



## Castaways can't be choosers – Homogenization of rafting assemblages on floating seaweeds



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### ABSTRACT

After detachment from benthic habitats, the epibiont assemblages on floating seaweeds undergo substantial changes, but little is known regarding whether succession varies among different seaweed species. Given that floating algae may represent a limiting habitat in many regions, rafting organisms may be unselective and colonize any available seaweed patch at the sea surface. This process may homogenize rafting assemblages on different seaweed species, which our study examined by comparing the assemblages on benthic and floating individuals of the furoid seaweeds *Fucus vesiculosus* and *Sargassum muticum* in the northern Wadden Sea (North Sea). Species richness was about twice as high on *S. muticum* as on *F. vesiculosus*, both on benthic and floating individuals. In both seaweed species benthic samples were more diverse than floating samples. However, the species composition differed significantly only between benthic thalli, but not between floating thalli of the two seaweed species. Separate analyses of sessile and mobile epibionts showed that the homogenization of rafting assemblages was mainly caused by mobile species. Among these, grazing isopods from the genus *Idotea* reached extraordinarily high densities on the floating samples from the northern Wadden Sea, suggesting that the availability of seaweed rafts was indeed limiting. Enhanced break-up of algal rafts associated with intense feeding by abundant herbivores might force rafters to recolonize benthic habitats. These colonization processes may enhance successful dispersal of rafting organisms and thereby contribute to population connectivity between sink populations in the Wadden Sea and source populations from up-current regions.

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### 1. Introduction

Floating seaweeds host a wide diversity of associated organisms during their journeys along the coasts and across the oceans (Clarkin et al., 2012a; Ingólfsson, 1995; Vandendriessche et al., 2006). Associates find shelter and/or food on host seaweeds, thereby facilitating travel for prolonged time periods. However, consumption, fouling and other diverse processes (e.g. solar radiation) limit the lifetime of floating seaweeds (Gutow, 2003; Rothäusler et al., 2011; Vandendriessche et al., 2007). Consequently, associates may frequently abandon degrading seaweed patches and colonize new rafts. Seaweeds are much scarcer in the neustonic realm than in benthic habitats. Given their need for an attachment substratum, associated organisms may unselectively attach to any floating object available at the sea surface. Indeed, obligate rafters (e.g. goose barnacles *Lepas* spp., Columbus crabs *Planes minutus*, or the isopod *Idotea metallica*) have been reported from many different types of floating objects, ranging from seaweeds to

wood and even abiotic substrata such as volcanic pumice and plastic debris (Bryan et al., 2012; Dellinger et al., 1997; Gutow and Franke, 2003; Minchin, 1996). A similar pattern of non-selectivity might also be expected for rafters on different species of floating seaweeds, which may select their attachment substrata opportunistically (Vandendriessche et al., 2006).

Studies of benthic habitats show that epibiotic assemblages can differ substantially among seaweed species (Buschbaum et al., 2006; Christie et al., 2007; Lutz et al., 2010; Taylor and Cole, 1994). These host-specific assemblages are probably not driven by divergent, host-specific succession, but more likely result from the high mobility and substratum preferences of many associated species (see e.g. Taylor, 1998), which allows them to select seaweeds they prefer for structural, chemical or positional traits. Consequently, a rapid turnover of associates leads to host-specific assemblages on benthic seaweeds.

On the one hand, host availability at the sea surface is likely much more restricted than in benthic habitats, possibly limiting selectivity of associated biota on floating seaweed patches. On the other hand, floating objects often accumulate in drift rows and fronts (Hinojosa et al., 2011; Ingólfsson, 1995), offering associated fauna ample opportunities

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to colonize new rafts. The restricted lifetime and limited availability of floating seaweed hosts at the sea surface likely favor homogenization of epibiotic assemblages over host-specific assemblages. Consequently, associate assemblages on floating seaweeds can be expected to differentiate less among hosts than those found on benthic seaweeds.

In most parts of the world, floating seaweeds originate from benthic habitats, with *Sargassum* from the Sargasso Sea as the lone exception (Rothäusler et al., 2012). When detached from their benthic substratum, seaweeds with gas-filled vesicles float to the sea surface. During this initial phase of rafting, important changes in the associated assemblage occur, mainly because many organisms living in benthic seaweeds drop off leaving only the most persistent species on the newly formed seaweed raft (Edgar, 1987; Gutow et al., 2009; Kingsford and Choat, 1985). This first wave of changes can start to homogenize assemblages, because non-persistent taxa (e.g. some gastropods and echinoderms) leave, regardless of the seaweed species. This process occurs very rapidly after detachment, and assemblages from floating seaweeds collected in the immediate vicinity of benthic seaweed beds therefore harbor typical associates from benthic habitats (Ingólfsson, 1995).

