches at the Belgian coast. In other words, the main question asked is 'What are the driving forces of variation within the invertebrate community associated with floating seaweeds, and what are their relative importances?' Furthermore, the temporal variation within populations of two abundantly encountered genera (*Gammarus* sp. and *Idotea* sp.) was analysed on the levels of size distribution and sexual maturity.

2. MATERIALS AND METHODS

2.1 Sampling

Monthly samples were collected from October 2002 until September 2004 on the Belgian Continental Shelf (BCS), in the southernmost part of the North Sea. Every other week, the RV Zeeleeuw sailed trajectories of ± 60 nautical miles across the Belgian part of the North Sea, thereby increasing the chance of floating seaweed encounters by sailing (as much as possible) perpendicular to the prevailing water currents. Samples were collected at distances of 0.6 to 19.3 nautical miles from the coastline, and were grouped according to their origin into (1) near shore samples (NS) from the Coastal Banks (<10 km off shore), and (2) off shore samples (OS) from the Flemish Banks and Hinder Banks (> 10 km off shore; Fig. 1). Sampling intensity was not equal over the seasons because bad weather often prevented the search for floating seaweeds (especially in the period Oct – Jan). For successful samplings (25 sampling days), the mean number of sampling points (and hence the amount of encountered seaweed clumps) was highest in the periods Feb-Apr and Jun-Sep. During these days, two scientists continuously looked out for seaweeds from the bridge of the research vessel. When clumps of floating seaweed were observed, a small assistance boat was lowered to the water surface and the seaweeds were gently approached, in order to avoid disturbance. Clumps of floating seaweed (minimum three per sampling occasion, and 1 to 4 sampling occasions per sampling date) were collected using a 300 μm mesh dip net with a ring diameter of 40 cm. The maximal size of the clumps was determined by the diameter of the dip net. As they could not be adequately sampled, larger seaweed clumps were left undisturbed. Three control samples (i.e. surface water samples without floating seaweed) were taken at each sampling position (>10 metres away from the nearest seaweed

clump). After each haul, the net was emptied, rinsed and its contents preserved in an 8% buffered formaldehyde-seawater solution.

Environmental variables measured included depth (Marimatech SeaSound 206C), sea surface temperature and salinity (thermosalinograph SBE21).
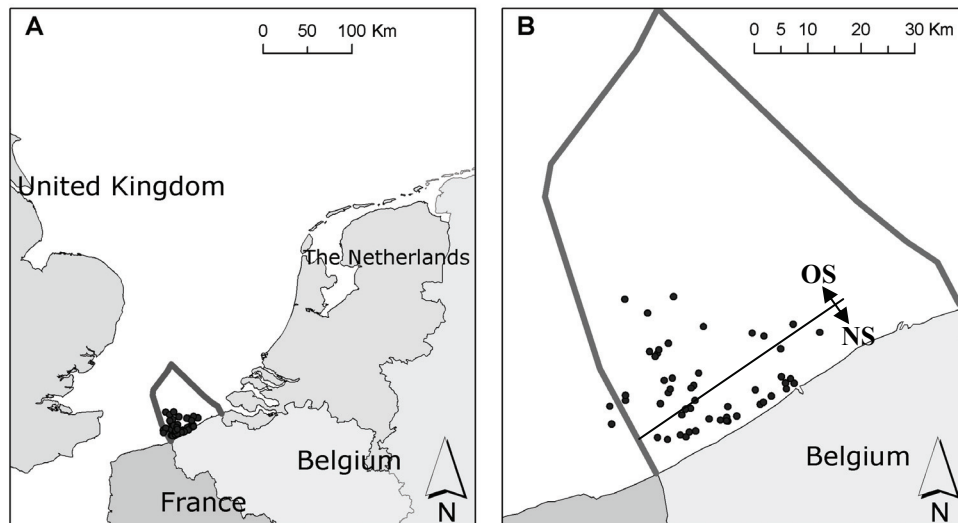

Fig. 1. Map of the sampling area (Belgian Continental Shelf) with indication of the sampling points (black dots) and the grouping of near shore samples (NS) and off shore samples (OS) (black line, B).

2.2 Data acquisition

In the laboratory, the preserved samples were rinsed in fresh water and sieved over a 1mm sieve (cf. Vandendriessche et al, 2006a). After sorting, all non-colonial and mobile macrofauna were identified – if possible – to species level. For certain taxa, further classification was done based on the life history stage, such as zoea, megalopa or post larval stage of decapods. Meiofauna and sessile organisms (such as harpacticoid copepods, acarines, nematodes, bryozoans and barnacles) were not counted. Certain species were reported on a higher taxonomical level (noted as 'sp.' – e.g. juveniles of the genus isopod *Idotea* were grouped); these taxa are further also referred to as 'species'. Species occurring in a wide length range were measured (standard length from the rostral tip to the last abdominal segment for crustaceans).

Raft volumes were quantified by water displacement per seaweed species. Floating objects other than seaweeds were lumped and referred to as 'rest'. The dominant species of seaweed were classified into two categories based on their color and epiphyte load (only determined for samples Oct

2002 – Sept 2003): recently detached or new seaweed (green, few epiphytes), and old seaweed (reddish brown, considerable epiphyte cover) (cf. Stoner & Greening, 1984; Parsons, 1986).

2.3 Data treatment

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 date and location (49 sampling occasions, 2 sample types). If necessary, a log (x + 1) transformation was performed to meet the required assumptions. Of all species, the added value of density was calculated by subtracting background neustonic values from seaweed sample values per sampling occasion (see Vandendriessche et al, 2006a). These values were expressed as individuals per litre of seaweed, and were further used in the analysis of the macrofaunal data.

