

Floating seaweed in the neustonic environment: A case study from Belgian coastal waters

Sofie Vandendriessche*, Magda Vincx, Steven Degraer

Marine Biology Section, Department of Biology, Ghent University, Krijgslaan 281-S8, 9000 Ghent, Belgium

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Abstract

Floating seaweeds form the most important natural component of all floating material found on the surface of oceans and seas. Notwithstanding the absence of natural rocky shores, ephemeral floating seaweed clumps are frequently encountered along the Belgian coast. From October 2002 to April 2003, seaweed samples and control samples (i.e. surface water samples from a seaweed-free area) were collected every other week. Multivariate analysis on neustonic macrofaunal abundances showed significant differences between seaweed and control samples in the fraction >1 mm. Differences were less conspicuous in the 0.5–1 mm fraction. Seaweed samples were characterised by the presence of seaweed fauna e.g. Acari, *Idotea baltica*, *Gammarus* sp., while control samples mainly contained Calanoida, Larvacea, Chaetognatha, and planktonic larvae of crustaceans and polychaetes. Seaweed samples (1 mm fraction) harboured considerably higher diversities ($\times 3$), densities ($\times 18$) and biomasses ($\times 49$) compared to the surrounding water column (control samples). The impact of floating seaweeds on the neustonic environment was quantified by the calculation of the added values of seaweed samples considering biomass and density. These calculations resulted in mean added values of 311 ind m^{-2} in density and $305 \text{ mg ADW m}^{-2}$ in biomass. The association degree per species was expressed as the mean percentage of individuals found in seaweed samples in proportion to the total density and biomass of that species (seaweed samples+control samples). Thirteen species showed an association percentage $>95\%$, and can therefore be considered members of the floating seaweed fauna.

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1. Introduction

The paper at hand focuses on the organisms associated with floating seaweed. The most spectacular and most thoroughly investigated neustonic seaweeds are undoubtedly the truly pelagic rafts of *Sargassum natans* and *S. fluitans*, as they can be found in the

western North Atlantic (Thiel and Gutow, 2005). *Sargassum* rafts provide a stable environment for their associated fauna and therefore harbour high diversities and numerous endemic species (e.g. Fine, 1970; Ryland, 1974; Stoner and Greening, 1984; Coston-Clements et al., 1991). More recently, several investigators also focused on uprooted coastal seaweeds floating at the surface such as *Ascophyllum nodosum*, *Fucus vesiculosus*, *Himantalia elongata*, *Chorda filum* and *Laminaria* spp. in the North Atlantic (Tully and O'Ceidigh, 1986; Davenport and Rees, 1993; Ingolfsson, 1995, 1998, 2000; Olafsson et al.,

* Corresponding author.

E-mail address: Sofie.Vandendriessche@UGent.be (S. Vandendriessche).

2001; Ingolfsson and Kristjansson, 2002; Gutow, 2003), *Macrocystis pyrifera* and *Sargassum* sp. in the Northern Pacific (Safran and Omori, 1991; Kingsford, 1995; Kokita and Omori, 1998; Hobday, 2000a,b,c) and *Carpophyllum maschalocarpum*, *Macrocystis pyrifera* in the Southern Seas (Edgar, 1987; Kingsford, 1992; Helmuth et al., 1994).

Notwithstanding the absence of natural rocky shores, clumps of detached coastal seaweeds are frequently encountered along the Belgian coast. These seaweeds originate from (1) the rocky coasts of northern France or southern England, passing along the Belgian coast by means of a residual current in a SW to NE direction through the English Channel; or (2) from the artificial hard substrates along the Belgian coast like harbour walls and groynes. As there are only few data on the fauna associated with these floating seaweeds, the present paper aims to assess whether the presence of floating seaweeds alters the species composition and species richness of the neuston in the Coastal Bank and Flemish Bank area off the Belgian coast. Furthermore, an attempt is made to quantify the association of the encountered species with the floating seaweed patches.

2. Materials and methods

2.1. Sampling

During daylight hours, samples were collected from autumn to early spring (October 2002 until April 2003) on the Belgian continental shelf (BCS), in the southernmost part of the North Sea. Every other week, the RV 'Zeeleeuw' sailed a trajectory of 60 nautical miles across the Coastal Bank and Flemish Bank area, thereby increasing the chance of floating seaweed encounters by sailing (as much as possible) perpendicular to the prevailing water currents (Fig. 1). Samples were collected at distances of 0.6 to 11.7 nautical miles from the coastline. The search for seaweed was also supported by an airplane on pollution control missions (carried out by the Management Unit of the North Sea Mathematical Models). Persistent bad weather conditions prevented sampling on several dates; sampling was successful on 03/10/2002–12/11/2002–13/12/2002–07/02/2003–27/02/2003–21/03/2003–04/04/2003–14/04/2003. On those 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 sur-

