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Potential contribution of surface-dwelling *Sargassum* algae to deep-sea ecosystems in the southern North Atlantic

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Abstract

Deep-sea ecosystems, limited by their inability to use primary production as a source of carbon, rely on other sources to maintain life. Sedimentation of organic carbon into the deep sea has been previously studied, however, the high biomass of sedimented *Sargassum* algae discovered during the VEMA Transit expedition in 2014/2015 to the southern North Atlantic, and its potential as a regular carbon input, has been an underestimated phenomenon. To determine the potential for this carbon flux, a literature survey of previous studies that estimated the abundance of surface water *Sargassum* was conducted. We compared these estimates with quantitative analyses of sedimented *Sargassum* appearing on photos taken with an autonomous underwater vehicle (AUV) directly above the abyssal sediment during the expedition. Organismal communities associated to *Sargassum fluitans* from surface waters were investigated and *Sargassum* samples collected from surface waters and the deep sea were biochemically analyzed (fatty acids, stable isotopes, C:N ratios) to determine degradation potential and the trophic significance within deep-sea communities. The estimated *Sargassum* biomass (fresh weight) in the deep sea (0.07 - 3.75 g/m^2) was several times higher than that

estimated from surface waters in the North Atlantic (0.024 – 0.84 g/m²). Biochemical analysis showed degradation of *Sargassum* occurring during sedimentation or in the deep sea, however, fatty acid and stable isotope analysis did not indicate direct trophic interactions between the algae and benthic organisms. Thus, it is assumed that components of the deep-sea microbial food web form an important link between the macroalgae and larger benthic organisms. Evaluation of the epifauna showed a diverse nano- micro-, meio, and macrofauna on surface *Sargassum* and maybe transported across the Atlantic, but we had no evidence for a vertical exchange of fauna components. The large-scale sedimentation of *Sargassum* forms an important trophic link between surface and benthic production and has to be further considered in the future as a regular carbon input to the deep-sea floor in the North Atlantic.

Keywords: *Sargassum*, sedimentation rate, carbon influx, microbial food web, protozoans, macrofauna, stable isotopes, fatty acids

1. Introduction

Oceans cover roughly 70% of the earth's surface and two third of their volume is deeper than 1000 m. Therefore, the deep sea can be considered the largest biome on earth. For a long time it was considered to be a single, featureless and stable environment, lacking barriers for the pelagic dispersal of species. Due to the absence of light, most of the deep-sea life is assumed to be heterotrophic and dependent on the production and sinking of organic matter from the surface waters to act as a carbon source (Johnson et al., 2007). Carbon flux decreases exponentially with depth (Suess, 1980). This creates a carbon-limited ecosystem, which leads to a low abundance of benthic organisms (Rex et al., 2006). Long-term studies have investigated surface primary production as well as sedimentation to the deep sea (e.g. Rowe and Staresinic, 1979; Krause-Jensen and Duarte, 2016). Trap measurements of carbon flux showed the importance of vertical energy transport and its resulting effect on deep-sea benthic ecosystems (e.g. Smith et al., 2006).

During the Vema-TRANSIT cruise with R/V Sonne in January 2015 we were especially interested in the potential dispersal of benthic organisms along the Vema Fracture Zone and the comparison of benthic communities between the Eastern and Western Atlantic basins. Since the potential dispersal of a large number of individuals over wide geographical ranges leads to a high gene flow, it was assumed that mainly cosmopolitan species exist (Gage and Tyler, 1991) and allopatric speciation was supposed to be a rare event (Palumbi, 1994). During the last four decades, different studies showed that the species diversity in deep-sea environments is high, but the underlying mechanisms are poorly understood (White, 1987; Palumbi, 1994; Rex and Etter, 2010). Today, the importance of water currents in the deep sea as possible pathways for

dispersal is basically understood (Dickson et al., 1982; Gage, 1996; Levin et al., 2001). For the tiny protists, the occurrence of similar genotypes has been shown in surface as well as deep-sea samples (e.g. Scheckenbach et al., 2005). Thus, potentially also sedimentation from surface aggregations (e.g. on the surface of floating macrophytes) could influence distribution patterns of some protists in the deep sea.

Sargassum floating mats form a unique ecosystem comprising the accumulations of holopelagic brown algae, *S. natans* (Linnaeus) Gaillon 1828 and *S. fluitans* (Børgesen) Børgesen 1914 (Laffoley et al., 2011; Huffard et al., 2014; Schell et al., 2015). Our interest in the wider importance of these floating systems for the abyssal areas was raised due to the detection of isolated branches of *Sargassum* on the seafloor even in single cores of multicorer samples from abyssal depths. The presence of relatively large clumps of *Sargassum* in photographs of the seafloor had already been reported by Schoener and Rowe (1970) and later in several publications (e.g. Wolff, 1979; Wei et al., 2012) giving clear evidence that *Sargassum* is sedimenting down to the deep sea. Rowe and Staresinic (1979) already estimated that 10% of organic carbon sedimented to the North Atlantic deep sea could be due to *Sargassum*. In their recent review, Krause-Jensen and Duarte (2016) concluded that macroalgae represent an important source of the overall carbon sequestered in the deep ocean. The means by which *Sargassum* sinks is still not completely understood; very little is known on the contribution of epifauna to the sedimentation process of *Sargassum*. The resulting accumulation of sedimenting *Sargassum* represents a potentially large and consistent carbon flux to deep-sea ecosystems. While the particular abundance and nature of holopelagic *Sargassum* is relatively unique to the North Atlantic (particularly the Sargasso Sea), the mechanism of large-scale sedimentation of macrophytes as a carbon flux is an important finding and is translated through the world's oceans (Krause-Jensen and Duarte, 2016). One can easily imagine that accumulations of *Sargassum* might influence distribution patterns of deep-sea fauna which is generally limited in carbon sources.

The importance of organic material as both a food source and habitat for sessile taxa on the ocean's deep-sea floor was highlighted by several authors (e.g. Wolff, 1979; Grassle and Morse-Porteous, 1987; Johnson et al., 2007; Bernardino et al., 2010). Usually, the origin of such organic material is not well defined. Fatty acids (FAs) can be used as biomarkers because they are transmitted between tissues of food and feeders almost without change (Howell et al., 2004; Iverson et al., 2009) and so allow interpretations about a specimens' diet (e.g. Dalsgaard et al., 2003; Peters, 2006; Würzberg et al., 2011). The usage of FAs as a biomarker approach relies on the assumption that some FAs can only be synthesized by certain organisms. They become traceable components of an animals' diet at higher trophic levels. Like the FA approach, stable isotopes can provide information about the long-term diet of organisms (Tieszen et al., 1983;

Ponsard and Arditi, 2000; Laakmann and Auel, 2010). Furthermore, it is a method to detect relative trophic levels as well as possible carbon sources of ecosystems through selective metabolic fractionations.

After our attention was attracted during the cruise by findings of leaflets of *Sargassum* in the small areas of MUC corers, we used the unique chance during the Vema-TRANSIT expedition, to get quantitative estimates of the *Sargassum* in the abyssal region using AUV photographing of the seafloor at the respective stations. Nano-, micro-, meio-, and macrofauna that were found on the surface of *Sargassum* were documented and compared within stations. Furthermore, we performed biochemical analysis on the surface and deep-sea samples, including C:N ratios as well as dry and ash-free dry weights to determine degradation that occurs during sedimentation. In addition, stable isotope and fatty-acid analysis of deep-sea macrofauna, *Sargassum* and sediment samples were conducted to investigate relative trophic levels and the potential of *Sargassum* as a direct food source for higher trophic levels.

We hypothesized that sedimented *Sargassum* could reach significant biomasses compared to floating *Sargassum* in surface waters. Derived from the observations that some sedimented *Sargassum* could still contained pigments, we assumed that sedimentation should be relatively high. Epifauna organisms or remains of it might be visible in sedimented *Sargassum*. Further, we presumed that biochemical signals of *Sargassum* can be traced in macrofauna organisms.

2. Material and methods

2.1 Sampling

Samples were collected during the VEMA Transit expedition on R/V Sonne (SO 237; December-January 2014/15) conducted to analyze potential biological and geological differences between the eastern and western basins of the equatorial Atlantic (Brandt et al., this issue; Devey et al., this issue). The cruise followed the southern edge of the westward-directed North Equatorial Current and the northwestward-directed Antilles Current located within the North Atlantic Subtropical Gyre which includes the Sargasso Sea (Fig. 1).