Effects of spatial (near shore, off shore) and temporal (seasonal) variation on the densities (added values) of the seaweed-associated species were examined using the non-parametric Kruskal-Wallis (KW) and Mann-Whitney U test (MWU), because the assumptions for parametric testing were not fulfilled. As only two samples represented the off shore autumn group, all autumn samples were excluded from the statistical analyses.

The assemblage structure of the seaweed-associated invertebrate fauna was investigated using 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). Patterns of association between macrofaunal abundances and environmental factors (depth, temperature, salinity) and other variables (sample site and date, sample volume and relative seaweed species abundance, clump age) were 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).

3. RESULTS

3.1 Environmental conditions

Seasonal variations in temperature and salinity were pronounced. Sea surface temperatures increased from a minimum of 5.5°C in winter to a maximum of 22.4°C in summer (KW p < 0.001 in both NS and OS samples). Winter temperatures differed significantly between OS and NS (MWU p = 0.002); no significant differences were observed in spring and summer samples (MWU p = 0.12 and 0.72, respectively). Salinity decreased from winter to spring, and increased again in summer (KW NS p = 0.01, OS p < 0.001). Significant effects of spatial variation were observed in summer samples, in which the salinity was higher in the OS samples (Table 1, MWU p = 0.001); no significant differences were observed in winter and spring samples (MWU p = 0.64 and 0.34, respectively).

Depth averaged 14.7 ± 0.6 m in near shore samples and 19.6 ± 0.6m in off shore samples (p< 0.001).

Table 1. Average sea surface temperatures (°C) and salinities (PSU) per sampling area and per season, reported with their standard error.

	season	N	surface temperature	salinity
Near shore	autumn (25/9 – 3/10)	13	16,9 ± 0,3	32,6 ± 0,4
	winter (7/2 – 27/2)	11	7,3 ± 0,2	33,7 ± 0,3
	spring (21/3 – 20/6)	27	14,8 ± 0,6	32,3 ± 0,3
	summer (1/7 – 4/9)	18	19,2 ± 0,4	33,4 ± 0,2
Off shore	autumn (25/9)	2	17,9	32,6
	winter (18/2 – 27/2)	7	5,7 ± 0,2	33,9 ± 0,1
	spring (4/4 – 5/6)	45	13,5 ± 0,5	32,6 ± 0,2
	summer (21/6 – 5/9)	60	18,8 ± 0,2	34,0 ± 0,1

3.2 Seaweed clumps

Clumps of floating seaweed consisted of one or more seaweed species like *Fucus vesiculosus* (Fv)*, Ascophyllum nodosum* (An)*, Halidrys siliquosa* (Hs), *Fucus spiralis* (Fs), *Himanthalia elongata* (He), *Cystoseira* sp. (Csp), filamentous green algae (fil. gr. algae), *Chorda filum* (Cf) and *Sargassum muticum* (Sm), and small amounts of other floating debris like reed, feathers, plastic, nylon, wood and cardboard.

During the sampling period, there were clear seasonal shifts in the relative abundances of the dominant seaweed species in both near shore samples and off shore samples (Fig 2). In the near shore samples, *A. nodosum* and *H. elongata* were quite abundant in autumn and winter samples, while spring and summer samples were mostly dominated by *F. vesiculosus* and *F. spiralis* (KW Fv p = 0.003, An

p < 0.001, He p = 0.003, Fs p = 0.02). In the off shore samples, *A. nodosum, H. elongata* and *F. vesiculosus* were dominant in autumn (few samples) and winter, while the abundances of *F. spiralis* and *S. muticum* became more important in spring and summer (KW Fv p = 0.007, An p = 0.19, He p = 0.18, Fs p < 0.001, Sm p = 0.001). Spatial differences were significant for Fv (MWU p = 0.002) and An (p = 0.002) in winter; for Fv (p = 0.03), An (p = 0.002), He (p = 0.07) and Sm (p = 0.004) in spring; and for Fv (p = 0.03) in summer.
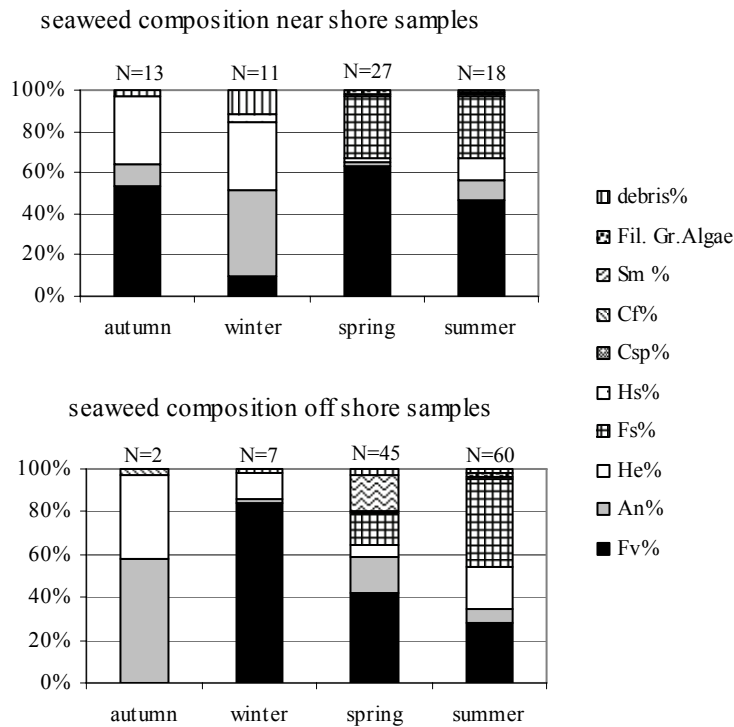