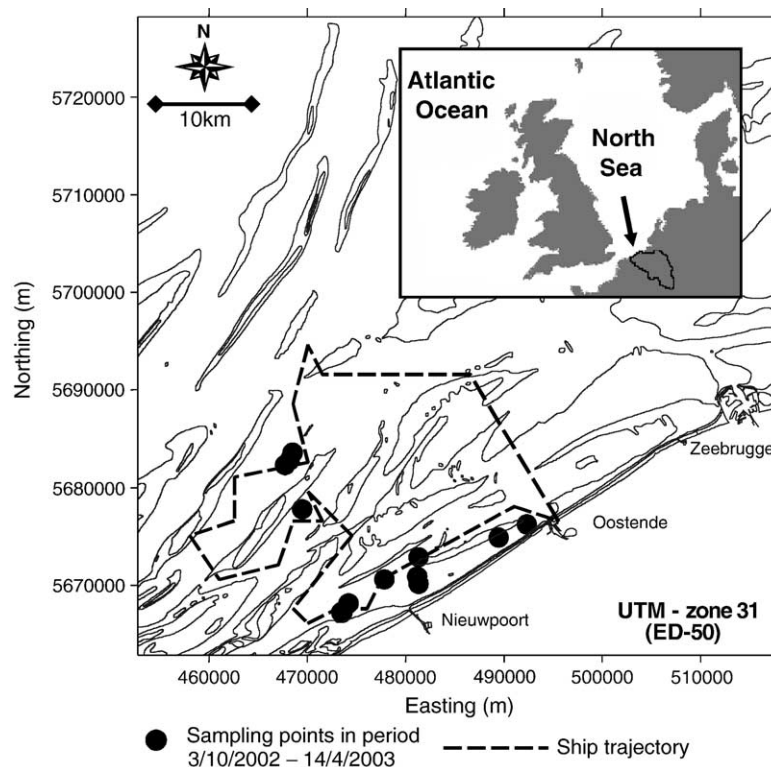


Fig. 1. Study area with indication of sampling occasions (black dots) and ship trajectory (interrupted line).

face and the seaweeds were gently approached, in order to avoid disturbance. Clumps of floating seaweed (minimum three per sampling occasion at one to four sampling occasions per sampling date) were collected using a 300 µm mesh dip net with a ring diameter of 40 cm. From a distance, the net was gently dipped under the clumps by means of an extensible handle. 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.

2.2. Data acquisition

In the laboratory, the preserved samples were rinsed in water, and sieved over a 1 mm and a 0.5 mm sieve. After sorting, all organisms 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. All animals were counted on species or stage level. Certain species were reported on a higher taxonomical level (noted as ‘sp.’ — e.g. juveniles of the genera *Gammarus* and *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) and their biomass was derived from regressions relating the standard length to Ash-free Dry Weight (ADW). ADW was determined as the difference between dry weight (60°C for 5 d) and ash weight (650°C for 2 h) for representative size distributions of the various species. For species caught in discrete life stages or occurring with a particular length, an average biomass value was assigned per stage or species. This value was determined by measuring the ADW of batches of animals belonging to a certain stage.

Densities and biomasses were expressed as numbers of individuals or mg ADW m⁻² sea surface area, respectively, to allow comparisons between seaweed samples and control samples (sessile fauna such as barnacles and bryozoans were omitted from biomass analysis). Diversity was calculated and expressed as expected number of species (Hurlbert, 1971) in order to minimise the effect of variations in sample size. Averages of density, biomass and diversity are reported with standard error.

2.3. Data treatment

Univariate two-way analysis of variance (ANOVA-STATISTICA software) was used to test for differ-

ences in diversity, density and biomass between seaweed samples (SWS) and control samples (CS), taking into account the different sampling occasions (black dots in Fig. 1). If necessary, a log (x+1) transformation was performed to meet the required assumptions.

Species abundance data of SWS and CS were subjected to non-metric multidimensional scaling ordination (MDS) and cluster analysis using the Bray-Curtis similarity measure. ANalysis Of SIMilarities (ANOSIM) was used to test the statistic for significant differences ($p < 0.05$) between groups and to identify the discriminating taxa (SIMilarity of PERcentages: SIMPER). Empty samples were excluded from the analyses and a presence-absence transformation was performed on the abundance data prior to the analyses. All community analyses were done using the Primer software (Clarke and Gorley, 2001).

Because the sampling strategy (dip net) always implies ‘contamination’ of seaweed samples with fauna from the surrounding water column, a bias is created in the dataset which may obscure patterns in community composition. An attempt was made to filter out that bias in a quantitative way by calculating the ‘added value’, in terms of density and biomass, of seaweed samples according to the following procedure: (1) for each sample type (SWS and CS), different replicates were taken per sampling occasion, (2) Two-Way ANOVA analyses (2 sample types, 13 sampling occasions) were used to determine which species were found significantly more in SWS than in CS, and can therefore be considered as seaweed fauna (if non-significant, the species can be considered as member of the background neustonic fauna); (3) added values of densities and biomasses of the seaweed fauna were calculated by subtracting background neustonic values of density and biomass from seaweed sample values (per sampling occasion). These values can be used to study floating seaweed-specific processes in detail, without the bias caused by the presence of surface water fauna. Furthermore, they give an indication of the degree of association of the encountered species with clumps of floating seaweed. That association degree per species can also be expressed as a percentage: per sampling occasion and per species, the percentage of individuals and mg ADW found in SWS was calculated in proportion to the total density and biomass of that species (SWS+CS) on that sampling occasion. Averaging out these values over all sampling occasions yielded the association degree.