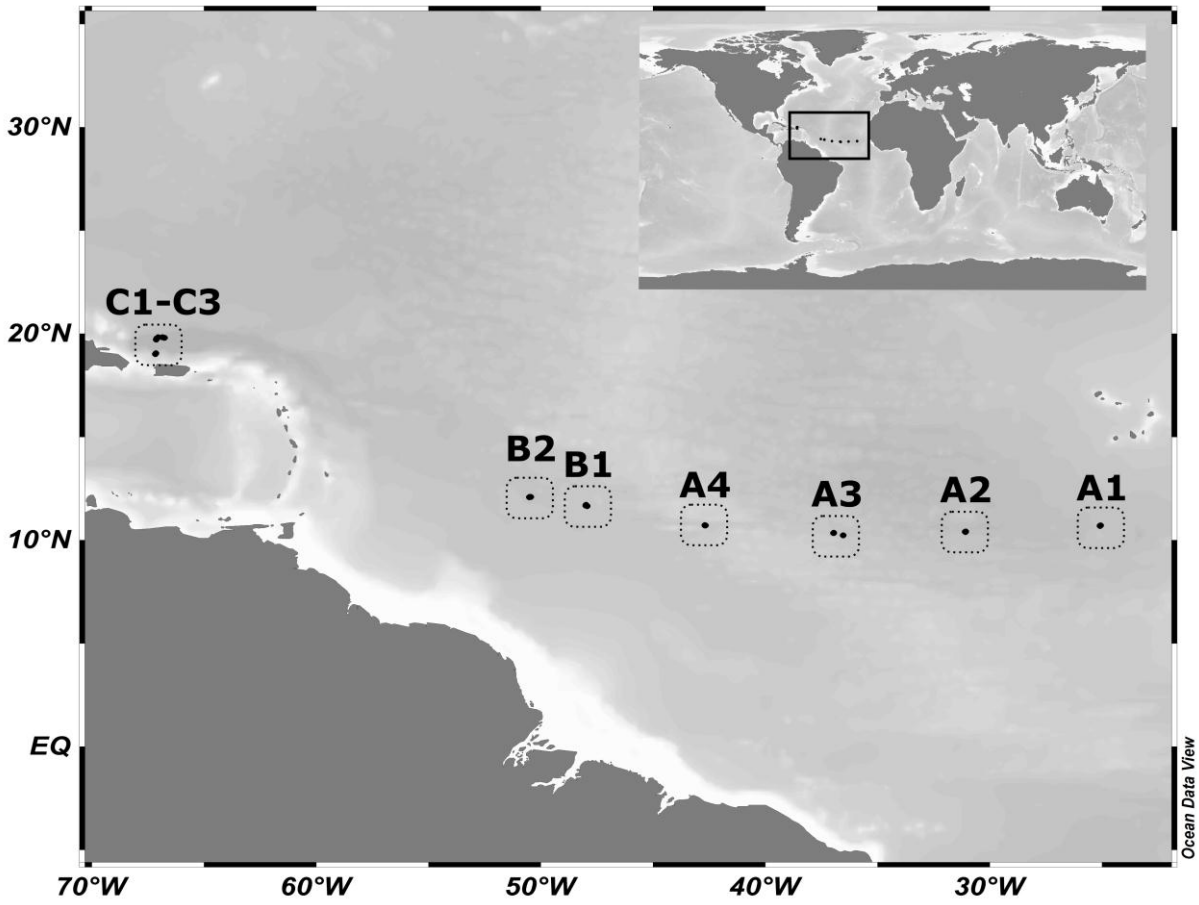

Figure 1 Sampling stations of VEMA Transit expedition with R/V Sonne (SO 237; December-January 2014/15). The details of sampling gear used at the different stations are given in Table 1. Station map was created with Ocean Data View (Schlitzer, 2012).

Samples of *Sargassum* were collected from the surface by means of a 10l bucket and fishing gear, while benthic deep-sea samples were collected by a camera-epibenthic sledge (C-EBS) (C-EBS, Brandt et al., 2013; Table 1). The nano-, micro-, meio- and macrofauna associated with the surface-collected *Sargassum* samples were microscopically investigated immediately after sampling (see below). Parts of the material collected from the surface as well as the deep sea were stored at -80°C to be used for later biochemical studies. Additionally, sediment sampled with a Multi-Corer (MUC) was used for biochemical studies. Deep-sea macrofauna, sampled by the C-EBS, were also used for stable isotope analysis.

Table 1 Station list of collected *Sargassum fluitans* from the surface and deep sea as well as stations sampled for sediment and fauna during the research cruise SO237. **A.** Surface samples. **B.** Deep-sea samples taken with the camera-epibenthic sledge (C-EBS) and Multi-Corer (MUC). **C.** Analysis of the oceanic floor by an automated underwater vehicle (AUV). Explanations of superscripts: ([1]) Samples used for biochemical analyses of *Sargassum* material collected from surface waters and degraded for approx. 1 ½ years under laboratory conditions in culture flasks; ([2]) *Sargassum* samples taken from surface waters; ([3]) sediment samples; ([4]) sampling of deep-sea macrofauna. *Sargassum* samples taken from surface waters (A) and the deep sea (B) were used to analyze associated fauna.

Area/ Site	Date/UTC Time	Depth [m]	Sampling	Latitude/Longitude
A. Surface samples				
A1/2	19.12.2014/ 11:32	Surface	Bucket	10°43.118'N/25°03.893'W
[1]A2/4	26.12.2014/ 12:16	Surface	Bucket	10°25.114'N/31°04.617'W
A2/4	28.12.2014/ 16:58	Surface	Bucket	10°24.481'N/31°05.318'W
[1, 2]A3/6	03.01.2015/ 14:54	Surface	Fishing gear	10°14.161'N/36°31.615'W
[1]A4/8	08.01.2015/ 19:10	Surface	Fishing gear	10°42.645'N/42°41.893'W
[1]B1/9	12.01.2015/ 00:51	Surface	Fishing gear	11°41.357'N/47°57.334'W
[1]C1/12	19.01.2015/ 00:54	Surface	Bucket	19°43.400'N/67°08.010'W
B. Deep-sea samples				
A1/2-6	20.12.2014	5520	C-EBS	10°42.330'N/25°05.580'W
A1/2-7	20.12.2014	5514	C-EBS	10°41.370'N/25°05.137'W
[3]A2/4-3	26.12.2014	5771	MUC	10°25.110'N/31°04.610'W
[2, 4]A2/4-8	27.12.2014	5735	C-EBS	10°24.161'N/31°06.205'W
[2, 4]A2/4-9	27.12.2014	5735	C-EBS	10°24.082'N/31°04.795'W
A3/6-7	02.01.2015	5085	C-EBS	10°20.659'N/36°57.010'W
A3/6-8	02.01.2015	5119	C-EBS	10°21.542'N/36°57.236'W
[3]A4/8-6	07.01.2015	5180	MUC	10°43.540'N/42°41.580'W
[2, 4]A4/8-4	06.01.2015	5176	C-EBS	10°43.000'N/42°39.910'W
B1/9-2	11.01.2015	4995	C-EBS	11°40.299'N/48°00.071'W
[2, 4]B1/9-8	12.01.2015	5004	C-EBS	11°39.014'N/47°56.168'W
[2, 4]B2/11-1	14.01.2015	5093	C-EBS	12°05.732'N/50°30.239'W
[2, 4]B2/11-4	14.01.2015	5130	C-EBS	12°04.753'N/50°30.348'W
[3]B2/11-5	14.01.2015	5091	MUC	12°05.400'N/50°26.980'W
C1/12-5	20.01.2015	8339	C-EBS	19°49.500'N/66°50.970'W
C1/12-6	21.01.2015	8340	C-EBS	19°48.490'N/66°45.440'W
C2/13-4	23.01.2015	8329	C-EBS	19°46.730'N/67°06.210'W
C2/13-5	23.01.2015	8082	C-EBS	19°49.850'N/67°02.910'W
C3/14-1	24.01.2015	4552	C-EBS	19°00.760'N/67°10.219'W
C3/14-2	25.01.2015	4930	C-EBS	19°03.044'N/67°08.650'W
C. AUV deployment			Dive Number	
A3/6-2	01.01.2015	5136	ABYSS 163	10°20.998'N/36°57.616'W
B1/9-6	12.01.2015	4977	ABYSS 165	11°42.58'N/47°59.07'W
B2/11-3	14.01.2015	5093	ABYSS 166	12°05.99'N/50°28.4'W

2.2 Biomass estimation of *Sargassum*

An estimation of the biomass of *Sargassum* in the deep sea was carried out for three stations of the VEMA expedition using photos taken by an automated underwater vehicle (AUV, HYDROID Inc.). The AUV was deployed for mapping purposes of the seafloor, using a Pike camera mounted with a 15mm Nikkor underwater lens, cropped to a focal length of 22mm providing a field of view of 41 degrees. All approximately 27000 photos from three AUV deployments were screened for *Sargassum* (Abyss 163: 1712 photos; Abyss 165: 2153 photos; Abyss 166: 145 photos). Out of these total 4010 *Sargassum*-containing pictures, every randomly chosen tenth

picture was quantitatively analyzed using ImageJ (https://imagej.nih.gov/ij/) regarding the surface area covered by *Sargassum* for those pictures. For a minimum estimation, *Sargassum* in the pictures was assumed to be only one layer thick. A program (Tiffy2tiff, GEOMAR, Kiel) was written in order to extract metadata from the photos regarding the coordinates of the AUV, depth, altitude above sea floor, and the pitch and roll for each photo. Based on the lens and metadata, the dimensions of each photo were calculated and inserted into ImageJ to determine the overall surface area of the *Sargassum* in each photo. The average surface area coverage per picture was calculated for each site and then compared with the ratio of *Sargassum* containing pictures to total pictures per AUV deployment to determine a total biomass per deployment. Surface collected *Sargassum fluitans* (stored frozen at -80°C until analysis in the home lab) were used to determine an average weight per centimeter squared (see below), to estimate the biomass of *Sargassum* per m^2 in each inspected photo.

2.3 Sedimentation rates of *Sargassum* algae

We carried out preliminary studies on the sedimentation of freshly collected *Sargassum fluitans* on board over a depth of only 20 cm revealing first estimates of about 35 sec/m sedimentation rate. Since there are very few data on sedimentation rates in the literature, we further analyzed sedimentation rates of *Sargassum*. In the absence of *S. fluitans*, we used a non-holopelagic marine species (tentatively identified as *Sargassum vulgare* C. Agardh 1820) which has a similar morphology to *S. fluitans. S. vulgare* was collected at the coast of the Canary Islands at depth of two meters attached to a rocky substrate. The algae showed no signs of decomposition or deterioration. In order to determine the maximum sedimentation rate, all bladders were cut from the plant. Four replicated experiments were carried out determining the rate of sedimentation over a distance of 10 meters close to the sampling area of the algae in the North Atlantic (Puerto de Mogan, Canary Islands). Depths and times were recorded using a Mares Smart dive computer, while free diving.