Shortly after floating seaweeds arrive at the sea surface, other organisms start to colonize, including sessile species that arrive as larval stages (e.g. hydrozoans, bryozoans or goose barnacles) and mobile species (e.g. decapod or peracarid crustaceans), the latter being relatively unselective with respect to substratum choice. Although some mobile species seem to prefer particular seaweed species, they also colonize less-preferred species (Vandendriessche et al., 2006). Isopods from the genus *Idotea* exemplify mobile rafters. Various *Idotea* species have repeatedly been found in large numbers associated with floating seaweeds in the NE Atlantic (Franke et al., 1999; Ingólfsson, 1995; Tully and Ó Céidigh, 1986; Vandendriessche et al., 2006). Clarkin et al. (2012b) showed that these isopods continuously colonize floating seaweeds. In general, rafting assemblages on floating seaweeds can be highly dynamic as rafts frequently break up and re-assemble in drift rows, where castaways may switch among rafts (Hobday, 2000). This process could homogenize raft assemblages with many species opportunistically holding onto a wide range of different seaweed species (Clarkin et al., 2012a).

While the assemblages on floating seaweeds have been relatively well-studied in the NE Atlantic (e.g. Clarkin et al., 2012a; Ingólfsson, 1995; Vandendriessche et al., 2006), few studies collected corresponding samples of benthic seaweeds and associated epibionts. However, understanding the different processes that shape the composition of the epibiotic assemblage on benthic and floating seaweeds requires comparative sampling. Clarkin et al. (2012b) showed that assemblages of associated isopods differ among benthic and floating seaweeds, indicating differential structuring processes in the two habitats. To compare entire epibiont assemblages on benthic and floating seaweeds we selected two structurally different, buoyant seaweeds, *Fucus vesiculosus* and *Sargassum muticum*. The structurally simpler *F. vesiculosus* occurs commonly throughout NW Europe on hard substrata of both rocky and sedimentary shores attached to epibenthic biogenic substrata such as mussel beds or artificial hard substrata. The morphologically complex *S. muticum* was introduced to Europe in the early 1970s with the first attached individuals found in southern Britain (Farnham et al., 1973). The species has successfully spread along the European Atlantic coast and is now common from Portugal (Engelen et al., 2008) to Scandinavia (Karlsson and Loo, 1999). Detached thalli of both species are frequently found floating in coastal waters (Franke et al., 1999; Thiel et al., 2011; Vandendriessche et al., 2006). Epibiont assemblages on benthic *S. muticum* are much more species-rich than those on *F. vesiculosus* from the same ecosystem (Buschbaum et al., 2006; Viejo, 1999; Whithers et al., 1975).

Here we investigated the mobile and sessile epibionts on benthic and floating seaweeds in the northern Wadden Sea (German Bight, North Sea), testing the following hypotheses: (1) The epibiotic assemblages differ between benthic and floating seaweeds due to a homogenization

of rafting assemblages from contrasting floating algal host species. (2) Homogenization of the rafting assemblages is caused by movements of mobile associates among floating algal hosts. Additionally, we analyzed the composition of the *Idotea* assemblages on floating seaweeds. A comparison with rafting *Idotea* assemblages from other N Atlantic regions helps in understanding the processes that shape the assemblage of these dominant mobile rafters.

## 2. Materials and methods

### 2.1. Study area

The study was performed in the List tidal basin (54°50'–55°10' N and 8°20'–8°40' E), a 400 km<sup>2</sup> semi-enclosed bight located at the Danish–German border in the northern Wadden Sea (south-eastern North Sea) (Fig. 1). The basin is enclosed by the island of Sylt in the south, the island of Rømø in the north, and by causeways connecting both islands to the mainland. A single tidal inlet (the Lister Deep) between both islands (spanning 2.8 km at its narrowest section where about 550 × 10<sup>6</sup> m<sup>3</sup> of seawater pass through with each tide) represents the only connection to the open North Sea. The water volume of the bight at mean tidal level is about 845 × 10<sup>6</sup> m<sup>3</sup>. The mean water depth in the List tidal basin is 2.7 m, but reaches up to 40 m in the main tidal channels (van Beusekom et al., 2008); the water column is homogeneously mixed most of the time (Hickel, 1980). Salinity remains comparatively constant and varies between 27 in spring and 31 in summer. Mean water temperatures are 15 °C in summer and 4 °C in winter. The tidal range is about 1.8 m with maximum current velocities of about 1.3 m s<sup>-1</sup> in the main tidal channels, and velocities generally below 0.1 m s<sup>-1</sup> on tidal flats (Backhaus et al., 1998). Tidal flats in the List tidal basin comprise only one third of the area. Thus, the major part of the basin is permanently submersed (Dolch and Hass, 2008).