3. Results

3.1. Neustonic fauna in presence and absence of floating seaweed

In total, 49 seaweed samples and 38 control samples were collected and analysed. Clumps of floating seaweed consisted of one or more seaweed species (*Fucus vesiculosus*, *Ascophyllum nodosum*, *Halidrys siliquosa*) and occasionally small amounts of other floating debris such as reed, feathers, plastic, nylon, wood and cardboard. Clump volume averaged 99 cm³ (range 8 cm³–360 cm³).

During the initial analysis of both seaweed and control samples, analyses were performed on a dataset, in which the 0.5 mm (0.5–1 mm) and the 1 mm (>1 mm) fractions were pooled. This approach resulted in an indistinct grouping of seaweed samples and control samples (results not presented in this paper). Therefore, we split up the dataset to obtain a more detailed view of the differences.

3.1.1. 1 mm fraction

Diversity (Fig. 2A) showed significantly higher values in seaweed samples (mean ES(100)=4.0) than in control samples (mean ES(100)=1.5) (ANOVA

$p < 0.001$). The variation due to sampling occasion and the combined effect were both significant ($p < 0.001$ and $p = 0.003$, respectively). Although the species richness seems relatively low, a total of 44 species were found in SWS and a total of 23 species in CS. However, only a few species were common in all samples and most species were only sporadically found. This trend was even more pronounced in the control samples.

Density (Fig. 2B) displayed the same trend as diversity: species abundances were significantly higher in seaweed samples (mean 404 ind m⁻²) than in control samples (mean 23 ind m⁻²) (ANOVA $p < 0.001$). The variation due to sampling occasion was significant ($p = 0.004$); the combined effect was not ($p = 0.1$). High densities in seaweed samples were mainly due to the dominance of small barnacles, halacarid mites, isopods (mainly *Idotea baltica*) and amphipods (mainly *Gammarus locusta* and *Gammarus crinicornis*).

Biomass (Fig. 2B) was substantially higher in seaweed samples (mean 329 mg ADW m⁻²) than in control samples (mean 7 mg ADW m⁻²) (ANOVA $p < 0.001$), which was mainly due to the dominance of large isopods (*Idotea baltica*: 58% of the total biomass), large amphipods (mainly *Gammarus locusta* and *Gammarus crinicornis*: 10% of the total biomass) and a few fish (*Chelon labrosus*: 27% of the total

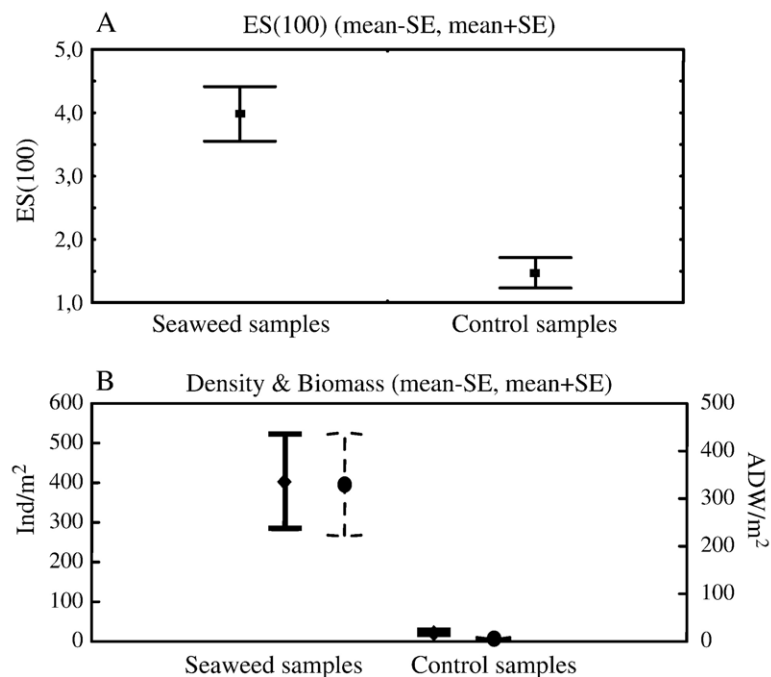


Fig. 2. Results of 1 mm fraction. (A) Plot of diversity expressed as expected number of species per 100 individuals (indication of mean and standard error). (B) Plot of density expressed as ind m⁻² surface area (full line — left Y-axis - indication of mean and standard error) and biomass expressed as mg ADW m⁻² surface area (dashed line — right Y-axis - indication of mean and standard error).

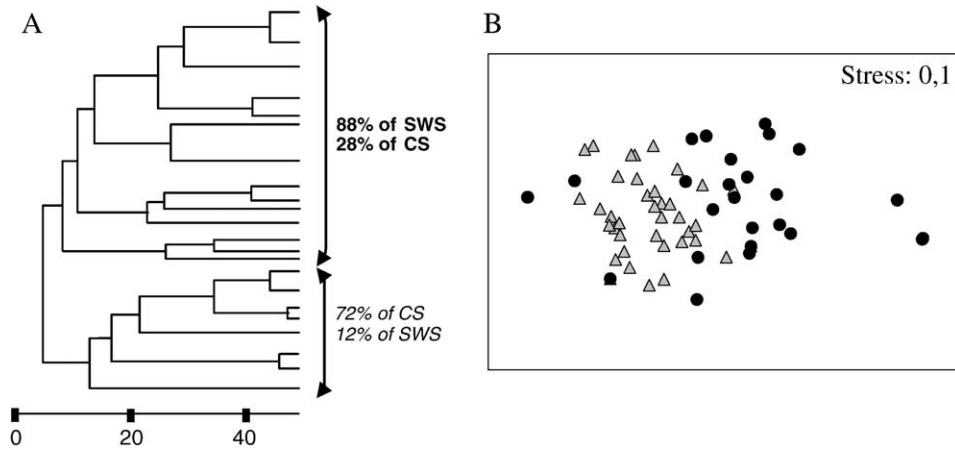


Fig. 3. (A) Simplified cluster (0–50% similarity): Bray-Curtis similarity/Presence-absence data/Group average sorting. (B) MDS plot: grey triangles represent seaweed samples (SWS); black dots represent control samples (CS).

biomass). The variation due to sampling occasion and the combined effect were both significant at $p < 0.001$.