2.4 Epifauna composition on floating *Sargassum*

Sargassum surface samples were collected from six stations (Table 1) during the cruise and analyzed to determine associated nano-, micro-, meio- and macrofauna immediately after sampling. For each surface sample, we selected a volume of 570 cm^3 per station for an analysis of meio- and macrofauna. The sessile fauna was separated from the mobile fauna, while the supernatant with the mobile fauna was sieved through three mesh sizes (1000µm, 500µm and 100µm). The samples were qualitatively examined for mobile micro- and macrofauna, prior to fixation of the selected volume in 96% ethanol. Observed species were photo-documented and fixed. Only organisms from 1000µm and 500µm have been analyzed so far. Quantitative

comparison between the six stations was not possible, thus, for standardization sessile fauna was investigated using a squared container with an area of 91.5 cm^2. Organisms were investigated using a light microscope and binocular. In addition, studies were carried out by scanning electron microscopy (some crustaceans, mollusks).

Nano- and microfauna was investigated in freshly collected samples suspended in sterilized seawater. Two sets of culture flasks at each station were used for qualitative studies. One set of replicates of about 4 cm^3 was transferred into 50 mL tissue culture flasks (Sarstedt, Nümbrecht, Germany) filled with 30 mL autoclaved seawater (35 PSU). In addition, about 10 cm^2 of the sample at each station were transferred to 600 mL tissue culture flasks. Culture flask were inspected under an inverted microscope (Zeiss Primovert with LD objectives of 10-40* magnification) immediately after collection of samples and in intervals of three days after inoculation.

2.5 Biochemical analyses of *Sargassum*

2.5.1 Fresh, dry and ash-free dry weights and C:N ratios

Frozen samples from both surface and deep-sea collected *Sargassum* were analyzed for fresh, dry and ash-free dry weight, as well as C:N ratios. Immediately after sampling, samples were stored at -80 °C. One "leaf" per sample, with three replicates each, was selected for the measurements. Fresh weights were determined after blotting with filter paper to remove free water droplets accumulated during thawing. For determining dry weights, samples were dried in a compartment dryer at 80 °C until weight became constant (approx. 19 hours). For determining the ash-free dry weight, dried samples were burned in a muffle furnace at 500°C for 3 hours. For the C:N analysis, dried samples were ground to a fine powder inside small glass containers and weighed into pressed tin capsules (3 mg). The total content of carbon and nitrogen was determined using an Organic Elemental Analyzer, Flash EA 2000 from Thermo Scientific. In addition, "leafs" of surface water collected *Sargassum* incubated for 18 months at 10°C were analyzed for C:N ratios and weights to estimate long-term degradation.

2.5.2 Fatty acid analysis

All tissue (including Polychaeta, Amphipoda, Decapoda, Asteroidea, Ophiuroidea) samples and *Sargassum fluitans* samples were lyophilized for 24 h, sediment samples for 48 h. Dry masses were then determined using a microbalance scale (Sartorius ISO 9001 (+/- 2 µg)), with samples being kept in a desiccator to prevent hydration during measurements. For the extraction, samples were transferred into glass vials with 4 ml of dichlormethane: methanol (DcM:MeOH) (2:1/v:v) for at least one week and stored at -30 °C. Afterwards, the solid parts were stored at -80 °C for the stable isotope analysis. An internal standard solution, Tricosanoic acid (S23:0),

with a concentration of 0.1 mg ml^{-1} was added based on the dry weight of the sample. To maintain an equal volume of sample, the standard solution was filled up with DcM:MeOH to a final volume of 1 ml before 1 ml of aqueous KCl solution (0.88 %) was added. The samples were then centrifuged for 15 min at 1200 rpm at 0 °C and then vaporized with N_2. Next, the samples were dissolved in 500 µl DcM:MeOH and an aliquot was stored as a backup. The rest was mixed with 1 ml of methanol with 3 % of concentrated Sulfuric acid (H_2SO_4) and heated up to 80 °C for 4 h to esterify the FAs into their methyl ester derivatives (FAMEs) (Kattner and Fricke, 1986). For the FAME extraction, 2 ml of distilled water and 1 ml hexane were added. The extraction with hexane, centrifugation for 10 min with 1200 rpm at 0 °C and vaporization with elemental nitrogen (N_2) was repeated three times for each sample. This was followed by dilution with hexane and the analysis in a gas chromatograph. The FAMEs were detected and identified using the retention times compared to those of Marinol, using the software Agilent OpenLab Data analysis, as well as analyzed manually afterwards. Dirt and blurred peaks were excluded.

2.5.3 Stable isotope analysis

Stable isotope analysis was conducted for *Sargassum fluitans* and sediment samples as well as for the sampled macrofauna including Polychaeta, Amphipoda, Decapoda, Asteroidea, Ophiuroidea. The *Sargassum fluitans* samples were roughly cleaned of epibionts and after defatting with DcM:MeOH, all samples were kept in a compartment drier for 24 h at 60 °C and were ground afterwards. To remove inorganic carbon, half of the total amount was treated with diluted Hydrogen chloride (HCl) (2 N) drop by drop until bubbling ceased (provoked by the reaction of HCl with calcium carbonate). The samples were then dried again for 24 h, whereas sediment samples were kept inside for 48 h. The non-acidified samples were used to analyze the $\delta^{15}N$ ratio and the acidified ones to analyze the $\delta^{13}C$ ratio. Aliquots (1 – 25 mg) were weighted and transferred into silver and tin capsules (HEKAtech, Germany), respectively. If enough material was available, triplicates of the samples were analyzed, using a CNHO- isotope- mass spectrometer (Nu Horizon Stable Isotope Mass Spectrometer, Nu Instruments Ltd., UK) linked to an elemental- analyzer (EURO- EA 3000, Euro Vector, Italy) in continuous flow configuration (set- up by HEKAtech, Germany). N_2 and carbon dioxide (CO_2) were used as standards for nitrogen and carbon respectively. Isotope and mass calibration were conducted by the use of the certified standards like IAEA- 600 Caffeine ($\delta^{13}C$ = -27.771 ‰ VPDB, SD 0.043; $\delta^{15}N$ = +1.0 ‰ air N_2, SD 0.2 ‰), IAEA- NO- 3 Potassium Nitrate ($\delta^{15}N$ = +4.7 ‰ air N_2, SD 0.2 ‰) and 2,5-bis (5-tert-butyl-2-benzoxazol-2-yl) thiophene (6.51 % N; 72.52 % C; HEKAtech, Germany). Values of the SIs are represented as δ-notations in per mil (‰) deviation representing the ratio of the heavier to the lighter isotope ($\delta^{15}N = {}^{15}N/{}^{14}N$, $\delta^{13}C = {}^{13}C/{}^{12}C$) (Fry 2006) relative to their

international standards (AIR for nitrogen, VPDB for carbon) (Fry and Peterson, 1987; Minagawa and Wada, 1984).

2.5.4 Statistics

One-way analyses of variance (ANOVA) tests were performed to check for significance in variation between the ratios of organic material weight to total weight of the different samples using software StatPlus. Two-way analyses of variances (ANOVAs) including two factors and an interaction between them were performed to test differences of fatty acid (FA) and stable isotope composition between the taxonomic groups and the three areas using the software R. The Shapiro-Wilk test was conducted to prove normal distribution. The Levene test was used to check for the homogeneity of variances. Outliers were detected using the Cooks distance. To gain specific information about the differences between the factor levels a Tukey's HSD post hoc test was performed. The confidence level was 95 %, so the significance level was 5 % ($\alpha = 0.05$). If the assumptions were not complied the significance level was raised up to 1 % ($\alpha = 0.01$). A principal component analysis (PCA) was performed using the software PASW Statistics 20.0 (SPSS) comparing the FA profiles between the different groups taking the ten most important FAs into account. This test requires a normal distribution, so an arcsine square root transformation was applied for the percentage data of the FAs.

3. Results

3.1. Biomass estimation of sedimented *Sargassum*

During the expedition, floating *Sargassum* could be observed on the surface in all regions; sedimented *Sargassum* could be detected in all EBS-C sledge samples and AUV recordings (Fig. 2A-I). Biomass of sedimented *Sargassum* was estimated for each of the three AUV deployment areas. An average surface area (m^2) of sedimented *Sargassum* per photo, total surface area (m^2) per site, total biomass (kg) per area, and biomass (g/m^2) was calculated (Table 2). The biomass was calculated using an average mass of 0.65 g/cm^2 taken from the frozen surface sample. *Sargassum* found at area B1 showed evidence of bioturbation (Fig. 2H), both in and around the algae, with large patches missing within the aggregation. This area also had the highest occurrence of macroscopically visible fauna in AUV photos, including fish, shrimp and holothurians. Area A3 had consistently larger patches of *Sargassum*, with little or no evidence of bioturbation. Macrofauna was visible in these photos, but at a much lower frequency.