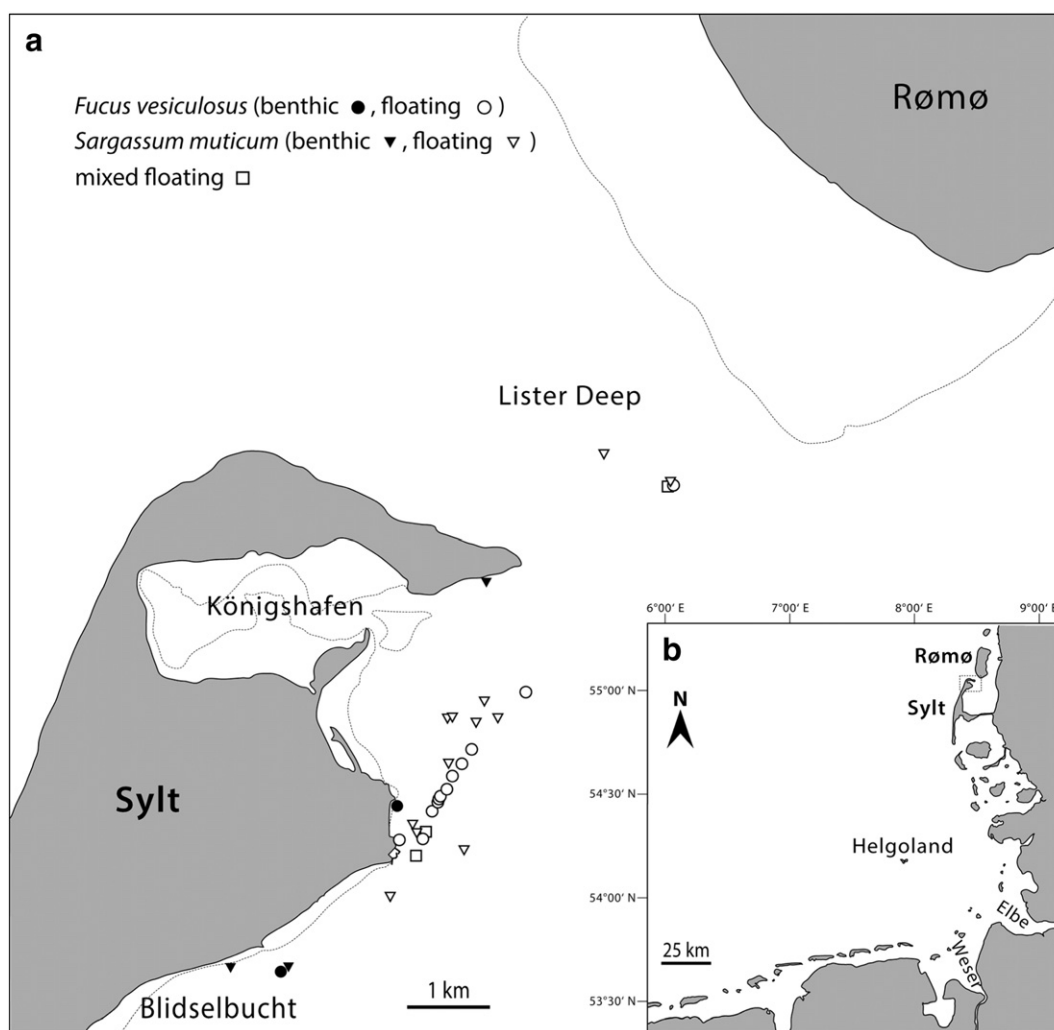
### 2.2. Sampling of benthic and floating algae

Benthic and floating thalli of *F. vesiculosus* and *S. muticum* were collected between 3 August and 22 October 2012. Benthic *F. vesiculosus* was collected in the intertidal zone of two rocky coastal groins (Fig. 1). Randomly selected individuals were collected during high tide when the thalli were fully submersed which enabled sampling of algae together with their associated community. We carefully enclosed individual thalli with the holdfast in a plastic bag prior detaching from the substratum with a knife. Benthic *S. muticum* was collected at three locations (Fig. 1) around low tide when the subtidal thalli were most easily accessible. For small thalli of *S. muticum*, we applied the same sampling procedure as for *F. vesiculosus*. Large thalli were carefully detached from the substratum and gently dragged into a large dip net (mouth opening: 4500 cm<sup>2</sup>; mesh size: 1 mm).

Floating seaweeds were collected in the tidal channels off List Königshafen and in the Lister Deep (Fig. 1). Patches of floating algae were captured with a single swoop of the dip net. Each patch of floating algae was carefully transferred into a plastic bag. All mobile organisms in the net that fell off the algal patch were also transferred into the respective bag. After collection in the field, the algal samples were immediately transported to the laboratory to analyze the mobile and sessile associates.