Fig. 2. Bar charts representing seaweed species composition (volume %) of floating seaweed clumps in the near shore and off shore region per season. *Fucus vesiculosus* (Fv), *Ascophyllum nodosum* (An), *Halidrys siliquosa* (Hs), *Fucus spiralis* (Fs), *Himanthalia elongata* (He), *Cystoseira* sp. (Csp), Filamentous green algae (Fil. Gr. Algae), *Chorda filum* (Cf), *Sargassum muticum* (Sm)

3.3 Invertebrate macrofauna

A total of 137 invertebrate taxa were recorded, of which 51 were terrestrial organisms. Forty-four species occurred frequently within floating seaweed patches; and 21 species were significantly more abundant within seaweed samples compared to control samples. Dominant taxa of the seaweed-associated fauna included gammarid amphipods (22% of added value), idoteid isopods (13%), decapod larvae and juveniles (63%), and insects (1%).

A negative correlation existed between seaweed volume and total invertebrate density in both the near shore and off shore samples (NS: Spearman R = -0.37, p = 0.002; OS: Spearman R = -0.41, p < 0.001) and in all seasons (all p < 0.01). Few species showed a significant correlation with seaweed volume: *Idotea emarginata* showed a positive correlation with seaweed volume in the near shore samples (Spearman R= 0.37, p = 0.002), while in the

Table 2. Results of Kruskall-Wallis and Mann-Whitney U tests for all seaweed-associated species, based on added values of densities. P-values in italics are significant. Nd: not determined (one of the groups has only zero-values)

	Kruskall - Wallis near shore	Kruskall - Wallis off shore	Mann - Whitney U winter	Mann - Whitney U spring	Mann - Whitney U summer
Total density (added value)	*0,02*	*< 0,001*	0,16	*0,02*	0,99
Amphipoda					
Gammarus locusta / G. crinicornis	*< 0,001*	*< 0,001*	0,28	0,27	*0,02*
Atylus swammerdami	0,22	0,44	0,37	0,95	*0,04*
Jassa sp.	*0,001*	0,7	0,21	0,13	0,1
Stenothoe marina	0,58	*< 0,001*	nd	*< 0,001*	0,58
Isopoda					
Idotea sp. Juv.	*< 0,001*	*0,03*	0,75	*0,003*	0,11
Idotea linearis	*< 0,001*	0,58	0,21	0,17	*< 0,001*
Idotea baltica	*< 0,001*	*0,03*	*0,026*	*< 0,001*	*0,01*
Idotea emarginata	*< 0,001*	0,79	*0,003*	0,62	0,77
Decapoda					
Liocarcinus holsatus MG	*< 0,001*	*0,001*	nd	0,13	*0,02*
Liocarcinus holsatus Juv.	*0,02*	*0,04*	nd	0,5	0,34
Pisidia longicornis MG	*0,016*	0,09	nd	0,76	*0,02*
Carcinus maenas MG	*< 0,001*	0,29	nd	*< 0,001*	0,94
Hippolyte varians PL	*0,03*	*< 0,001*	nd	0,39	0,28
Palaemon elegans PL	*0,001*	*< 0,001*	nd	0,19	0,89
Insecta					
Helophorus aquaticus	0,9	*< 0,001*	0,07	0,84	0,07
Psyllidae sp.	0,12	*< 0,001*	*0,03*	nd	nd
Scatopsidae sp.	*0,01*	*< 0,001*	*0,04*	0,27	0,58
Sciaridae sp.	0,47	*0,001*	0,07	0,67	0,43
Aphididae sp.	0,1	*< 0,001*	nd	*0,01*	0,21

off shore samples, *Stenothoe marina* (Spearman R = 0.21, p = 0.03) and juveniles of *Idotea baltica* (Spearman R = 0.25, p = 0.008) showed a positive correlation, and postlarvae of *Palaemon elegans* (Spearman R = -30, p = 0.001), Psyllidae (Spearman R = -19, p = 0.04) and Aphididae (Spearman R = 0.21, p = 0.02) showed a negative correlation.

The overall correlation between seaweed volume and diversity (ES(100)) was positively significant (Spearman R = 0.29, p < 0.001). When regions and seasons were analysed separately, positive significant correlations were only encountered in the off shore samples (Spearman R = 0.36, p < 0.001) and in spring (Spearman R = 0.49, p < 0.001).

For most of the associated species, there was a clear temporal variation in their abundance, although the intensity of the variation in some cases varied depending on the sampling area (Fig. 3 & Table 2). The overall density was highest in the near shore samples (mean 2104 Ind/l vs. 1364 Ind/l), and increased from winter (mean 33 Ind/l) to summer (2167 Ind/l). The most abundant amphipods, *Gammarus locusta / G. crinicornis*, showed a significant seasonal signal in both sampling areas with highest densities in summer. Summer densities, however, were significantly different between sampling areas (MWU p = 0.02). Differences between seasons were only significant in near shore samples for *Jassa* sp. (KW p = 0.001), whereas seasonality in *Stenothoe marina* was most pronounced in the off shore samples (KW p < 0.001), where highest densities were recorded in spring (mean 18 Ind/l).

Temporal variation was pronounced in both sampling areas for *I. baltica* and *Idotea* juveniles, but was only significant in near shore samples for *I. linearis* and *I. emarginata*. Spatial variation was obvious in *I. baltica*, for which significant differences in abundance between sampling areas were observed in winter (MWU p = 0.03), spring (MWU p < 0.001) and summer (MWU p = 0.01). Seasonal patterns in abundance were similar for *I. baltica, I. emarginata* and *I. juveniles*, with high abundances in autumn and winter, while *I. linearis* was found more sporadically.