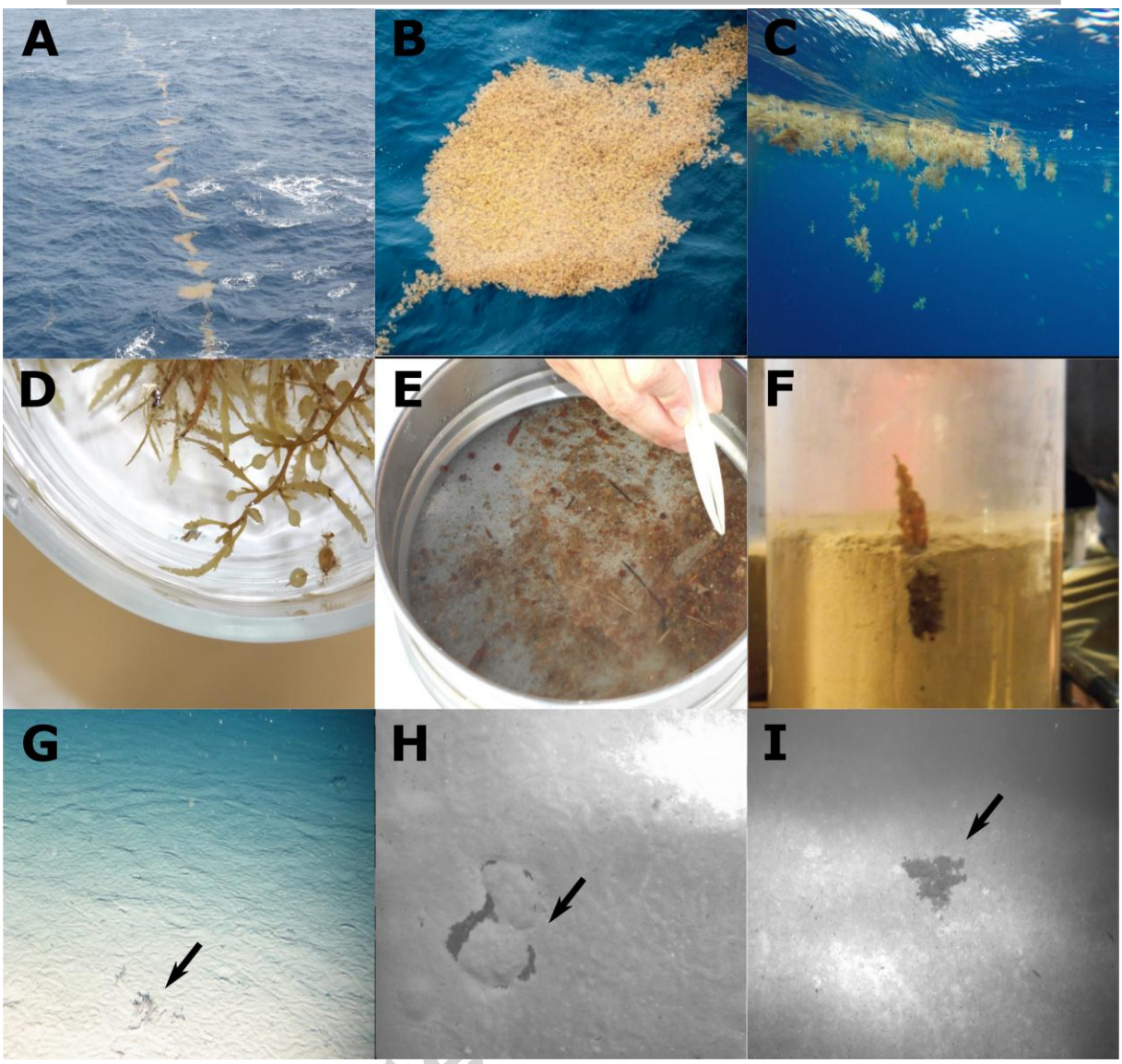

Figure 2 A, B *Sargassum* algae aligned along Langmuir circulation. **C:** Beginning of sedimentation of *Sargassum* algae. **D:** Collected sample of *Sargassum fluitans* from surface waters. **E:** Pieces of sedimented *Sargassum* algae collected by C-EBS. Samples were sieved (300 µm) to remove sediment. **F:** Thallus of *Sargassum* collected in sediment core by a Multi-Corer (MUC) from the deep sea. **G:** Photo of *Sargassum* on sea floor taken by C-EBS at 5100 m depth (area A3). **H, I:** Photos of sedimented *Sargassum* algae on seafloor taken by AUV from around 5000 m water depth and a nominal altitude of 8 m above the seafloor (areas B1 and A3, respectively).

Area B2 had the least amount of *Sargassum* in the photos. Aggregations were sparse, with only small branches in most photos. There were significant differences in substrate quality noted in AUV photos with soft sediment dominating in the first two AUV deployments while mostly rock with little sediment overlay dominated the last deployment (area B2). The area B2 was at the center of the VEMA transform fault (VTF) and, unfortunately, only a small area could be inspected by this AUV dive. Multiple faults were visible in the photos, which were suggested by the geological survey to be tectonically active.

Table 2 *Sargassum* biomass (fresh weight) in the abyssal of the southern North Atlantic estimated from photos taken by AUV deployments.

Area/Site/ Dive No.	Depth (m)/Area (km^2)	No. of photos taken	No. of photos with *Sargassum*/ photos analyzed	Average biomass of *Sargassum* per photo with *Sargassum* (g)	Average surface area per analyzed photo (m^2)	Total surface area (m^2) of photos from a deployment	Total biomass in deployment area (kg)	Biomass per deploy-ment area (g/ m^2)
A3/6-2/ Abyss 163	5136/4.5	9217	1712/171	1161	0.18	306.0	1989.3	3.75
B1/9-6/ Abyss 165	4977/0.2	9576	2153/215	335	0.05	111.1	722.5	1.29
B2/11-3/ Abyss 166	5093/23	8112	145/14	241	0.04	5.4	35.0	0.07

3.2 Abundance estimation of surface *Sargassum* from literature

3.3 Sedimentation rate of *Sargassum*

Preliminary experiments carried out during the expedition onboard, revealed an estimated rate of sinking of freshly collected *Sargassum fluitans* (all bladders removed to estimate maximum sinking rate) of 2.5 km per day (undisturbed). With this estimated sinking rate a sample of *Sargassum* (ø 10 cm) would take between 2 and 2.5 days to reach abyssal depths. We investigated the maximum sedimentation rate of *Sargassum vulgare* in more detail at the coast of the Canary Islands. The experiments revealed an average rate of 2 m min^{-1} (± 0.48) estimated during four 10-meter runs. Based on these tests at maximum sedimentation, it would take a sample of *Sargassum* approximately 1.7 days to reach a depth of 5,000 meters, resulting in a sedimentation rate of approximately 2,900 m per day.

3.4 Epifauna composition on floating *Sargassum*

3.4.1 Meio- and macrofauna

From the floating *Sargassum* collected at the six stations, individuals belonging to five different phyla were found, including Caenogastropoda (Gastropoda), Cheilostomatida (Bryozoa), Leptothecata (Cnidaria), Polycladida (Plathelminthes) and Sabellida, Phyllodocida, Clitellata (Annelida) (Table 3). Preliminary results indicated the presence of epibiotic bryozoans (genus *Membranipora* de Blainville, 1830), and the annelid worm *Spirorbis* sp. at all sampled stations. There was little variation in the diversity of the sessile and motile fauna between the different stations with the most common sessile organisms being *Spirorbis* sp. and *Jellyella* cf. *tuberculata* (Bosc, 1802). The most common motile organism was the gastropod *Litiopa melanostoma* Rang, 1829, which was found at all sites except for site 8. However, juveniles and veliger stages of this species were only found at the two easternmost stations. Site 8 in area 4 (A4/8) was the only site where we detected the crab *Portunus sayi* (Gibbes, 1850). An undetermined shrimp was found with heavy infections by bopyrid isopods. The copepod *Scutellidium* cf. *longicauda* and the isopod *Carpias minutus* were the most frequent crustaceans.

Table 3 Recorded meio-and macrofauna from sampled surface *Sargassum fluitans*. For site 4 at sampling area 2 we collected *Sargassum* twice: on the 26th of December 2014 (*) and on the 28th of December (**).

***Sargassum* community from surface samples**	**Surface stations (area/site)**						
	A1/2	*A2/4	**A2/4	A3/6	A4/8	B1/9	C1/12
Gastropoda - Caenogastropoda							
Litiopa melanostoma Rang, 1829	X	X	X	X		X	X
Gastropoda - Opistobranchia							
Doto sp.	X						
Polychaeta - Sabellida							
Spirorbis sp.	X	X	X	X	X	X	X
Polychaeta - Phyllodocida - Nereididae	X				X		
Clitellata	X	X					X
Gymnolaemata - Cheilostomatida							
Jellyella cf. *tuberculata* (Bosc, 1802)	X	X	X	X	X	X	X
Rhabditophora - Polycladida							
Gnesioceros sp.		X		X		X	X
Hydrozoa - Leptothecata							
Clytia sp.	X	X					
Aglaopheniidae sp.				X	X	X	X
Crustacea - Maxillopoda - Harpacticoida							
Scutellidum cf. *longicauda* (Philippi, 1840)	X	X	X	X			X
Paralaophonte cf. *congenera* (G.O. Sars, 1908)	X	X		X			
Harpacticus cf. *gurneyi* Jakubisiak, 1933	X	X			X		X
Dactylopusia cf. *tisboides* (Claus, 1863)			X				X
Crustacea - Maxillopoda - Poecilostomatoida							
Macrochiron cf. *sargassi* G.O. Sars, 1916					X	X	X
Crustacea - Malocostraca - Decapoda							
Portunus sayi (Gibbes, 1850)					X		
Hippolyte cf. *coerulescens* (Fabricius, 1775)	X		X		X		
Latreutes fucorum (Fabricius, 1798)					X	X	X
Crustacea - Malacostraca - Isopoda							
Isopoda sp. 1				X			
Isopoda sp. 2							X
Isopoda sp. 3							X
Carpias minutus (Richardson, 1902)		X	X	X	X	X	

3.4.2 Micro- and nanofauna

The surface of *Sargassum* was densely populated at all areas investigated. Among protists associated with floating *Sargassum fluitans*, we found representatives of nearly all phylogenetic groups (Table 4). Regarding diversity, heterotrophic flagellates dominated including cryptomonads, apusomonads, thaumatomonads, ancyromonads, choanoflagellates, stramenopiles, cercomonads, bodonids, euglenids and dinoflagellates. Remarkable was the record of the filasterean *Ministeria vibrans*, which was confirmed by molecular studies (18S rDNA) and high resolution video-enhanced microscopy. Some "rhizopod" species appeared including foraminiferans, labyrinthulids, different forms of heteroloboseans and rhizarians. There were obvious differences in the diversity observed for the different samples, sites 2 (area A1) and 8 (area A4) contained the largest number of taxa, though quantitative estimates were not carried out. After one week of cultivation, ciliates comprising representatives of very

different taxonomic groups dominated the community in all raw cultures. A few epiphytic diatoms present in all samples represented the autotrophic fraction of epiphytes.