The cluster dendrogram and the MDS plot both revealed the same two groups (Fig. 3): (1) a group comprising the majority of seaweed samples (SWS) and (2) a group comprising most of the control samples

(CS). ANOSIM analysis indicated that these groups were significantly different ($R = 0.32$, $p < 0.001$).

3.1.2. 0.5 mm fraction

Diversity (Fig. 4A) was higher in seaweed samples (mean $ES(100) = 3.2$) than in control samples (mean

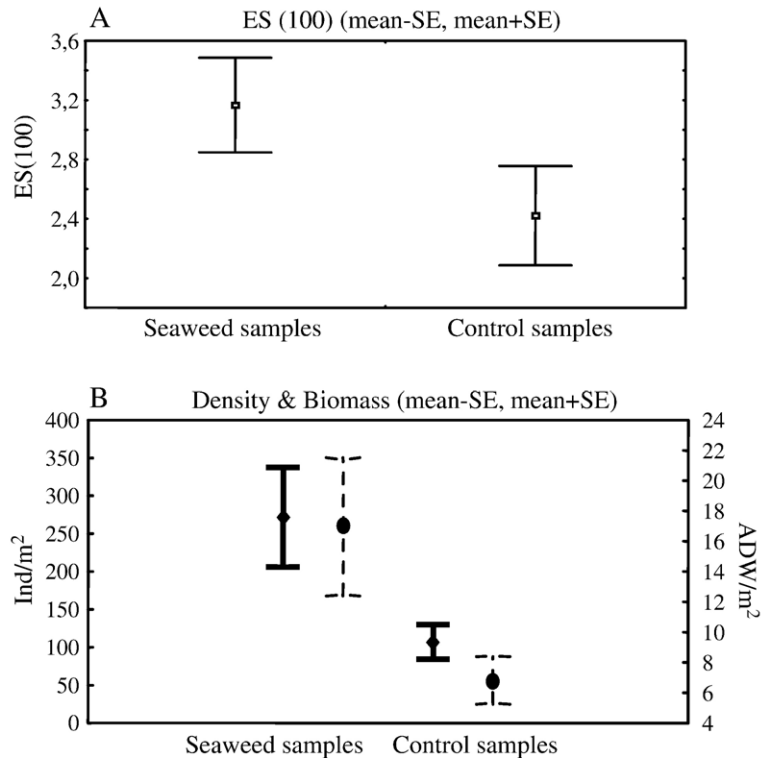


Fig. 4. Results of 0.5 mm fraction. (A) Plot of diversity expressed as expected number of species per 100 individuals (indication of mean and standard error). (B) Plot of density expressed as ind m^{-2} surface area (full line — left Y-axis - indication of mean and standard error), and plot of biomass expressed as mg ADW m^{-2} surface area (dashed line — right Y-axis - indication of mean and standard error).

ES(100)=2.4). This difference was not quite significant (two-way ANOVA, $p=0.07$). The variation due to sampling occasion was significant ($p<0.001$); the combined effect was not ($p=0.4$).

Density (Fig. 4B) was higher in seaweed samples (mean 272 ind m^{-2}) than in control samples (mean 107 ind m^{-2}), but again this trend was not confirmed by a two-way ANOVA ($p=0.051$). The variation due to sampling occasion was significant ($p<0.001$); the combined effect was not ($p=0.9$).

Biomass (Fig. 4B) confirmed the trend observed in the 1 mm fraction: biomass was higher (ANOVA $p=0.01$) in seaweed samples (mean 17 mg ADW m^{-2}) than in control samples (mean 7 mg ADW m^{-2}). Note, however, that the biomass was only 2.5 times higher, whereas in the 1 mm fraction, biomass was almost 50 times higher. The variation due to sampling occasion and the combined effect were both highly significant ($p<0.001$).

Neither cluster analysis, nor MDS revealed the two groups that were established at the $>1 \text{ mm}$ level (Fig. 5).