The occurrence of crab larvae was highly seasonal: they appeared in spring, in very high densities for *Liocarcinus holsatus* and *Carcinus maenas* (mean 997 Ind/l and 261 Ind/l, respectively), and were found until the end of summer. Crab juveniles (*L. holsatus*) and postlarvae of prawns (*Hippolyte varians* and *Palaemon elegans*) also started to appear in spring but reached their highest densities in summer. Spatial variation was not significant for prawn larvae and juvenile crabs, but was present in summer for megalopae of *L. holsatus* and *Pisidia longicornis* (MWU p = 0.02 for both) and in spring for *C. maenas* (MWU p < 0.001).

Only few insect taxa were found significantly more in seaweed samples compared to the surrounding water column, and these were only found on a few occasions. Generally, the densities were higher in off shore samples: spatial variation was significant for Psyllidae sp. and Scatopsidae sp. in winter (MWU p = 0.03 and 0.04, respectively), and for Aphididae sp. in spring (MWU p = 0.01).
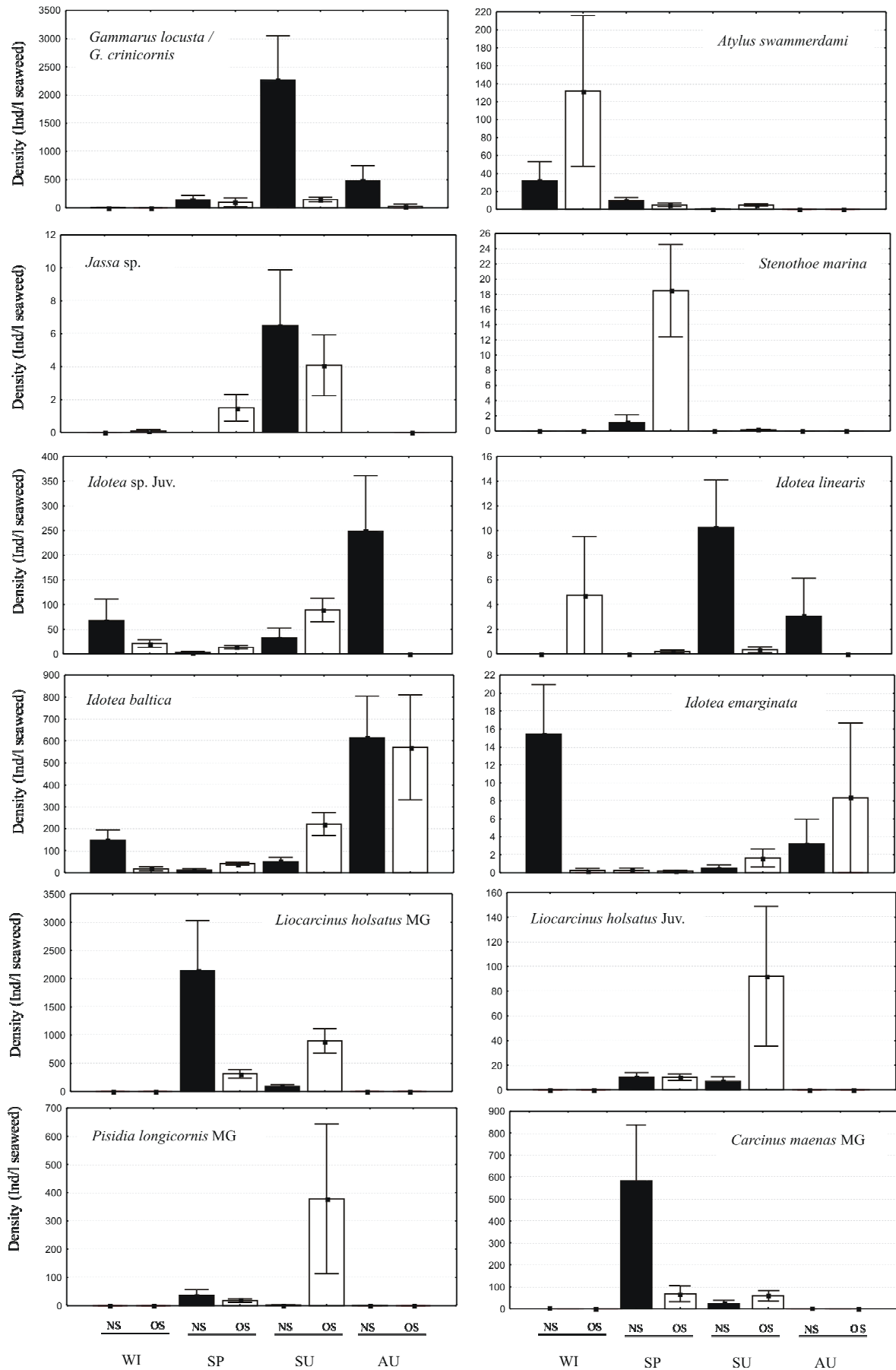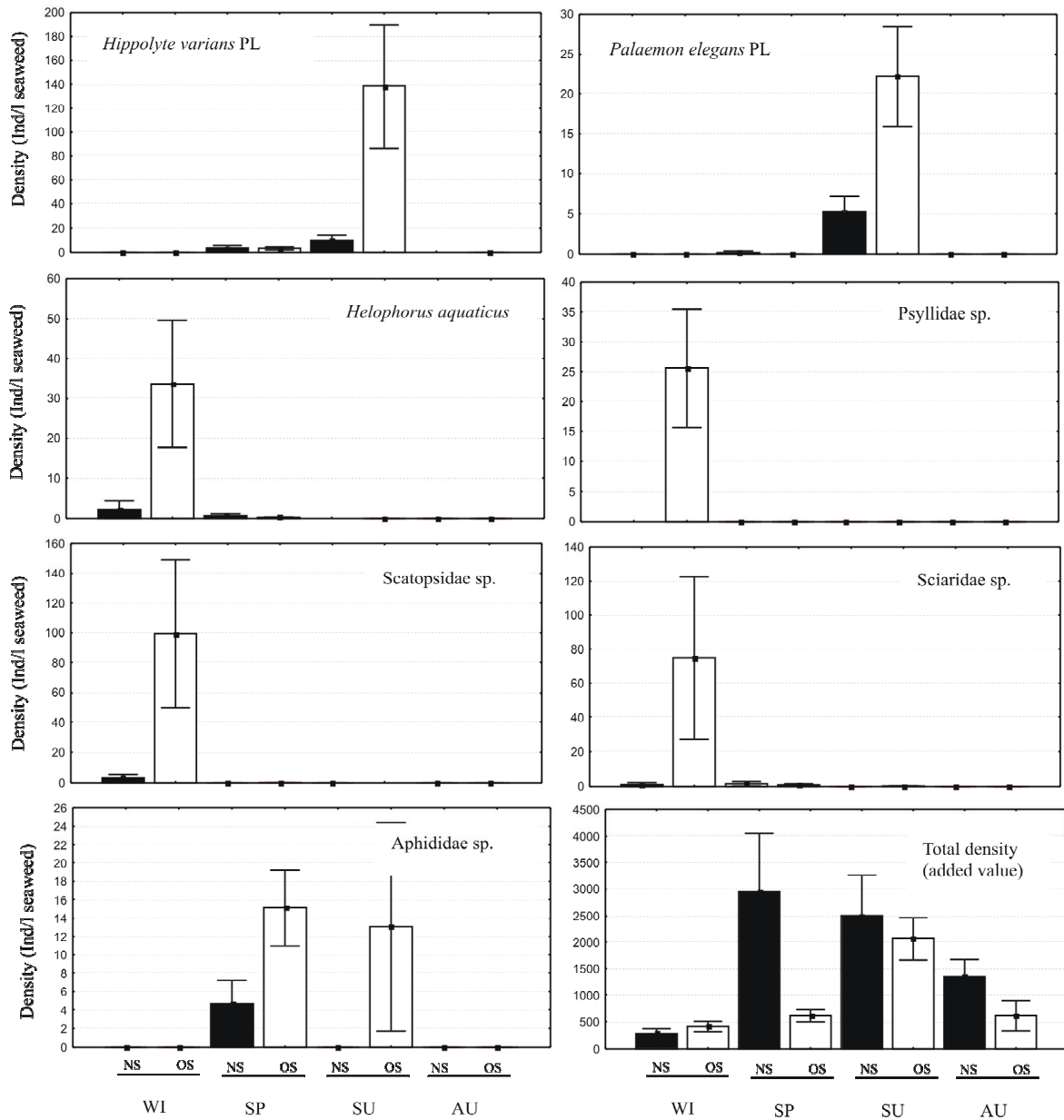
Fig. 3. Spatial (near shore = black bars, off shore = white bars) and temporal variation within abundances of invertebrate macrofauna, with Y-error bars representing standard error.