Table 4 Recorded protists from sampled surface *Sargassum fluitans*. Taxonomic groups summarized following Adl et al. (2012).

***Sargassum* community from surface samples**	**Surface stations (area/site)**				
	A1/2	*A2/4	A3/6	A4/8	B1/9
Incertae sedis					
Kiitoksia sp.				X	
Cryptomonadida					
Goniomonas sp.				X	
Apusomonadida					
Amastigomonas sp.	X				
Ancyromonadida					
Ancyromonas sp.	X				
Fabomonas tropica Glücksman & Cavalier-Smith, 2013					X
Amoebozoa					
Undet. amoebid	X	X	X	X	X
Undet. vannellid				X	
Undet. dactylopodid			X		
Thecamoeba sp. 1	X	X		X	
Thecamoeba sp. 2		X		X	
Vahlkampfia			X		
Filasterea					
Ministeria vibrans Tong, 1997		X			
Choanoflagellata					
Monosiga-like	X				
Stephanoeca sp.	X				
Salpingoeca tuba Kent, 1880	X				
Salpingoeca cf. *frequentissima* Zacharias, 1894	X				
Salpingoeca sp.			X	X	X
Excavata - Euglenida					
Anisonema-like 1	X	X	X	X	X
Anisonema-like 2	X	X	X	X	X
Petalomonas sp.			X		
Peranema sp.			X		
Excavata - Kinetoplastea					
Neobodo designis (Skuja, 1948) Vickerman, 2004	X	X	X	X	X
Neobodo curvifilus (Larsen & Patterson, 1990) Moreira et al. 2004	X				X
Rhynchomonas nasuta (Stokes, 1888) Klebs, 1892	X				
Bodo sp.				X	X
Excavata - Heterolobosea					
Percolomonas cosmopolitus (Ruinen, 1938) Fenchel & Patterson, 1986	X				
Vahlkampfia sp.		X			
Stramenopiles - Dictyochophyceae					
Ciliophrys sp.					X
Pteridomonas danica Patterson & Fenchel, 1985	X		X	X	
Stramenopiles - Actinophyridae					
Actinophrys sp.				X	
Stramenopiles - Bicosoecida					
Caecitellus sp.			X		X
Cafeteria roenbergensis Fenchel & Patterson, 1988	X	X	X	X	X
Pseudobodo sp.	X	X	X	X	X
Stramenopiles - Labyrinthulomycetes					
Labyrinthulids			X		
Rhizaria - Foraminifera					
Rotaliidae	X				
Reticulomyxa-like					X
Globigerina-like	X				
Rhizaria - Thaumatomonadida					

Thaumatomonas sp.	X			X	
Glissomonas-like			X	X	X
Massisteria marina Larsen & Patterson, 1990			X	X	X
Rhizaria - Metromonadea					
Metromonas sp. 1	X	X	X	X	
Metromonas sp. 2	X				
Metopion sp.				X	
Alveolata - Dinoflagellata					
undet. Dinoflagellata	X				
Ciliophora - Hypotricha					
Euplotes sp. 1	X	X	X	X	
Euplotes sp. 2	X	X	X		
Diophrys sp.	X		X	X	
Dysteria sp.	X		X	X	
Aspidisca sp.	X			X	
Ciliophora - Stichotrichia					
undet. Stichotrichid		X	X	X	
Ciliophora - Suctoria					
Suctoria undet.			X		
Ciliophora - *Protocruzia*					
Protocruzia sp.		X	X		
Ciliophora - Scuticociliata					
Cinetochilum sp.	X				
Cristigera setosa Kahl, 1928	X				
Ciliophora - Oligotrichia					
undet. Oligotrichia	X				
Ciliophora - Karyorelictea					
Trachelorаphis sp.	X				
Pleuronema sp.	X				
Litonotus sp.	X				
Blepharisma-like			X		
Ciliophora - Peritrichia					
Cothurnia-like	X				

For site 4 at sampling (area 2) we collected twice *Sargassum:* on the 26th of December 2014 and on the 28th of December. For the protist community we only determined protist communities from the 26th of December 2014 (*). In area C1, protists were present but could not be analyzed in detail due to time constraints onboard.

3.5 Biochemical analysis of *Sargassum*

3.5.1 Fresh, dry and ash-free dry weights and C:N ratios

Weights were measured from two floating *Sargassum* samples stored at -80°C (three replicates), five surface material samples that were stored at 10°C for degradation (three replicates), and seven deep-sea samples stored at -80°C (three replicates). Values for the fresh, dry and ash free dry weights were averaged between the three sample types (surface material, surface material degraded, deep-sea material). Using the ash-free dry weight, the percentages of organic material to total weight were calculated and then averaged resulting in 64.0 (± 6.2) % for surface material, 46 (± 5.2) % for surface material degraded material, and 54 (± 9.7) % for deep-sea material. The ratio of organic weight to total weight showed significant differences within all the three sample types (one-way ANOVA, $p<0.001$). The C:N ratios were determined for each sample weighed, and averages were calculated based on sample location (Fig. 3). Due to high variance there was no significant difference between the three sample types (one-way ANOVA, $p>0.05$).

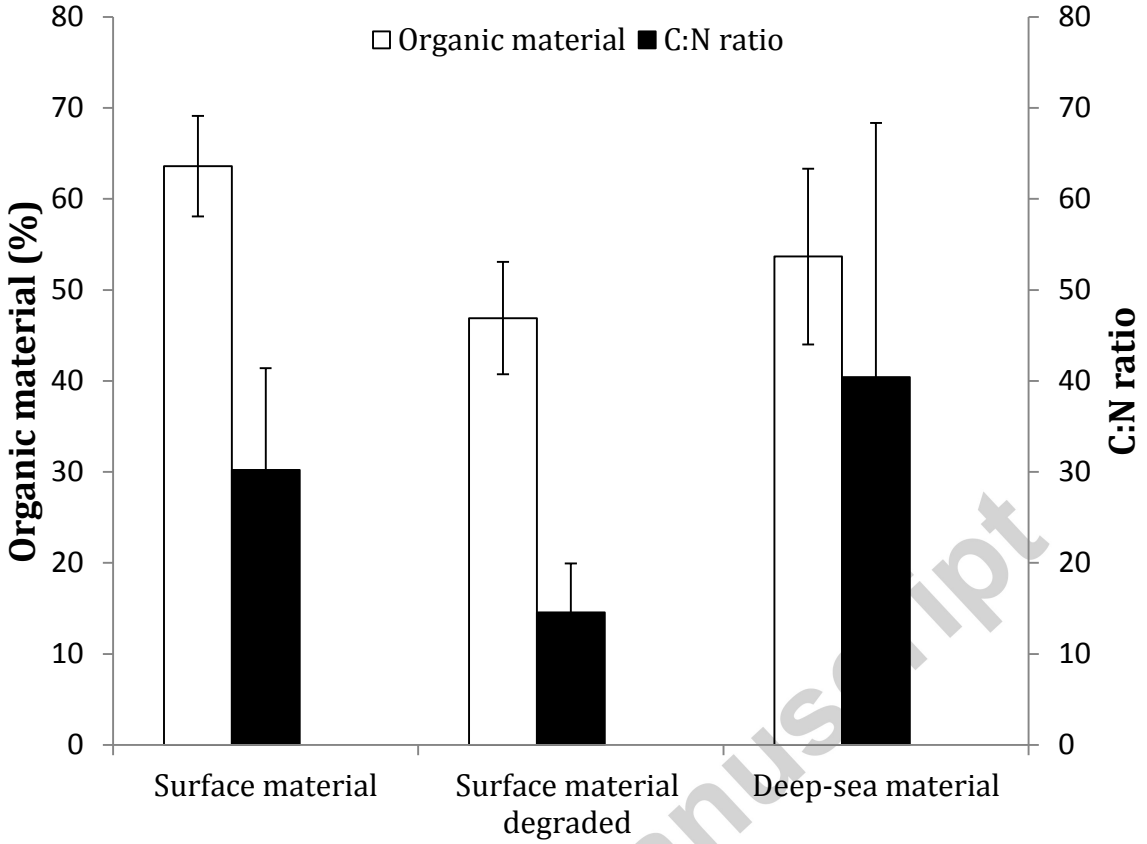

Figure 3 Percentage of organic material for surface material, surface material degraded, and deep-sea material of *Sargassum* samples (left axis, white columns), and C:N ratio (right axis, black columns).

3.5.2 Fatty acid analysis

Stations were pooled from one area for the analysis. The variability within the samples of *Sargassum* was high and no significant difference between the depths could be detected. The five most abundant fatty acids (FAs) in the *Sargassum* samples were 16:0, 18:0, 18:1(n-9), 20:4(n-6) and 22:6(n-3) with ranges of 9.9%- 39.1%, 3.4%- 11.7%, 4.1%- 10.9%, 1.3%- 20.8% and 1.2%- 10%, respectively (Table S1). Having a closer look at the ten most abundant FAs in all analyzed samples, the *S. fluitans* samples revealed a low and not consistent FA composition neither between the depths, nor between areas (Fig. 4).