3.1.3. Species assemblages in fractions and groups

The differences in species composition between the two fractions in the SWS and CS can be derived from Table 1: both fractions of the control samples and the 0.5 mm fraction of the seaweed samples were mainly dominated by planktonic organisms such as calanoid copepods, larvaceans, chaetognaths and invertebrate larvae (e.g. polychaete larvae and cypris larvae), while the 1 mm fraction of SWS was mainly characterised by non-planktonic fauna e.g. Cirripedia, *Littorina mariae*, *Mytilus edulis*, Acari, *Gammarus locusta*, *Gammarus crinicornis*; *Idotea baltica*, *Idotea linearis* and *Idotea emarginata*. SIMPER analysis of 1 mm data showed a very high average dissimilarity between seaweed samples and control samples (95.4%). The isopod *Idotea baltica* (seaweed samples) and calanoid cope-

Table 1

Relative abundances of the five most important taxa in different fractions (1 and 0.5 mm) and groups (SWS and CS)

	1 mm		0.5 mm	
SWS	Cirripedia	25%	Calanoida	64%
	Acari	16%	Acari	13%
	Isopoda	15%	Cirripedia	5%
	Amphipoda	12%	Cypris	5%
	Cypris	11%	Larvacea	4%
	rest	21%	rest	9%
CS	Chaetognatha	22%	Calanoida	67%
	Insecta	10%	Larvacea	3%
	Ctenophora	14%	Cnidaria	10%
	Calanoida	12%	Polychaeta	5%
	Polychaeta (larvae)	19%	Ctenophora	10%
	rest	23%	rest	6%

pods (control samples, not identified to species level) were the most discriminating taxa (contribution percentages: Table 2).

3.2. Added value of floating seaweed

In order to calculate the added values concerning density and biomass, Two-Way ANOVA analyses were performed on density and biomass data per species, taking into account two sample types (SWS-CS) and 13 sampling occasions. The results concerning effect 1 (Table 2) indicate that some species always displayed higher densities and biomasses in SWS compared to CS, independent of sampling time and/or place. A calculation of the added values of these species clearly shows that *Idotea baltica* was not only a good indicator of seaweed samples (see SIMPER), it also seems to be an important contributor to the added values of seaweed samples (1 mm fraction: Table 2). Other contributors to density (mean added value 311 ind m^{-2}) and biomass (mean added value $305 \text{ mg ADW m}^{-2}$) were amphipods (*Gammarus* sp., *G. locusta*, *G. crinicornis* and *Atylus swammerdami*), other idoteid isopods (*Idotea emarginata* and *Idotea* sp. juv.), fish (*Chelon lab-*

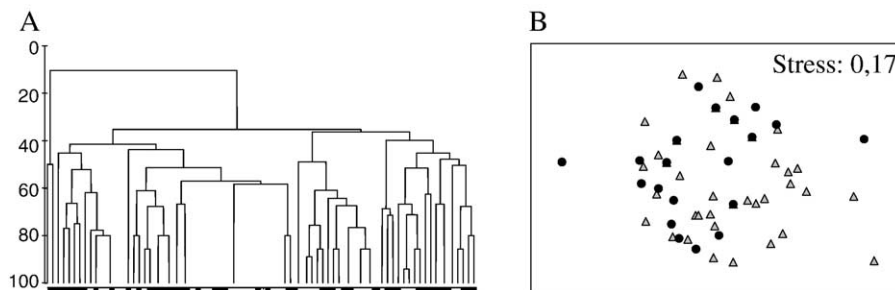


Fig. 5. (A) Simplified cluster (samples represented by black or white squares): Bray-Curtis similarity/Presence-absence data/Group average sorting. Black squares: SWS, white squares: CS. (B) MDS plot: grey triangles represent seaweed samples (SWS); black dots represent control samples (CS).

Table 2

ANOVA results (effect of sample type: SWS vs. CS, effect of sampling occasion not represented) concerning density and biomass (significant values: $p < 0.05$: italic) per species

	ANOVA (effect1: SWS/CS)		Added value		Association degree percentage	SIMPER Contribution %	
	density p-value	biomass p-value	density ind/m ²	biomass mg ADW/m ²		SWS	CS
<i>Elminius modestus</i>	<0.001	nam	100.8	nam	95.8	10.9	nd
Acari sp.	<0.001	nam	63.5	nam	100	27.6	nd
<i>Idotea baltica</i>	<0.001	<0.001	40	177.9	97.2	37.5	nd
<i>Sagitta</i> sp.	0.54	0.58	bg	bg	bg	nd	24.2
<i>Idotea</i> sp. Juv.	<0.001	<0.001	17.8	4.2	95.8	8.7	nd
<i>Atylus swammerdami</i>	<0.001	<0.001	13.8	14.9	100	5.6	nd
Scatopsidae sp.	<0.001	0.08	12	bg	93.8	nd	nd
Sciaridae sp.	0.02	0.35	9.6	bg	83.8	nd	nd
Calanoida sp.	0.31	0.29	bg	bg	bg	nd	38.4
<i>Pleurobrachia pileus</i>	0.14	nam	bg	nam	bg	nd	18.7
mean added value/sample			311.4	305.3			

Only the 10 most abundant (>2.5 ind m⁻²) and most frequently occurring ($>10\%$ of samples) species represented; species ordered by decreasing density — mean added values of all species with significantly higher density-biomass in SWS compared to CS, with their mean association degree (percent of the total number of individuals/mg ADW found in seaweed samples) — SIMPER contribution percentages of discriminating species per sample type.

nam: no available measurements, bg: background values (ANOVA non-significant), nd: non-discriminating in SIMPER analysis.

rosus), barnacles, halacarid mites, mussels and even some insects. Other organisms (e.g. *Pleurobrachia pileus*, *Sagitta* sp., calanoid copepods and some insects) were not found significantly more in seaweed samples and can be considered as background fauna, with a ‘uniform’ distribution in the neuston of Belgian coastal waters.