3.4 Community structure

A two-way ANOSIM based on the densities (added values) of seaweed-associated invertebrate macrofauna revealed significant differences between seasons and sampling areas (R = 0.26 and 0.22, respectively, with a significance level of 0.1% in both cases). Pairwise tests between seasons indicated that the degree of separation between seasons (R –values ranging between 0.29 and 0.68) is, except for the comparison spring-summer (R = 0.14), higher than between sampling areas. The MDS plot with seasons as factors reflected the temporal variation, but indicated that there is a larger variability within the spring samples (average similarity 28.5%) compared to the other seasons

(average similarity autumn: 48.4%, winter: 34.7%, summer: 32.5%) (Fig. 4). SIMPER analysis showed that the contributions to similarities between seasons can be attributed to the presence and abundance of (1) *I. baltica, Idotea* juveniles and *G. locusta / G. crinicornis* in autumn, of (2) *I. baltica, I. emarginata, Idotea* juveniles and *A. swammerdami* in winter, of (3) *L. holsatus* megalopae and juveniles, *I. baltica, Idotea* juveniles, *G. locusta / G. crinicornis, C. maenas* megalopae and *Aphididae* sp. in spring, and of (4) *L. holsatus* megalopae and juveniles, *I. baltica, Idotea* juveniles, *G. locusta / G. crinicornis* and *H. varians* postlarvae in summer. As for sampling areas, *G. locusta / G. crinicornis, I. baltica* and *L. holsatus* megalopae contributed for 75% to similarity between groups, but near shore samples were additionally characterised by *Idotea* juveniles and *C. maenas* megalopae, while off shore samples also contained *L. holsatus* juveniles, *P. longicornis* megalopae and *A. swammerdami*.
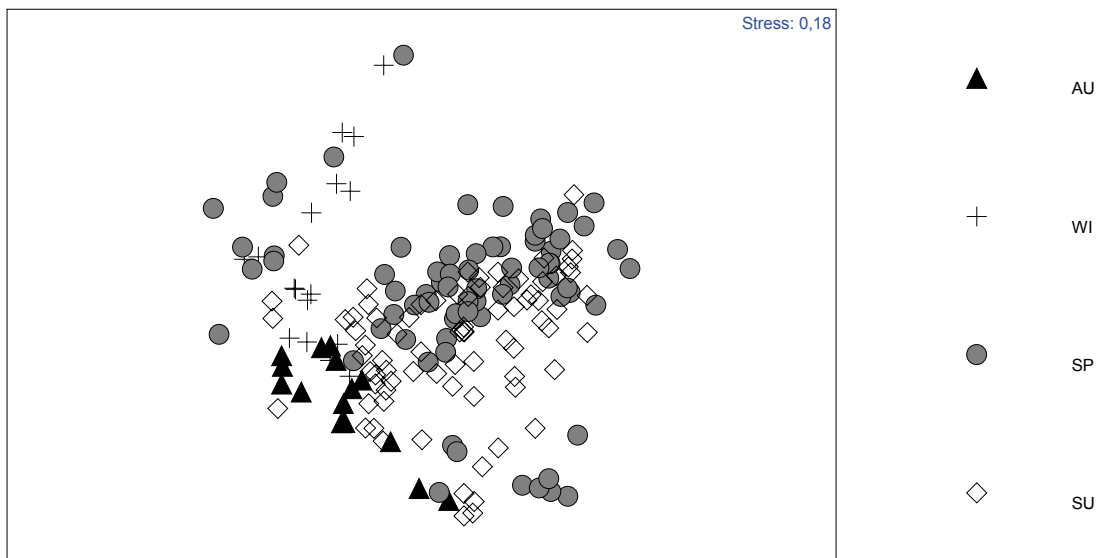

Fig. 4. MDS plot of seaweed samples, with seasons as factors.

The multivariate patterns of invertebrate density data were compared to environmental parameters (seaweed volume, relative abundances of seaweed constituents, surface water temperature and salinity, distance to shore and depth). RELATE indicated a significant correlation between the standardised Euclidean distance matrix of the variables and the similarity matrix of macrofaunal data ($p = 0.003$). 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 samples, a combination of four variables best explained the macrofaunal assemblage: % *Fucus vesiculosus*, % *F. spiralis*, sea surface temperature and water depth. However, the matching coefficient was rather low (Rho = 0.26), implying that there were other factors that strongly structured the assemblage. One of these factors might be the age of the seaweeds, which was investigated using a subset of the data (Oct 2002 – Sept 2003). The ANOSIM results, however, indicated a minor impact of seaweed age (R = 0.1).

3.5 Gammarus sp. / Idotea sp.

Two crustacean genera were abundantly associated with floating seaweeds all through the year: *Gammarus* with mixed populations of *G. crinicornis* and *G. locusta*, and *Idotea* with *I. baltica, I. emarginata* and *I. linearis*. *Idotea* juveniles (<7mm) were grouped because the different genera were hard to distinguish at small sizes. The temporal variation within the populations of these two genera was investigated on the levels of size distribution and sexual maturity (data autumn 2002 – spring 2004).

Gammarus locusta / G. crinicornis

Idotea baltica /I. linearis / I. emarginata/ Idotea juveniles
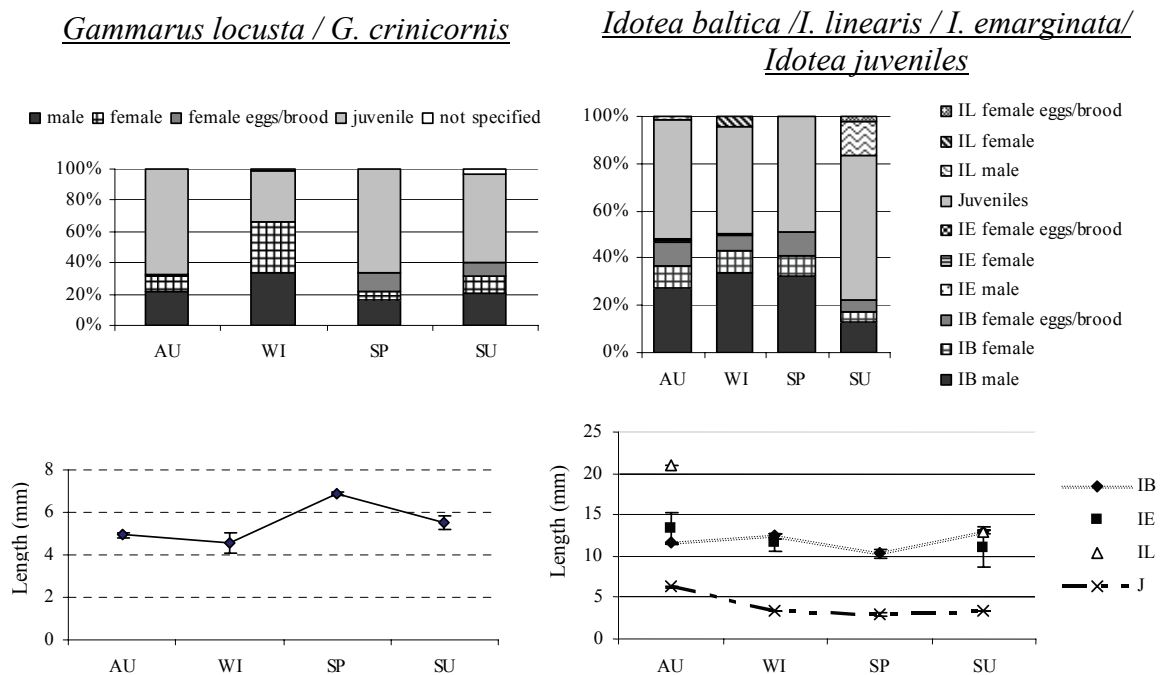