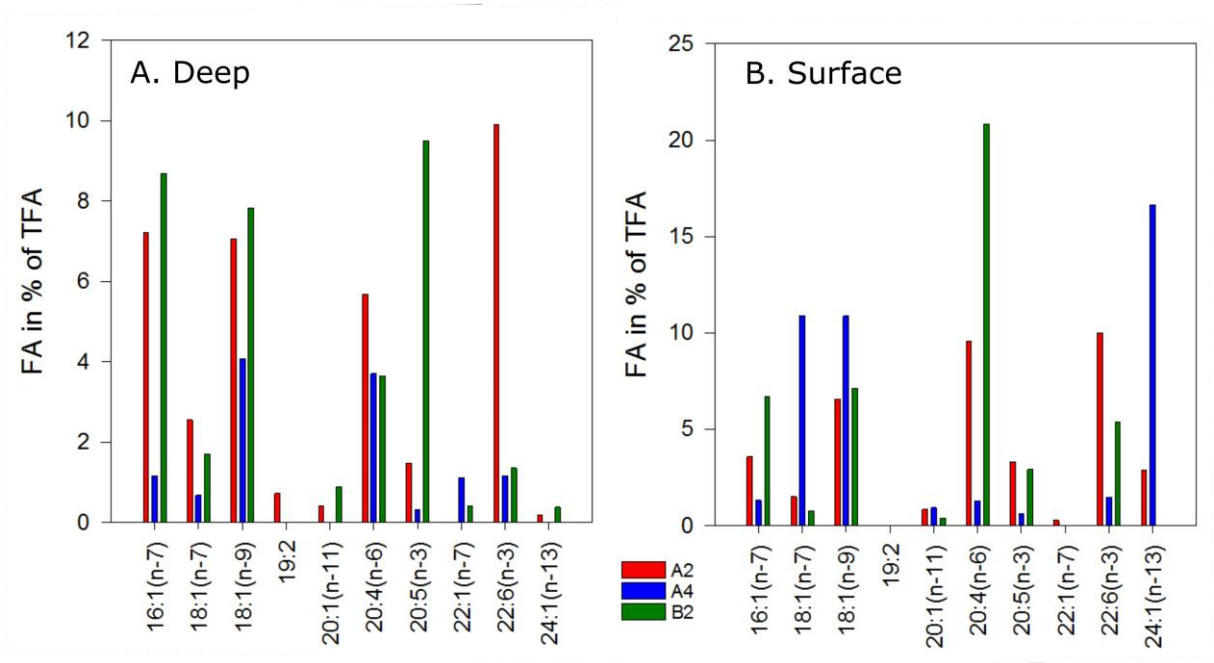

Figure 4 Mean values of *Sargassum fluitans* sampled in the deep sea (A) and surface (B) for the ten most abundant fatty acid [%] of total fatty acid contents (TFA) from the three different areas.

3.5.3 Stable isotope analysis

The stable $\delta^{15}N$ values revealed a clustered picture for each sampled group (Fig. 5). Therefore, significant differences between the sediment, the *Sargassum* samples and the abyssal specimens could be detected. The $\delta^{13}C$ values showed a wide range among the groups from -16‰ to -19‰ but were consistent within each taxonomic group (Fig. 5). Only the sediment samples revealed a statistic-supported separation from all other groups. However, no obvious difference between the eastern and western side of the Mid-Atlantic Ridge (MAR) was detectable.

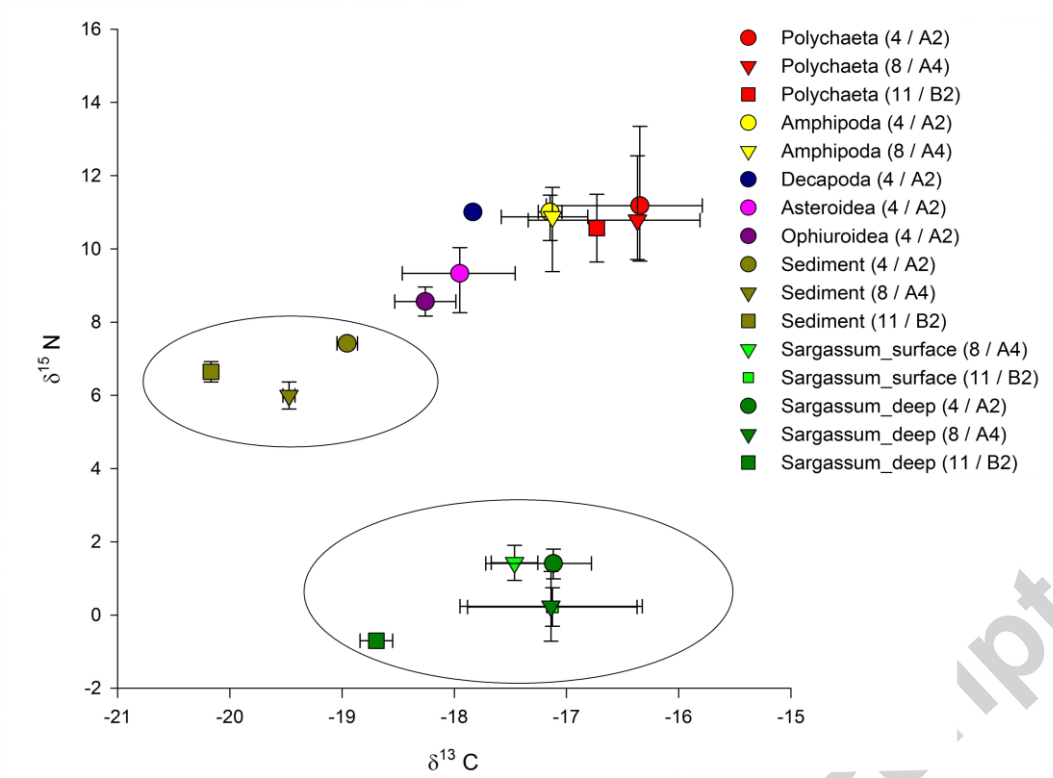

Figure 5 Biplot overview of stable isotope composition for organisms of different taxa, sediment and *Sargassum fluitans* at different stations (site/area), minimum and maximum values served as error bars. The symbol color indicates the kind of sample, while the shape of symbols indicates the sample origin. Sampling sites and respective sampling area are given in brackets.

To determine the relative trophic levels of the taxa, sampled in area A2, the mean $\delta^{15}N$ values were compared (Figure S1). The *Sargassum fluitans* material showed the lowest values (0.31‰ for *Sargassum*_surface/ 0.82‰ for *Sargassum*_deep) followed by the sediment samples (6.68‰). The mean value of the sediment samples (6.7‰) was used as the baseline of the enrichment process, thus, two relative trophic levels scarcely could be identified.

4. Discussion

Mass occurrences of *Sargassum* are well known from the North Atlantic and Gulf of Mexico (e.g. Butler et al., 1983; Gower and King, 2008) and can also form inundation events (Schell et al., 2015). Floating mats of *Sargassum* can be aggregated by Langmuir circulations and in areas of converging currents (Haney, 1986). With increasing biomass, there is an accumulation of organic nutrients and a development of communities within these mats (e.g. Huffard et al., 2014). Earlier studies revealed an increase of diversity of benthic communities in habitats which are enriched with *Sargassum* (e.g. Smith and Hessler, 1987; Grassle and Morse-Porteous, 1987). It was argued that sedimentation of these algal mats offer a potential food source for deep-sea communities (Schoener and Rowe, 1970; Wolff, 1979; Turner and Rooker, 2006). To get an idea

regarding the relative importance of sedimented *Sargassum* biomass, we tried to relate our own estimates of sedimented *Sargassum* biomass with that reported for floating *Sargassum*.

4.1 Biomass estimation of *Sargassum*

4.1.1 Estimation of floating *Sargassum* biomass from literature

For a comparison with sedimented *Sargassum*, we reviewed available quantitative estimates of floating *Sargassum* in the North Atlantic. Free floating species of *Sargassum*, like that found in the Gulf of Mexico and the North Atlantic, have been studied since at least the 1830's, and have been part of marine lore, as in the naming of the Sargasso Sea (Gower and King, 2008). Various groups, like NOAA (http://www.noaa.gov) and the Sargasso Sea Alliance (http://www.sargassoalliance.org), in conjunction with the Bermuda government, have compiled previous reports, as well as conducted primary research (neuston pulls) to determine abundance, positioning and movement of *Sargassum* algae within the Gulf of Mexico and North Atlantic (Schell et al., 2015). Data were also collected from NOAA, NASA, and ESA satellites using MODIS and MERIS imaging (Stoner, 1983; Butler and Stoner, 1984; Gower and King, 2008; Siuda, 2011). There are a few abundance estimates available for different years and periods (Table 3). Separate tows conducted and published by Stoner (1983) that occurred between 1977 and 1981 compared the average *Sargassum* biomass of the Sargasso Sea, the Bahamas and the Gulf Stream. These results were compared with tows made by Parr in the 1930's for the same areas, and concluded that the overall biomass of pelagic *Sargassum* had decreased over a period of about 50 years (Stoner, 1983). However, a later publication by Butler and Stoner (1984) questioned this conclusion on the basis that Stoner did not consider seasonal variation of *Sargassum* abundance. Gower and King's (2008) studied the movement of free floating *Sargassum* between the Gulf of Mexico and Atlantic Ocean using satellite-imaging data and Medium Resolution Imaging Spectrometer (MERIS) from the European Space Agency. They calibrated the satellite data with ship measurements from the corresponding months (Gower and King, 2008). The MERIS study also referenced previous studies by Parr in the 1930's of free floating *Sargassum* in the western North Atlantic (Parr, 1939 cited in Gower and King, 2008). During fall, quantities of *Sargassum* were greater in the North Sargasso Sea (average of 0.27 g/m^2) than in the South (0.03 g/m^2), while the reverse was noted for spring (0.12 and 0.18 g/m^2 respectively). It was also shown that there was an increased overall abundance during fall, with an average biomass of 0.30 g/m^2 throughout the year (Siuda, 2011). Siuda (2011) used 1999 individual neuston-tow pulls conducted from 1973 to 2010 by SEA from Woods Hole Oceanographic Institute to determine local and seasonal differences. A recent review of Schell et al. (2015) clearly showed strong annual fluctuations of floating *Sargassum* biomass determined by neuston tows during autumn studies with peaks in recent years causing inundation events. We summarized all data

available to us in Table 5, where we tried to standardize the estimates of *Sargassum* biomass (fresh weight) by the different authors as biomass per m^2.