### 2.3. Analysis of benthic and rafting assemblages

Mobile organisms were washed off the algal thalli with seawater over a 500 µm sieve. The wet weight (WW) of each thallus (including sessile epibionts) was determined with an analytical balance (±0.1 g). In addition to *F. vesiculosus* and *S. muticum* we found the buoyant brown algae *Ascophyllum nodosum* and *Himanthalia elongata*, the red alga *Gracilaria vermiculophylla*, leaves of the seagrasses *Zostera marina* and *Zostera noltii*, as well as coastal cormophytes (*Salicornia europaea*,



**Fig. 1.** (a) Positions in the Sylt-Rømø Bight where benthic thalli and floating seaweed patches were collected between August and October 2012. (b) Location of the Sylt-Rømø Bight in the German Bight (North Sea).

*Suaeda maritima*) entangled in the floating patches. For patches that consisted of more than one species the WW was determined for all patch-forming macrophytes individually.

The algae were inspected for sessile epibionts with the naked eye and a stereo microscope. All epibionts were identified alive to the lowest taxonomic level possible and recorded qualitatively (presence/absence). Peracarid crustaceans (amphipods and isopods) were enumerated. Individuals that could not be identified alive were preserved in 5% formalin-seawater solution, and later transferred to and stored in ethanol for later species identification. For isopods of the genus *Idotea*, we could not identify small juveniles to the species level and therefore classified them as juvenile *Idotea* spp.

#### 2.4. Statistical analyses

Benthic thalli consisted of either *F. vesiculosus* or *S. muticum*. Floating patches often comprised various species of seaweeds and cormophytes. A floating patch was assigned to either *F. vesiculosus* or *S. muticum* when the respective species dominated the patch by at least 80% of the total WW. For simplification, we refer to those patches as “floating *Fucus*” and “floating *Sargassum*”, respectively. Algal epiphytes on those patches were considered members of the associated assemblage. If the share of the dominating algal species was less than 80% of the WW, the patch was classified as “mixed floating” and excluded from the multivariate comparison of the associated epibiota (see below). In total, we analyzed

12 replicate samples each for benthic and floating *Fucus* and *Sargassum* (i.e., a total of 48 samples) and classified three samples as mixed floating.

We tested relationships between seaweed biomass and species richness of the epibiotic assemblage with linear regression. Because algal biomass varied among the samples, we estimated maximum number of associated species from sample-based species accumulation curves generated from 999 permutations using the software package PRIMER 6. The maximum number of species was estimated by non-linear regression as the upper asymptote of the curves. Asymptotes were determined using a generalized Weibull cumulative distribution function (Flather, 1996) that produced fits with consistent  $R^2 > 0.99$ .

We visualized structural similarity of the associated assemblages using non-metric multi-dimensional scaling (nMDS) generated from presence-absence data followed by an analysis of similarity (ANOSIM). nMDS and ANOSIM were based on Simpson's dissimilarity index (Simpson, 1943 adjusted by Lennon et al., 2001) because the samples from different hosts differed in species richness (see Results). Simpson's index is more robust to missing species than the often used Bray-Curtis index and thus provides a more conservative estimate of dissimilarity (Koleff et al., 2003).

A similarity percentage (SIMPER) analysis identified those species that contributed most to the dissimilarity between assemblages from different hosts/habitats. Because in its original formulation (Clarke, 1993) SIMPER was based on Bray-Curtis dissimilarities, we had to

**Table 1**  
Frequencies of occurrence (%) and mobility status (mobile/sessile) of epibiotic species on benthic thalli and floating patches of *Fucus vesiculosus* and *Sargassum muticum* as well as on mixed floating patches collected in the northern Wadden Sea. x indicates presence of species in mixed floating samples.