Fig. 5. Left: bar chart of population composition and line plot of seasonal variation in length (mean and standard error) in *Gammarus locusta / G. crinicornis*. Right: bar chart of population composition and line plot of seasonal variation in length (mean and standard error) in *Idotea baltica* (IB), *I. emarginata* (IE), *I. linearis* (IL) and *Idotea* juveniles (J)

In the analysed specimens of *Gammarus*, sexes were generally first recognised from a size of 2 - 5mm. Maximum sizes were 22mm in males and 15.4mm in females. A high percentage of juvenile individuals were present in *Gammarus locusta / G. crinicornis* all through the year (31 – 67%) with highest numbers in spring. Nevertheless, mean length increased by 2 mm in spring, compared to autumn and winter, indicating the presence of larger adults. The bar chart in Fig. 5 indicates that reproducing adults (large males and females carrying eggs and embryos) were found in highest relative abundances in spring and summer, whereas especially reproducing females were virtually

absent in autumn and winter. Males and ovigerous females were generally larger (mean lengths of 8.2 and 8.8mm, respectively) compared to immature adults (mean 6.2mm).

Of all encountered idoteid isopods, *Idotea emarginata* and *I. linearis* only constituted a small proportion (0.8 and 0.5%, respectively), so it can be assumed that juveniles (43.8%) were almost all *I. baltica* (56.5% adults). *Idotea linearis* was only sporadically found (males and non-reproducing females in autumn and winter), but were most abundant in summer (16.2% of total *Idotea* population). In summer, all females were carrying eggs or embryos. As for *I. emarginata*, males were only found in small proportions (0.02 – 0.7%) in autumn, winter and summer, while non-reproducing and reproducing females were only found in autumn and summer (0.02 – 0.18% and 0.23 – 0.02%, respectively). Adult length stayed within the range of 10-15mm all year through.

Idotea juveniles were found in large numbers throughout the year, with the highest mean relative abundance in summer (61%). Similarly, the presence of reproducing adults was continuous, indicating a year-round reproduction. The average lengths of adults and juveniles were highest in autumn (11.6 and 6.3mm) and lowest in spring (10.3 and 3mm), in which the reproduction was most intense.

4. DISCUSSION

The observed seasonal patterns within seaweed-associated communities are due to a combination of physical and biological processes, including seasonal shifts in water temperature and reproduction periods, which regulate the availability of larvae and juveniles (Dempster, 2005). At the Belgian coast, invertebrate densities generally increased after winter to peak in spring (near shore samples) and summer (off shore samples). This pattern is very pronounced for the different species of decapods: crab megalopae and juveniles, and prawn postlarvae started to appear in spring and were found abundantly throughout the summer. However, adults were seldomly found in the vicinity of floating seaweeds and were not found significantly more than in the surrounding water column, suggesting that megalopae and juveniles leave the floating seaweeds to recruit to the water column or the benthos. Crab larvae and prawn postlarvae are known associates of floating seaweeds and drift seagrass (e.g. Kingsford & Choat, 1985; Franke et al, 1999), on which they hitchhike to shallow coastal waters before metamorphosis (Wehrtmann & Dittel, 1990; Thiel & Gutow, 2005b).

In gammarid amphipods and idoteid isopods, all developmental stages of maturity were represented, and most species were found throughout the year. *Atylus swammerdami* was found abundantly in off shore winter samples, but showed no significant seasonal pattern. *Jassa* sp. and *Stenothoe marina* were found more sporadically, in summer and spring, respectively. The *Gammarus crinicornis / G. locusta* species group was found throughout the year, with highest densities in summer. The increase in densities followed an increase in the proportion of reproducing adults in spring, resulting in a considerable input of juveniles in summer. Similarly, the highest proportions of

Idotea juveniles were also found in summer (61%), as reproduction was most intense in spring, although continuous throughout the year like in other idoteids (e.g. Healy & O'Neill, 1984; Salemaa, 1986; Tully & O'Ceidigh, 1986; Abello & Frankland, 1997). However, overall *Idotea* densities were highest in autumn and winter, unlike in other idoteid populations with continuous reproduction (e.g. Healy & O'Neill, 1984), where highest densities were reached in May-September. Apparently, the densities of *I. baltica* and *I. emarginata* were not correlated with water temperature, and high numbers of adults and juveniles per litre of seaweed could be found, even in winter (Tully & O'Ceidigh, 1986). The high densities in autumn can partly be attributed to the recruitment of the new generation to the seaweed, but may also result from new recruitments from the littoral zone (Salemaa, 1979; Tully & O'Ceidigh, 1986). It has been reported that *I. baltica* migrates to over-winter in off shore sublittoral waters, during which they may encounter floating seaweeds with which they stay associated (Salemaa, 1986). The reproduction of gammarid amphipods and idoteid isopods by incubating developing embryos is an advantageous strategy for rafting organisms, since it allows the persistence of local populations on a floating item (Highsmith, 1985; Helmuth et al, 1994; Thiel & Gutow, 2005b).