Table 5 Biomass estimates (fresh weight) for *Sargassum* recorded from the North Atlantic by different authors.

Source	Biomass	Year	Location	Area for recalculation	Biomass recalculated [g/m^2]
Parr (1939)	7 million tons	1933	North Atlantic	41.5 M km^2	0.169
	11 million tons	1934	North Atlantic	41.5 M km^2	0.265
	4 million tons	1935	North Atlantic	41.5 M km^2	0.096
Stoner (1983)	74 mg/m^2	1977-1981	Sargasso Sea		0.074
	165 mg/m^2	1977-1981	The Bahamas		0.165
	280 mg/m^2	1977-1981	Gulf Stream		0.28
Gower and King (2008)	1 million tons	2002-2008	Gulf of Mexico	1.6 M km^2	0.625
	1 million tons	2002-2008	North Atlantic	41.5 M km^2	0.024
Siuda (2011)	0.39 g/m^2	1977-2010	North Sargasso Sea		0.39
	0.21 g/m^2	1977-2010	South Sargasso Sea		0.21
Schell et al. (2015)	0.17 g/m^2	1995-2013	South Sargasso Sea		0.17
	0.23 g/m^2	2014/2015	South Sargasso Sea		0.23
	0.25 g/m^2	2011/2012	South Sargasso Sea		0.25
	0.0027 g/m^2	1992-2013	West. Trop. North Atlantic		0.0027
	0.07 g/m^2	2011	West. Trop. North Atlantic		0.07
	0.84 g/m^2	2014	West. Trop. North Atlantic		0.84

With the literature reviewed in this study, there are consistent findings of large quantities of holopelagic *Sargassum* throughout the North Atlantic, Caribbean Sea and Gulf of Mexico. Studies looking into the abundance of *Sargassum* have regularly shown these quantities, leading to the assumption that, while seasonal variances occur, there is a consistent supply of *Sargassum* throughout these waters to serve as a potential carbon flux to the deep sea through sedimentation. These findings are supported by the amount and frequency of *Sargassum* noted during the present expedition. Other studies have shown that these floating aggregations of algae can support a large diversity of marine organisms in surface waters (Fine, 1970; Settle, 1993), as they provide feeding grounds, refuge areas and, thus, increase habitat complexity (Fine, 1970; Kingsford, 1995).

The interactions between these organisms could possibly lead to nutrient enrichment of the *Sargassum* mats, as well as an enhanced primary production indicated by findings of 20:5(n-3) as a diatom marker in the sediment. Normally equatorial oceans are generally considered to be oligotrophic and therefore exhibit a lower total primary production rate than coastal or polar areas. In contrast, Uitz et al. (2010) found increased microplankton concentrations (diatoms) in the studied area which could explain the higher proportions of 20:5(n-3) found in the organisms and in the sediment. The increased amount of organic matter could be explained by the influence of the NECC transporting nutrients and POM from the coastal areas of the African and American continents. This assumption is also supported by the theory of Oschlies and Garcon (1998) who predicted an increase of primary production in areas of strong eddy kinetics which are found in

the studied region. Furthermore, trophic interactions on *Sargassum* might initiate the sedimentation process by removal of the bladders through grazing and degradation (Fig. 2C). The resulting vertical transfer of energy includes not only the *Sargassum* itself, but potentially also the community of organisms on its surface.

4.1.2 Biomass estimates of sedimented *Sargassum*

Three different AUV deployments during the VEMA Transit expedition showed the presence of *Sargassum* algae on the seafloor at high abundances, which was additionally confirmed by qualitative samples of *Sargassum* taken with the camera of the C-EBS as well as by the sledge. Analysis of the AUV photos revealed a biomass density of up to 3.75 g/m^2 and the lowest density of 0.07 g/m^2. These results fall within the biomass previously estimated for *Sargassum* at the surface (Table 5). While area B1 showed a 20 times higher biomass density compared to the estimated surface density, one needs to consider that surface communities of *Sargassum* tend to aggregate in large mats, some noted to be over a kilometer in length, and are not evenly distributed through the North Atlantic. Variation in the appearance of *Sargassum* between the different sites and stations could show differences in the role that it plays, depending on the surrounding organisms. The *Sargassum* found at area A3 had a consistently larger biomass per clump than the other two areas (B1, B2), with little signs of bioturbation. However, at area B1, the majority of *Sargassum* found had signs of bioturbation surrounding it (Fig. 2H). We assume that this might be caused by the treatment of *Sargassum* by benthic animals (Schoener and Rowe, 1970; Wolff, 1979), although we had no direct photographic evidence. Schoener and Rowe (1970) presented the first direct evidence for high abundance of *Sargassum* in the abyssal. They found *Sargassum* clumps of varying sizes in varying degrees of degradation at 33 of 150 stations in the western North Atlantic off North Carolina by a camera survey. Here we present the first quantitative data indicating the high potential contribution of *Sargassum* to the matter flux in the southern part of the North Atlantic. We consider AUV studies to be a very useful tool to quantify sedimented macroalgae and to get a better insight into particle flux from the surface to deep-sea communities.

4.1.3 Sedimentation of *Sargassum*

Sedimentation rates of *Sargassum* determine how viable it could be as a source of carbon for deep-sea ecosystems. If the rate is too slow, there might be a decrease in usable carbon and nutrients, either due to degradation, or consumption by other organisms in the water column. The rate of sedimentation found in this study is in theory a maximum potential sedimentation rate, based on the removing of all bladders (pneumatocysts) from the algae, thus, decreasing the buoyancy. The two different sedimentation tests conducted, the preliminary one on board the

R/V *Sonne* cruise with *S. fluitans* and the study at the Canary Islands using *S. vulgare*, showed similar rates (5000 m in 48 hours). Both of these tests removed all the bladders from the plants, and while they were done with two different species, we assume that similar results would occur with other morphometrically similar species of algae. It must be noted, however, that a maximum sedimentation rate with all bladders being removed is unlikely to be found naturally. That leaves an important question as to what causes the initial sedimentation of the algae. It is possible that some of the bladders need to be removed before the initiation of sedimentation begins, however, as previously mentioned, the nutrification and development of surface dwelling organisms on the algae can have an effect on the sinking rates, potentially initiating the sedimentation process (Turner and Rooker, 2006). Moreover, the compression of bladders with increasing depth will further reduce the buoyancy of the algae.

Schoener and Rowe (1970) determined sedimentation rates of *Sargassum* preserved in 10% Formalin 3.3 (2.8-4.0) cm/sec and calculated a sedimentation to 5000 m depth to occur within 41 hours. This value is in the same range as our estimates using live specimens. It is not known what caused a change in its specific gravity. Schoener and Rowe (1970) argued that there could be changes in the integrity of the air bladders at a critical shallow depth which would result in rapid sinking or there might be a high specific gravity by slow degradation. Johnson and Richardson (1977) have shown in experiments with pressure chambers that the depth, at which the whole *Sargassum* plants lost their positive buoyancy and sank, appeared to be an inverse function of the rate of hydrostatic pressure change, indicating that the slower the plant descent the shallower the depth at which sinking occurred due to positive buoyancy loss. They calculated that, once negatively buoyant, *Sargassum* will sink to the sea floor in about 40 h. This value is again in the same range as estimated in the present study. In accordance with Johnson and Richardson (1977) we argue sedimentation may occur via several mechanisms: 1) fragmentation of weed clumps due to wave action with the subsequent sinking of the older parts which are more heavily populated by epibenthic micro- and macroorganisms (Fig. 2C; Tables 3 and 4); 2) diseased *Sargassum* may lose its buoyancy; 3) entrainment of *Sargassum* clumps in the zones of convergence and down welling associated with Langmuir circulation cells and large scale down welling. For vital *Sargassum*, Woodcock (1993) hypothesized that the algae may be adapted to a cyclic submergence in the wind-induced vertical currents, returning to the surface only when the currents are less than the plant's rise rate. This phenomenon might support the maintenance of their holopelagic life.

The well preserved *Sargassum* clumps in the AUV photos might be explained by a steady sedimentation and replacement of degraded material at relatively high rates or a very slow degradation rate. The biochemical data support this ambivalent view. However, several facts support the first explanation: 1) macrofauna is known to feed on and destroy *Sargassum* in the

deep (e.g. Schoener and Rowe, 1970; Wolff, 1979; Grassle and Morse-Porteous, 1987); 2) macrofauna was present at relatively high abundances at the three investigated areas (Brandt et al., this issue; Riehl et al. this issue) and might have fed at least indirectly on *Sargassum* (see below); 3) traces of macrofauna activities around *Sargassum* clumps were recorded (Fig. 2H).