The added value can be expressed as an absolute value: in density, for example, *I. baltica* had an added value of 40 ind m⁻², meaning that in the presence of seaweed, 40 more individuals can be found per m² than in the absence of seaweed. Another way of expression is by calculating the mean percentage of individuals and mg ADW found in SWS in proportion to the total density and biomass (Table 2). For *I. baltica*, that mean density percentage was 97.2%, meaning that 97.2% of all individuals were found on floating seaweeds. Some species were even exclusively found in seaweed samples (100% association) and were completely absent from the surrounding surface waters (e.g. the amphipod *Atylus swammerdami*, the beetle *Helophorus aquaticus*, and halacarid mites).

4. Discussion

4.1. Size fractions

In accordance with previous studies on the fauna associated with floating seaweed (Tully and O’Ceidigh, 1986; Ingolfsson, 1998, 2000), all organisms larger than 0.5 mm were rinsed from the seaweeds. In the

present study, the 1 and 0.5 mm fractions were separated. Analysis of the two fractions indicated substantial differences between seaweed samples and control samples in the 1 mm fraction, whereas these differences were less pronounced in the 0.5 mm fraction. The smallest fractions of seaweed samples and control samples were both characterised by high percentages of calanoid copepods (64% in SWS and 67% in control samples). These copepods were not identified up to species level, but variation at this level is improbable as this study and the study of Ingolfsson (1998) both indicate that calanoid copepods are not in essence associated with floating seaweed but are common in the surrounding neuston.

The similarity between taxa of SWS and CS at the 0.5 mm level was probably due to the passive movement of the identified planktonic organisms in the water column. It is known, however, that smaller animals such as some species of harpacticoid copepods can cling to, or even seek, passing seaweed clumps (Yeatman, 1962; Ingolfsson and Olafsson, 1997; Olafsson et al., 2001). In the present study, no such colonisers were encountered. Therefore, differences between control samples and seaweed samples are best discerned at the 1 mm level.

In conclusion, it can be stated that the 0.5 mm fraction of seaweed samples and control samples, and the 1 mm fraction of control samples are mainly composed of ‘background neustonic fauna’, whereas the 1 mm fraction of seaweed samples is populated by ‘seaweed fauna’.

4.2. Seaweed samples versus control samples

Most authors acknowledge the effect of drifting vegetation on the habitat complexity in the neustonic environment and, consequently, on the neustonic species composition (Tully and O'Ceidigh, 1986; Locke and Corey, 1989; Davenport and Rees, 1993; Kingsford and Choat, 1985; Kingsford, 1992, 1995; Shaffer et al., 1995; Ingolfsson, 1998; Hobday, 2000a,b). However, dip net control samples for statistical verification of the differences between seaweed fauna and surface water fauna have rarely been taken. Ingolfsson (1998) took a single control sample per sampling site and found that Calanoida, Decapoda larvae, Cirripedia larvae and Cladocera were not significantly more common in clumps of floating seaweeds than in the control samples. Shaffer et al. (1995) collected five drift vegetation samples and five control samples per sampling date and found that seaweed samples were dominated by epiphytic organisms, while calanoid copepods were found significantly more in open water. In the study at hand, three control samples per sampling site were taken, in which Calanoida were also typically found. Kingsford and Choat (1985), Kingsford (1992) and Kokita and Omori (1998) collected seaweed samples and control samples, but used a purse seine net or a 2m diameter ring net and mainly focussed their research on fish. Consequently, their results are hard to compare with the results of the present study. In general, the conclusions of Ingolfsson (1998), Shaffer et al. (1995) and the present study are the same: there are significant differences between the species compositions and species abundances of seaweed samples and control samples.

The cluster dendrogram and MDS plot of Fig. 2 show a clear grouping of seaweed samples and control samples. However, some of the control samples resembled seaweed samples due to the presence of non-planktonic animals such as *Idotea baltica*, *Gammarus* juveniles and *Gammarus crinicornis*, while some of the seaweed samples resembled control samples due to the absence of seaweed species. If non-planktonic organisms were found in control samples, it was only in very low abundances (max 0.4 ind m⁻²). Their presence may have been due to two factors: (1) *Idotea baltica* and *Gammarus locusta* were observed swimming freely at the surface (Tully and O'Ceidigh, 1986, and pers. obs.). So, *I. baltica* and *G. locusta* probably swim around at the surface in the vicinity of seaweed clumps and can therefore occasionally be found in control samples taken near floating seaweeds; and (2) some of the control samples contained small amounts of

debris other than floating seaweed (e.g. reed, plastic and feathers), to which the non-planktonic species can cling. The absence of seaweed-associated species in some seaweed samples cannot be explained at present.

4.3. Diversity, density and biomass (1 mm fraction)

An attempt was made to take variation due to differences in sampling occasion (spatial and/or temporal variation) into account by using a two-way ANOVA (2 groups, 13 sampling occasions). The 0.5 mm fraction showed little difference in density, diversity and biomass between seaweed samples and control samples. There was, however, a significant effect of sampling occasion. In the 1 mm fraction, both the effect of sample type and the effect of sampling occasion were significant. There was also a combined effect (except in density), which indicates that spatial and/or temporal variation intensified the differences between seaweed samples and control samples.