	Mobility (m = mobile; s = sessile)	<i>Fucus vesiculosus</i>		<i>Sargassum muticum</i>		Mixed
		Benthic N = 12	Floating N = 12	Benthic N = 12	Floating N = 12	Floating N = 3
<b>Porifera</b>						
<i>Halichondria panicea</i> (Pallas, 1766)	s			91.7	41.7	
<i>Leucosolenia</i> sp.	s			8.3		
<i>Sycon ciliatum</i> (Fabricius, 1780)	s			50.0		
<b>Coelenterata</b>						
<i>Clytia hemisphaerica</i> (Linnaeus, 1767)	s	8.3	8.3	100.0	8.3	
<i>Coryne muscoides</i> (Linnaeus, 1761)	s					x
<i>Laomedea angulata</i> Hincks, 1861	s				8.3	
<i>Metridium senile</i> (Linnaeus, 1761)	s			75.0	16.7	
<i>Obelia longissima</i> (Pallas, 1766)	s		25.0		5.0	x
<i>Obelia geniculata</i> (Linnaeus, 1758)	s	58.3	16.7	8.3	16.7	
<b>Nemertea</b>						
Nemertea indet.	m	8.3				
<b>Annelida</b>						
<i>Autolytus</i> sp.	m			8.3		
<i>Capitella</i> sp.	m			8.3		
<i>Harmothoe imbricata</i> (Linnaeus, 1767)	m			25.0		
<i>Lepidonotus squamatus</i> (Linnaeus, 1758)	m			8.3		
<i>Nereis diversicolor</i> (Müller, 1776)	m	25.0		8.3		
<i>Polydora ciliata</i> (Johnston, 1838)	m	33.3	8.3	41.7	66.7	x
<i>Proceratea cornuta</i> (Agassiz, 1884)	m		8.3	16.7	8.3	
<b>Mollusca</b>						
<i>Aplysia fasciata</i> Poiret, 1789	m			25.0		
<i>Cerastoderma edule</i> (Linnaeus, 1758)	s	16.7		8.3	8.3	
<i>Crepidula fornicata</i> (Linnaeus, 1758)	m	16.7		16.7		
<i>Crassostrea gigas</i> (Thunberg, 1793)	s	66.7		50.0		
<i>Eubrancheus exiguus</i> (Adler & Hancock, 1848)	m				8.3	
<i>Hydrobia ulvae</i> Pennant, 1777 ( <i>Peringia ulvae</i> (Pennant, 1777))	m	41.7	16.7	33.3	16.7	
<i>Littorina fabalis</i> (Turton, 1825)	m	25.0				
<i>Littorina littorea</i> (Linnaeus, 1758)	m	75.0		16.7		
<i>Littorina obtusata</i> (Linnaeus, 1758)	m	8.3				
<i>Macoma balthica</i> (Linnaeus, 1758)	s	8.3		16.7		
<i>Mya arenaria</i> Linnaeus, 1758	s	33.3		16.7		
<i>Mytilus edulis</i> Linnaeus, 1758	s	66.7		66.7	33.3	x
<b>Crustacea</b>						
<i>Apherusa bispinosa</i> (Bate, 1857)	m	50.0		91.7	58.3	
<i>Apohyale prevostii</i> (Milne Edwards, 1830)	m	50.0		16.7		
<i>Austrominius modestus</i> (Darwin, 1854)	s	33.3	25.0		8.3	x
<i>Balanus crenatus</i> Bruguière, 1789	s	75.0		91.7	8.3	
<i>Cancer pagurus</i> Linnaeus, 1758 (megalopa)	m			8.3		x
<i>Caprella linearis</i> (Linnaeus, 1767)	m			75.0	8.3	
<i>Caprella mutica</i> Schurin, 1935	m			33.3		
<i>Carcinus maenas</i> (Linnaeus, 1758) (megalopae and early crab stages)	m	50.0	75.0	75.0	91.7	x
<i>Cheirocratus</i> sp.	m			8.3		
Cumacea indet.	m			8.3		
<i>Eriocheir sinensis</i> Milne Edwards, 1853 (megalopae)	m		25.0		50.0	x
<i>Gammarus locusta</i> (Linnaeus, 1758)	m	58.3	100.0	25.0	91.7	x
<i>Gitana sarsi</i> Boeck, 1871	m			16.7		
<i>Hemigrapsus sanguineus</i> (De Haan, 1835)	m	16.7				
<i>Idotea baltica</i> Pallas, 1772	m	8.3	91.7	8.3	75.0	x
<i>Idotea chelipes</i> (Pallas, 1766)	m		25.0		41.7	x
<i>Idotea emarginata</i> (Fabricius, 1793)	m		50.0		25.0	x
<i>Idotea granulosa</i> Rathke, 1843	m				8.3	
<i>Idotea linearis</i> (Linnaeus, 1766)	m		50.0		75.0	x
<i>Idotea metallica</i> Bosc, 1802	m		8.3		16.7	x
<i>Idotea neglecta</i> Sars, 1897	m		25.0			
<i>Jaera albifrons</i> Leach, 1814	m	25.0				
Janiridae indet.	m		8.3			
<i>Jassa marmorata</i> Holmes, 1903	m			41.7		
<i>Liocarcinus holsatus</i> (Fabricius, 1798)	m		8.3			
<i>Metopa pusilla</i> Sars, 1892	m			58.3		
<i>Microprotopus maculatus</i> Norman, 1867	m	16.7		100.0	41.7	
<i>Monocorophium acherusicum</i> (Costa, 1853)	m	50.0	8.3	100.0	75.0	
<i>Pagurus bernhardus</i> (Linnaeus, 1758)	m			8.3	8.3	
<i>Palaemon longirostris</i> Milne Edwards, 1837	m		16.7			
<i>Praunus flexuosus</i> (Müller, 1776)	m				25.0	
<i>Semibalanus balanoides</i> (Linnaeus, 1767)	s	25.0				

Table 1 (continued)