A few insect families were found significantly more in seaweed samples compared to control samples. The presence of insects was sporadic and probably the result of swarming during a period of off shore winds, driving the insects to sea (Bowden & Johnson, 1976). Unable to return, the insects are forced to land on the sea surface. The presence of living insects on floating seaweeds and their absence in the neuston may be the result of three mechanisms: (1) insects land equally on seaweed and surface water but the ones on the seaweed can survive longer, (2) insects are preprogrammed to land on a vegetation-like surface and avoid landing on the water surface or (3) insects were associated with beached seaweed and were trapped when the seaweed became resuspended. As the abundant insect species (*Helophorus aquaticus*, Psyllidae sp., Aphididae sp., Scatopsidae sp. and Sciaridae sp.) were winged and are not typically seen on decaying seaweed, aerial introduction is most probable. Insects blown out to sea provide a considerable amount of organic matter to the surface water, and if associated with drifting vegetation, they might colonise distant shores (Bowden & Johnson, 1976; Peck, 1994). Because the association of insects is quite coincidental, the properties of the seaweed clumps will be of little importance. The most important cause of variation is probably the aerial insect composition at the time of off shore winds.

The BIO-ENV analysis confirmed the role of surface temperature as a driving factor for seasonal variation, but also put forward the relative abundances of *Fucus vesiculosus* and *Fucus spiralis* in the individual seaweed clumps. Results showed that the availability of these seaweed species is spatially and temporally influenced (*F. vesiculosus* had high relative abundances in autumn, spring and summer in near shore samples, and in winter, spring and summer in off shore samples; whereas *F. spiralis* showed considerable proportions in spring and summer only, in both regions). The spatial and temporal limitations in the availability and abundance of these seaweeds may in turn

influence the abundance and presence of invertebrate macrofauna that prefer these species above others as food and/or habitat (cf Vandendriessche et al, 2006b).

A final factor selected during the BIO-ENV was depth, which is linked to the spatial variation between seaweed samples. It is highly unlikely that depth itself is a major factor influencing the invertebrate species assemblage, as most species colonised the floating seaweeds from the surrounding water column. Depth, however, reflects the spatial differences between sampling areas; in the present study the different sandbank systems. These sandbank systems are prone to different current regimes, and the sampled seaweed clumps may therefore have entirely different origins, ages and traveling trajectories. Moreover, because the Belgian coastline possesses no natural hard substrates of itself (seaweeds only grow on harbor walls and groynes), it is doubtful that distance to shore shows any relation with distance traveled. So it can be hypothesised that in this case, spatial variation is a function of raft history, which is likely to be highly complex given the tidal regime at the English Channel and the Belgian coast.

An attempt was made to assess the impact of seaweed age by grouping the dominant seaweeds (usually *F. vesiculosus* or *A. nodosum*) per clump according to colour and epiphyte load. The age groups, however, only showed minor differences between the invertebrate communities, which was to be expected as most clumps were composed of more than two algal species. Because seaweed clumps often converge or break up, the constituting seaweeds of a clump may have different ages and origins, so age of the seaweeds may differ even within clumps (Ingólfsson, 1998). Although age and origin of a clump are, in most cases, hard to assess, they may still be of great importance to colonising invertebrates, especially to herbivores feeding on epiphytes and on the seaweeds themselves. Stoner and Greening (1984), for example, found that the effects of age on the permanently floating *Sargassum* were more important than the effects of clump size, and were mainly due to a higher degree of food availability and shelter resulting from a larger epiphyte load in older plants. Furthermore, Cronin and Hay (1996) stated that the susceptibility of seaweeds to herbivores is largely dependent on the history (dessication, UV-exposure) of the seaweeds.

Based on the invertebrate species composition of the analysed floating seaweed clumps, it can be assumed that the clumps were in an advanced successional stage (Ingólfsson, 1995; Thiel, 2003; Thiel & Gutow, 2005b): there were only few littoral species (e.g. *Mytilus edulis, Tergipes tergipes*) left and new colonisers (e.g. *Idotea baltica, Gammarus crinicornis / G. locusta*) were abundant and reproducing.

Although the effect of variation linked to the size of the clumps was a major factor following the BIO-ENV analysis in Vandendriessche et al (2006b), it was not selected as important structuring variable in the present study. Again, only few species were found to show a positive correlation; and the positive correlation was significant for species richness and clump size. Similar results were obtained by Ingólfsson (1998), who found a positive correlation between density and clump size for intertidal species, but not for benthic or pelagic species. In that particular study, the correlation

between clump size and diversity of the associated species was also highly significant. These findings affirm the hypothesis that correlations vary greatly depending on the origin of the seaweeds and the association degree and behaviour of the associated species, and that they are probably a reflection of the history of the clump rather than being the result of its structural complexity (Ingólfsson, 1998; Vandendriessche et al, 2006b).

When investigating fauna associated with floating seaweeds, a number of structuring factors can be discerned like spatial and temporal variation, clump size and composition, age and origin. Still, there always remains a proportion of the variation that can only result from coincidences during the course of the journey of the floating seaweeds (e.g. washing ashore, convergence with and exchange between other clumps, disturbance during storms). Furthermore, some factors can be discerned but are hard to quantify (e.g. age and traveling history). Consequently, floating seaweeds constitute a complex system in the neuston, with varying but still considerable effects on the associate invertebrate fauna. Of all variation, only a part can be quantified and attributed to measurable sources of variation (matching coefficient of only 0.26 in the present study), while a large part of the variation results from structuring factors that are hard (e.g. clump age) or even impossible (e.g. number of convergence or divergence events between clumps) to quantify.

As a conclusion, it can be stated that, in the present study, the sea surface temperature and the seaweed species composition were important sources of variation, while variation in depth reflected the traveling history of the seaweed clumps. The clump volume also played a role in structuring the invertebrate assemblages, but that effect was very species-specific. Other factors like clump age, the occurrence of storms, convergences or divergences of clumps and beaching incidents were hard or even impossible to measure, but probably had considerable consequences with regard to the associated invertebrates. These results reflect the complexity of the habitat formed by floating seaweed clumps at the sea surface.

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