Clumps of floating seaweeds recovered off the Belgian coast seem to harbour a significantly higher species richness than the surrounding surface water (mean expected number of species per 100 individuals: 4.46 in SWS, 2.0 in CS; only 1 mm fraction considered). Even though a high number of species were found in total (44 in SWS, 23 in CS), the majority of species were sparsely represented. Individual samples, however, were often dominated by one of the minor species groups, especially in control samples. This pattern in species range could be attributed to the discontinuous distribution of neustonic fauna in the sea surface layer, for example due to swarming behaviour or the formation of windrows (Holdway and Maddock, 1983), and/or to the effect of spatio-temporal variation (see the previous paragraph).

Besides a higher number of species ($\times 3$), samples of floating seaweed off the Belgian continental shelf had significantly higher densities ($\times 18$) and biomasses ($\times 49$) than control samples. Both rocky shore fauna and colonising subtidal, benthic and epibenthic fauna contributed considerably to total densities, whereas high biomasses were mainly due to the abundant presence of actively colonising fauna (isopods, amphipods and fish). According to Ingolfsson (1998), some of these colonisers display a clump-seeking behaviour: they seek (1) shelter from predators such as large fish or birds (Kokita and Omori, 1998); (2) a food source: the associated macrofauna (Tully and O'Ceidigh, 1989) or the seaweed itself, although it should be noted that some herbivores such as *I. baltica* destroy their own habitat by feeding on the seaweed (Gutow, 2003); or (3)

a substrate for attachment. Other organisms, such as insects (Davenport and Rees, 1993), accidentally end up on floating seaweeds because of their tendency to seek or to hold on to vegetation. The success of these colonisers on floating seaweeds may be due to the lack of endemic neustonic species utilising the habitat (Locke and Corey, 1989).

4.4. Added value of floating seaweed

The analyses above clearly indicate that the presence of floating seaweed strongly increased the diversity, density and biomass of the neustonic macrofauna, especially in the 1 mm fraction. However, due to the sampling method, floating seaweed samples are always ‘contaminated’ with fauna from the surrounding neuston. In future research on the macrofauna associated with floating seaweed (e.g. spatial and temporal variation), it is necessary to be able to determine the ‘added value’ of floating seaweed in the neuston in terms of density and biomass; in this study averages of 311 ind m^{-2} and 305 mg ADW m^{-2} , respectively. These values were obtained by performing Two-Way ANOVA analyses and by subtracting background neustonic values of density and biomass from seaweed sample values (see data treatment). In this way, a distinction was made between ‘true seaweed fauna’ such as *Idotea baltica*, *Atylus swammerdami* and *Gammarus crinicornis* and ‘background fauna’ such as calanoid copepods, some insects, ctenophores, chaetognaths and pelagic larvae of barnacles and polychaetes. To be able to perform such an action, both floating seaweeds and the surrounding neuston should, as in the present study, be sampled in a representative way in order to compensate for aggregation behaviour of neustonic fauna and sampling artefacts. In this study, the Two-Way ANOVA analyses only yielded positively significant p-values, meaning that fauna are attracted to floating seaweeds.

The calculation of the added values in density and biomass provides not only a more accurate dataset to study seaweed specific fauna, it also gives an indication of the degree of association of the encountered species with the floating seaweeds. That degree of association can also be expressed as a percentage. The calculated percentages indicate that thirteen species (>95% association) strongly depended on the presence of floating seaweed. This seaweed dependency was already clear for species such as *Idotea baltica*, *Idotea emarginata* and *Gammarus locusta* (e.g. Tully and O’Ceidigh, 1986; Davenport and Rees, 1993; Ingolfsson, 1995, 1998, 2000; Gutow, 2003; Gutow

and Franke, 2003; Salovius et al., 2005), but has not yet been reported for *Gammarus crinicornis*, *Chelon labrosus* and *Helophorus aquaticus*. Their strong association degrees in the present study are an invitation to more intensive samplings and to a detailed study of fauna associated with floating seaweed in Belgian coastal waters.

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References

- Clarke, K.R., Gorley, R.N., 2001. PRIMER v5: User manual/tutorial, PRIMER-E. Plymouth Marine Laboratory, UK. 91 pp.
- Coston-Clements, L., Settle, L.R., Hoss, D.E., Cross, F.A., 1991. Utilization of the *Sargassum* habitat by marine invertebrates and vertebrates — a review. National Marine Fisheries Service, NOAA, Southeast Fisheries Science Center. Beaufort Laboratory, Beaufort NC. 32 pp.
- Davenport, J., Rees, E.I.S., 1993. Observations on neuston and floating weed patches in the Irish Sea. Est. Coast. Shelf Sci. 36, 395–411.
- Edgar, G.J., 1987. Dispersal of fauna and floral propagules associated with drifting *Macrocystis pyrifera* plants. Mar. Biol. 95, 599–610.
- Fine, M.L., 1970. Faunal variation on pelagic *Sargassum*. Mar. Biol. 7, 112–122.
- Gutow, L., 2003. Local population persistence as a pre-condition for large-scale dispersal of *Idotea metallica* (Crustacea, Isopoda) on drifting habitat patches. Hydrobiologia 503, 45–48.
- Gutow, L., Franke, H.-D., 2003. Metapopulation structure of the marine isopod *Idotea metallica*, a species associated with drifting habitat patches. Helgol. Mar. Res. 56, 259–264.
- Helmuth, B., Veit, R.R., Holberton, R., 1994. Long-distance dispersal of a subantarctic brooding bivalve (*Gaimardia trapesina*) by kelp-rafting. Mar. Biol. 120, 421–426.
- Hobday, A.J., 2000a. Age of drifting *Macrocystis pyrifera* L.C. Agardh rafts in the Southern California Bight. J. Exp. Mar. Biol. Ecol. 253, 97–114.