	Mobility (m = mobile; s = sessile)	<i>Fucus vesiculosus</i>		<i>Sargassum muticum</i>		Mixed
		Benthic N = 12	Floating N = 12	Benthic N = 12	Floating N = 12	Floating N = 3
<b>Pycnogonida</b>						
<i>Anoplodactylus petiolatus</i> (Krøyer, 1844)	m				8.3	
<i>Nymphon brevistrore</i> Hodge, 1863	m			8.3		
<b>Bryozoa</b>						
<i>Alcyonidioides mytili</i> (Dalyell, 1848)	s			16.7	25.0	
<i>Bowerbankia gracilis</i> Leidy, 1855	s				25.0	
<i>Bowerbankia imbricata</i> (Adams, 1798)	s				50.0	
<i>Conopeum reticulatum</i> (Linnaeus, 1767)	s	16.7		8.3	8.3	x
<i>Electra pilosa</i> (Linnaeus, 1767)	s	66.7	58.3	100.0	83.3	x
<i>Membranipora membranacea</i> (Linnaeus, 1767)	s					x
<b>Tunicata</b>						
<i>Aplidium glabrum</i> (Verill, 1871)	s			41.7		
<i>Molgula manhattensis</i> (De Kay, 1843)	s	16.7		41.7	33.3	
<i>Styela clava</i> Herdman, 1881	s			66.7		x
<b>Chlorophyta</b>						
<i>Berkeleya rutilans</i> (Trentepohl ex Roth) Grunow 1880	s		25.0	91.7	66.7	x
<i>Bryopsis</i> sp.	s			8.3		
<i>Chaetomorpha</i> spp.	s	16.7		91.7	66.7	
<i>Enteromorpha</i> spp. Link	s	33.3	41.7	83.3	50.0	x
<i>Ulva lactuca</i> Linnaeus 1753	s			91.7	41.7	
<b>Phaeophyceae</b>						
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier 1851	s					x
<i>Ectocarpus</i> spp. Lyngbye	s			100.0	41.7	
<i>Elachista fucicola</i> (Velley) Areschoug 1842	s	100.0	16.7	8.3		x
<i>Giffordia granulosa</i> (Smith) Hamel 1939	s			41.7		
<i>Pilayella</i> sp.	s			25.0	41.7	
<b>Rhodophyta</b>						
<i>Acrochaetium secundatum</i> (Lyngbe) Nägeli 1858	s	8.3		25.0		
<i>Antithamnion</i> sp.	s	16.7		25.0	8.3	
<i>Ceramium nodulosum</i> (Lightfoot) Ducluzeau 1806	s	16.7				
<i>Ceramium rubrum</i> Agardh 1811	s	16.7	8.3	100.0	25.0	x
<i>Chondrus crispus</i> Stackhouse 1797	s				8.3	
<i>Erythrotrichia</i> spp.	s	16.7		88.3	8.3	
<i>Goniotrichum alsidii</i> (Zanardini) Howe 1914	s	8.3		16.7	33.3	
<i>Polysiphonia</i> spp.	s	33.3	16.7	100.0	75.0	x
<i>Polytrichium</i> sp.	s	8.3				
unidentified crustose red alga	s		8.3			
<b>Others</b>						
<i>Asterias rubens</i> Linnaeus, 1758	m			8.3		
<i>Pedicellina</i> sp.	s		8.3	33.3	25.0	
<b>Pisces</b>						
<i>Belone belone</i> (Linnaeus, 1761)	m				8.3	
<b>Phycinae</b>						
<i>Cyclopterus lumpus</i> Linnaeus, 1758	m		41.7	8.3	16.7	x
<i>Spinachia spinachia</i> (Linnaeus, 1758)	m		8.3		8.3	x
<i>Syngnathus rostellatus</i> Nilsson, 1855	m		16.7		50.0	
<i>Gasterosteus aculeatus aculeatus</i> Linnaeus, 1758	m					x

adapt it for use with Simpson's dissimilarity. To do this, all species that occurred in only one of two contrasted samples were assigned the same contribution to the dissimilarity. The contribution of each species was calculated as the number of species that occurred only in just a single sample divided by the Simpson's dissimilarity value. The overall average contribution of a species was then calculated as the mean of all contributions of this species determined from pairwise contrasting of each sample from one category with each sample from the other category. Analyses were run in the library *vegan* (Oksanen et al., 2013) in the freely available R software (R Core Team, 2013), using a modified version of the SIMPER routine (available upon request).