4.2 Epifauna composition on *Sargassum*

The analysis of floating *Sargassum* revealed a diverse community. Regarding the epiphytic meio- and macrofauna, the random occurrence of the shrimp *Latreutes fucorum*, the polychaete *Platynereis dumerilli*, the turbellarian *Planocera* cf. *pellucida* and the nudibranch gastropod *Doto* sp. fits well with the observations of previous studies (e.g. Weis, 1968; Fine, 1970; Stoner and Greening, 1984; Huffard et al., 2014). It has been shown that many organisms known to be found in the Sargasso Sea also occur further south and east of the Atlantic as previously described, where mats of floating *Sargassum* can still be found. The recorded meio- and macrofauna might well be responsible for the destruction of bladders of *Sargassum* directly or indirectly by feeding and thereby stimulating microbes which destroy the algal cell layers (Johnson and Richardson, 1977).

Regarding the nano- and microfauna, a community structure was found as it is typical for marine sediments (e.g. Arndt et al., 2000). Many taxa we observed were also recorded from oceanic detritus (Patterson et al., 1993; Arndt et al., 2003). Thus, a potential transatlantic distribution of benthic protists by *Sargassum* would be possible. The preliminary studies revealed that most of the recorded taxa belong to ubiquitously distributed protists (e.g. Patterson and Lee, 2000). The protistan fauna obviously contributes to a diverse microbial food web on the *Sargassum* surface. Some peritrichous ciliates feed on pico- and nanoplankton surrounding the *Sargassum,* several choanoflagellate species and stramenopile heterotrophic flagellates feed on the surrounding bacterioplankton. All other protists, however, belonged to surface dwelling forms feeding on attached bacteria and algae stimulating the degradation of *Sargassum* by exerting a strong grazing pressure on bacteria biofilms. Several protist species were found to survive drastic increases in hydrostatic pressure occurring during sinking (Živaljić et al., this issue), thus, the grazing impact might continue during the sedimentation process of *Sargassum*, as several representatives have been found alive on sedimenting detritus from deep-sea samples (Patterson et al., 1993; Arndt et al., 2003).

To check, whether the epiphytic fauna from the surface might give rise to the population of the deep-sea benthos, we did preliminary studies on blades of *Sargassum* collected by the C-EBS (meio- and macrofauna) or the Multi-Corer. Several blades were inspected for meio- and macrofauna and three blades obtained from undisturbed MUC cores revealed no protists in direct observations or cultures. Though we did not find any species identified by our

investigations of surface samples of *Sargassum*, at least several nanoprotists we found on the floating *Sargassum* have been recorded from the deep sea (e.g. *Neobodo* spp., *Cafeteria* sp., Patterson et al., 1993; Arndt et al., 2003; Scheckenbach et al., 2010). Thus, a potential contribution of protists sedimenting with *Sargassum* to the oceanic floor cannot be ruled out at least for some nanofauna species. Regarding the epiphytic meio- and macrofauna on sedimented *Sargassum*, we could not record any organism. These finding might be influenced by the sampling technique which has potentially washed away attached organisms. Future studies with more refined methods are necessary to study this matter. At the moment, we have to assume that even though there are high densities of a very diverse epifauna on floating *Sargassum*, only a few organisms might be transferred to the deep-sea communities.

4.3 Biochemical analysis and potential carbon flux from sedimented *Sargassum*

4.3.1 Fresh, dry and ash-free dry weights and C:N ratios

The analysis of dry and ash-free dry weights showed significant differences between samples collected at the surface and those collected from the deep sea. Samples that were collected from the surface and immediately stored at -80°C had a higher percentage of organic content than samples collected from the surface and degraded for 18 months at 10°C and deep-sea samples, stored at -80°C. It should be expected that degradation is noted between the surface sample immediately frozen and the surface sample stored at 10°C for 18 months. Furthermore, degradation was also seen in the deep-sea samples that were frozen at -80°C immediately after sampling. This could be a result of degradation on the way of sedimentation or due to degradation in the abyss. Since the sinking rate is relatively high when bladders are destructed, it has to be assumed that the major part of the degradation takes place in the abyssal sediment. While destruction of *Sargassum* blades at 10°C for 18 months was very obvious, visual inspection of the *Sargassum* collected directly from the abyss showed only little destruction, and plant structures remained intact (see discussion above).

C:N ratios found in our study were typical of marine plants, however, with high variance even between similar samples. Literature cites values of between 4 and 10 for marine phytoplankton, between 15 and 50 for holopelagic *Sargassum* depending on if it is found in the neritic zone or the open ocean, and a general tendency for higher values with increasing depth (Müller, 1977; Atkinson & Smith, 1982; Meyers, 1994; Lapointe 1995). Due to high variability, our results of the C:N analysis did not show statistically significant differences between the surface *Sargassum* and deep-sea samples. This has to be addressed in future studies.

4.3.2 Fatty acids (FA) analysis

Macroalgae, like *S. fluitans,* are often characterized by distinct FA compositions affecting organisms of higher trophic levels. This makes them a useful biomarker to reveal information about food webs (Graeve et al., 2001). Unfortunately, the FA composition of the *S. fluitans* samples was not consistent, thus no specific FA or a distinct composition could be detected. This could have various reasons; maybe it is due to seasonal differences in polyunsaturated FAs (PUFAs) signatures for *S. fluitans* (Turner and Rooker, 2006) influenced by light intensity, salinity, temperature and available nutrients (Thompson et al., 1990; Thompson et al., 1992). It could also be due to the material biochemically changing during the floating time, aging, and sinking processes (Mintenbeck et al., 2007; Galloway et al., 2012; Galloway, 2013) or an increased microbial abundance (McArthur et al., 1992; Chen et al., 2008). Also the associated epibionts could affect the FA measurements and lead to scattered results. From freshwater systems it is known that bacterivorous protists might change the PUFA signature (Martin-Creuzburg et al., 2005). We found large numbers of bacterivorous protists being active at the surface of *Sargassum* feeding on attached bacteria.

The PCA of the ten most abundant FAs (16:1(n-7), 18:1(n-7), 18:1(n-9), 20:1(n-11), 22:1(n-7), 24:1(n-13), 19:2, 20:4(n-6), 20:5(n-3) and 22:6(n-3)) revealed a clear separation of the different taxa showing a clustered picture of the Opheliidae (Polychaeta), Porcellanasteroidae (Asteroidea) and Ophiuridae (Ophiuroidea), but a scattered image for the seven different Amphipoda families. Different taxonomic groups have distinct FA patterns consistent within the groups. The fatty acid 20:4(n-6) had the biggest proportion followed by 18:1(n-9) and 16:1(n-7). This pattern is also found by Khotimchenko (1991) for *Sargassum*. Furthermore, 20:4(n-6) is discussed to be a biomarker for the entire taxonomic group of brown algae (Hanson et al., 2010). Turner and Rooker (2006) hypothesized that heterotrophs utilizing the *S. fluitans* rely more on the enhanced phytoplankton production and the associated epibionts, and some analyzed organisms showed higher proportions of those FAs. Our own investigation on the components of the microbial food web indicates that the majority of microbes take advantage of the biofilm on the surface of *Sargassum* blades. This leads to the assumption that, at least for some organisms, *S. fluitans* could serve as a food source in the studied region.

4.3.3 Stable isotope (SI) analysis

Considering the SI results in this study, the very low $\delta^{15}N$ values of the *S. fluitans* samples (mean value= 0.5 ‰) and the relatively large gap before the first analyzed megafaunal group (Ophiuridea= 8.6 ‰), it is unlikely that the macroalgae serve as a direct food source for higher trophic levels, while it possibly might be consumed by protists. Protists are known to upgrade

the food quality for higher trophic levels (Martin-Creuzburg et al., 2005, 2006). The abyssal seafloor as a food limited habitat is suggested to generate mainly opportunistic feeders using every available food source including wood falls (e.g. Becker et al., 2009; Hoyoux et al., 2009). Therefore, a gap of 2.5 relative trophic levels between the possible food source and the small sized Ophiuridae seem to be very unlikely. The sediment with its organic matter (and the microbial food web on *Sargassum*), however, leads to a more justified result considering the SI. FAs are faster incorporated than the heavy isotopes. Therefore, the slightly increased amounts of 20:4(n-6) could be a signal of the algal material whereas no sign could be detected in the SI patterns. However, microbes (bacteria and protists) in the upper sediment layers can rapidly alter FAs during deposition via biodegradation and/or chemical degradation as a consequence of the created surrounding (Eclinton, 1973). Regardless of whether *S. fluitans* is directly or indirectly used as a food source for metazoans, the floating algae have likely a very significant impact on the environment, on the surface as well as in the deep sea.

5. Conclusion

Deep-sea ecosystems are generally limited by carbon availability. We add quantitative estimates suggesting that floating *Sargassum* could act as an important input of organic carbon to the deep sea in the southern North Atlantic. While previous studies had looked at carbon flux into the deep sea, the sedimentation rates and potential for large quantities of macrophytes to significantly contribute to this flux has been rarely studied (for a recent review see Krause-Jensen and Duarte, 2016). We show that there is a large biomass of sedimented *Sargassum* algae on the seafloor which can be in the same range as that at the surface and should play an important role for benthic production – sinking rates of *Sargassum* are probably high (~2 days to 5000m water depth) allowing little time for degradation or consumption. While these are only estimates, the results show that a significant part of the production of *Sargassum* at the surface waters eventually reaches the deep sea, at least in the area of the southern North Atlantic covered during the Vema-TRANSIT expedition. Analysis of fatty acids and stable isotopes indicate that macrofauna might not directly consume *Sargassum* in the abyssal, but probably via the components of the abyssal microbial food web including bacteria and protists (probably several trophic levels) as it is known already for macrofauna making use of wood falls (Becker et al., 2009; Hoyoux et al., 2009). The particular phenomenon of large-scale sedimentation of *Sargassum* as a regular carbon input has to be much more considered. Further studies are needed to determine to what extent deep-sea organisms rely on this source of energy.

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