- Hobday, A.J., 2000b. Persistence and transport of fauna on drifting kelp (*Macrocystis pyrifera* L.C. Agardh) rafts in the southern California Bight. *J. Exp. Mar. Biol. Ecol.* 253, 75–96.
- Hobday, A.J., 2000c. Abundance and dispersal of drifting kelp *Macrocystis pyrifera* rafts in the Southern California Bight. *Mar. Ecol. Prog. Ser.* 195, 101–116.
- Holdway, P., Maddock, L., 1983. A comparative survey of neuston: geographical and temporal distribution patterns. *Mar. Biol.* 76, 263–270.
- Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52, 577–586.
- Ingólfsson, A., 1995. Floating clumps of seaweed around Iceland: natural microcosms and a means of dispersal for shore fauna. *Mar. Biol.* 122, 13–21.
- Ingólfsson, A., 1998. Dynamics of macrofaunal communities of floating seaweed clumps off western Iceland: a study of patches on the surface of the sea. *J. Exp. Mar. Biol. Ecol.* 231, 119–137.
- Ingólfsson, A., 2000. Colonization of floating seaweed by pelagic and subtidal benthic animals in southwestern Iceland. *Hydrobiologia* 440, 181–189.
- Ingólfsson, A., Kristjánsson, B.K., 2002. Diet of juvenile lump sucker (*Cyclopterus lumpus*) in floating seaweed: effect of ontogeny and prey availability. *Copeia* 2, 472–476.
- Ingólfsson, A., Olafsson, E., 1997. Vital role of drift algae in the life history of the pelagic harpacticoid *Parathalestris croni* in the northern North Atlantic. *J. Plankton Res.* 19, 15–27.
- Kingsford, M.J., 1992. Drift algae and small fish in coastal waters of northeastern New Zealand. *Mar. Ecol. Prog. Ser.* 80, 41–55.
- Kingsford, M.J., 1995. Drift algae: a contribution to near-shore habitat complexity in the pelagic environment and an attractant for fish. *Mar. Ecol. Prog. Ser.* 116, 230–297.
- Kingsford, M.J., Choat, J.H., 1985. The fauna associated with drift algae captured with a plankton-mesh purse seine net. *Limnol. Oceanogr.* 30, 618–630.
- Kokita, T., Omori, M., 1998. Early life history traits of the gold-eye rockfish, *Sebastes thompsoni*, in relation to successful utilization of drifting seaweed. *Mar. Biol.* 132, 579–589.
- Locke, A., Corey, S., 1989. Amphipods, Isopods and surface currents: a case for passive dispersal in the Bay of Fundy, Canada. *J. Plankton Res.* 11, 419–430.
- Olafsson, E., Ingólfsson, A., Steinarsdóttir, M.B., 2001. Harpacticoid copepod communities of floating seaweeds: controlling factors and implications for dispersal. *Hydrobiologia* 453/454, 189–200.
- Ryland, J.S., 1974. Observations on some epibionts of Gulfweed, *Sargassum natans* (L.) Meyen. *J. Exp. Mar. Biol. Ecol.* 14, 17–25.
- Safran, P., Omori, M., 1991. Some ecological observations on fishes associated with drifting seaweed off Tohoku coast, Japan. *Mar. Biol.* 105, 395–402.
- Salovius, S., Nyqvist, M., Bonsdorff, E., 2005. Life in the fast lane: macrobenthos use temporary drifting algal habitats. *J. Sea Res.* 53, 169–180.
- Shaffer, J.A., Doty, D.C., Buckley, R.M., West, J.E., 1995. Crustacean community composition and trophic use of the drift vegetation habitat by juvenile splitnose rockfish *Sebastes diploproa*. *Mar. Ecol. Prog. Ser.* 123, 13–21.
- Stoner, A.W., Greening, H.S., 1984. Geographic variation in the macrofaunal associates of pelagic *Sargassum* and some biogeographic implications. *Mar. Ecol. Prog. Ser.* 20, 185–192.
- Thiel, M., Gutow, L., 2005. The ecology of rafting in the marine environment I. The floating substrata. *Oceanogr. Mar. Biol. Annu. Rev.* 42, 181–264.
- Tully, O., O’Ceidigh, P., 1986. The ecology of *Idotea* species (Isopoda) and *Gammarus locusta* (Amphipoda) on surface driftweed in Galway Bay (west of Ireland). *J. Mar. Biol. Ass. UK* 66, 931–942.
- Tully, O., O’Ceidigh, P., 1989. The ichthyoneuston of Galway Bay (west of Ireland): II. Food of post-larval and juvenile neustonic and pseudoneustonic fish. *Mar. Ecol. Prog. Ser.* 51, 301–310.
- Yeatman, H.C., 1962. The problem of dispersal of marine littoral copepods in the Atlantic Ocean, including some redescription of species. *Crustaceana* 4, 253–272.