We tested whether differences in species composition among hosts/habitats resulted from nestedness or species turnover. If nestedness occurs, species-poor samples (i.e. habitats/hosts) should represent random subsets of species-rich samples (Atmar and Patterson, 1993; Ulrich et al., 2009), otherwise, species turnover drives differences in

composition among sites. We combined all samples from the same host-category to display the entire specific epibiotic assemblage. Nestedness analyses were carried out using the NODF index (Almeida-Neto et al., 2008), the most robust among the several proposed metrics (Ulrich et al., 2009). The observed NODF value was compared with 10,000 null values obtained from randomized matrices, using the 'quasiswap' algorithm that preserves both species occurrences and sample richness (Ulrich and Gotelli, 2007). Because NODF depends on the size and degree of fill of the matrix, we z-normalized for comparisons. Analyses were carried out using the routine 'oecosimu' implemented in the library *vegan* (Oksanen et al., 2013) in R (R Core Team, 2013).

The multivariate analyses and the nestedness analysis were performed for the entire epibiotic assemblages as well as separately for the mobile and sessile epibiota. We considered those species capable of rapid movement among algal hosts by active crawling and swimming as mobile (Table 1). Sessile species (e.g., bivalves, hydroids and



bryozoans) maintain specific and firm connections to their substrata and are, thus, unable to rapidly traverse even minor distances between temporarily aggregating floating seaweed patches. For the multivariate analyses we homogenized the entire data set by strictly combining species on the next-higher taxonomic level if not all individuals could be identified to the species level (e.g., *Idotea* spp., *Bivalvia*, *Ectocarpales*). The mixed floating samples were considered in the nMDS but not in the subsequent analyses because they were compositionally too heterogeneous to represent true replicates.

### 3. Results

#### 3.1. Size and composition of benthic and floating seaweed patches

Seaweed median biomasses were 90 g (range: 32.0–1030.7 g) for benthic seaweeds and 137.8 g (range: 10.8–1573.8 g) for patches of floating seaweeds. Median biomasses were 139.0 g (range: 74.8–371.0 g) for individuals of benthic *F. vesiculosus* and 58.5 g (range: 10.8–358.9 g) for floating patches dominated by *Fucus*. *S. muticum* had a median weight of 47.5 g (range: 32.0–1030.7 g) for benthic individuals and 246.0 g (range: 76.8–1573.8 g) for floating patches dominated by this seaweed.

The specific contribution of other buoyant macrophytes to the WW of floating algal patches dominated by *Fucus* or *Sargassum* varied between <1 and 12%. In mixed floating patches the furoid seaweeds *A. nodosum* and *H. elongata* contributed up to 58 and 29%, respectively, to total patch weight. The specific contributions of all other buoyant macrophytes (see Section 2.3) to the WW of floating patches were generally low, with maximum values of 3%.

#### 3.2. Epibiont species on benthic and floating seaweeds

A total of 96 species, including algae, invertebrates and fishes, were associated with benthic and floating *Fucus* and *Sargassum* (Table 1). Four additional species were recorded on mixed floating patches. 13

species occurred only on *Fucus*, whereas 38 species were exclusively associated with *Sargassum*. We found 45 species that occurred on both algal hosts. 34 species occurred only on benthic seaweeds, 27 species only on floating seaweeds, and 39 species on both benthic and floating seaweeds.

For benthic ( $R^2 = 0.60$ ,  $p < 0.01$ ) and floating ( $R^2 = 0.54$ ,  $p < 0.01$ ) *Fucus* as well as for floating *Sargassum* ( $R^2 = 0.66$ ,  $p < 0.01$ ), the species number increased with increasing WW of the algal substratum, whereas this relationship was not evident for benthic *Sargassum* ( $R^2 = 0.02$ ,  $p = 0.64$ ; Fig. 2). The maximum species richness estimated from species accumulation curves was almost twice as high on *Sargassum* as on *Fucus* (Fig. 3). Additionally, the species richness of the epibiotia was on average 13% (*Sargassum*) and 31% (*Fucus*) higher on benthic than on floating algae. Estimated maximum species richness was 44.9 (95% confidence interval, CI: 43.7–46.2) and 38.1 (CI: 36.3–39.9) on benthic and floating *Fucus*, respectively. On benthic and floating *Sargassum* estimated species richness was 78.4 (CI: 75.1–81.7) and 68.1 (CI: 64.3–71.9). Non-overlapping 95% CI indicate significant differences in species richness of the epifauna between the two host species as well as between benthic and floating conspecific thalli.

We classified 53 species as mobile and 47 species as sessile (Table 1), and documented 28 sessile and 30 mobile species associated with *Fucus*. *Sargassum* had 40 sessile and 43 mobile species. A total of 21 mobile and 25 sessile species occurred on both seaweed species. 38 sessile and 35 mobile species occurred on benthic algae, 35 sessile and 31 mobile species on floating algal patches and 13 mobile and 26 sessile species on both benthic and floating seaweeds.

Considering the entire epibiotia (including both sessile and mobile species), the samples from benthic *Fucus* and *Sargassum* formed distinct clusters in the nMDS-plot indicating clear compositional differences between assemblages (Fig. 4a; Table 2). The characteristic epiphytes on *Fucus* (*Elachista fucicola*) and *Sargassum* (ectocarpalean brown algae) as well as the sponge *Halichondria panacea*, which occurred exclusively on *Sargassum*, contributed most to differences between epibiotic assemblages on the two benthic hosts (Table 3).

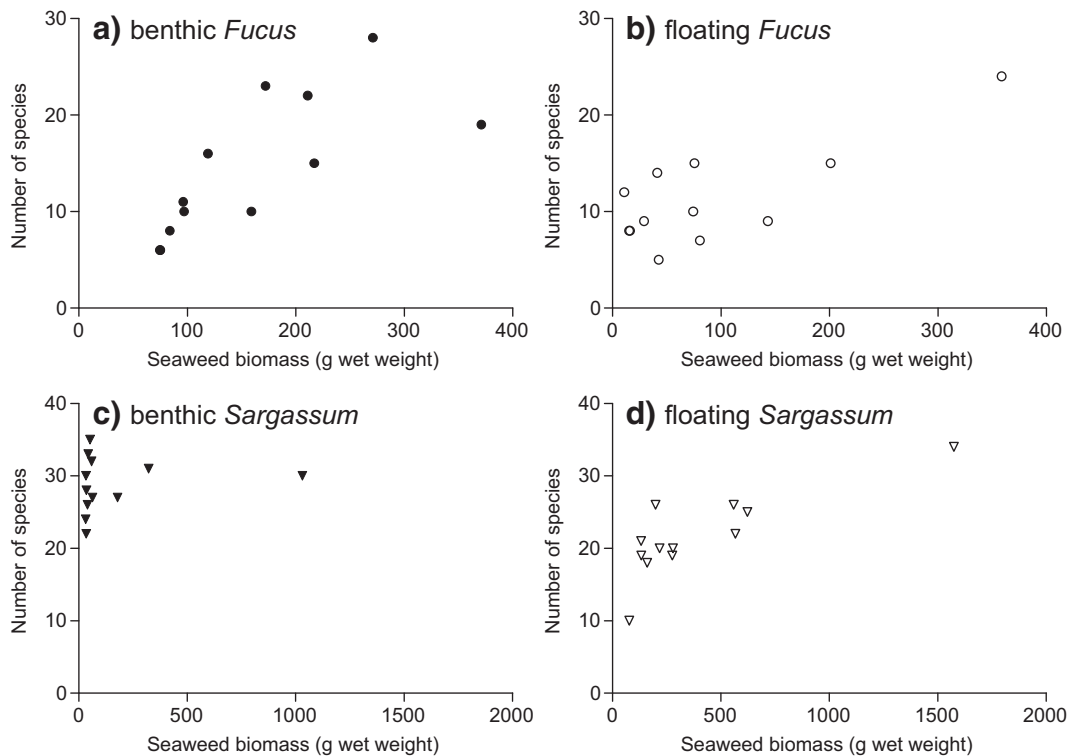
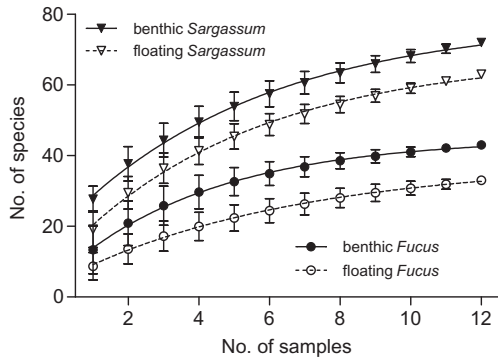


Fig. 2. Relationship between species richness of the epibiotic assemblage and wet weight of benthic thalli (a and c) and floating patches (b and d) of *Fucus vesiculosus* (a and b) and *Sargassum muticum* (c and d) collected in the northern Wadden Sea.



**Fig. 3.** Species accumulation curves (999 permutations) for estimating the maximum number of epibiotic species on benthic thalli and floating patches of *Fucus vesiculosus* and *Sargassum muticum* collected in the northern Wadden Sea.

The epibiota varied within host species between benthic and floating thalli (Table 2). On both algal hosts the difference between the benthic and the rafting epibiota was mainly due to the occurrence of idoteid isopods on almost every floating patch whereas common benthic epifauna such as bivalves, barnacles, caprellid amphipods and the epiphyte *E. fucicola* were almost entirely absent from the floating patches (Table 3).

The rafting assemblages on floating *Fucus* and *Sargassum* were indistinguishable (Table 2). Samples from the mixed floating patches associated closely with the other samples from floating patches in the nMDS-

plot, indicating similar rafting assemblages (Fig. 4a). The situation was similar when considering only mobile epibiotic species (Fig. 4b). The assemblages differed between benthic thalli but not between floating patches of *Fucus* and *Sargassum* (Table 2). Again, idoteid isopods were primarily responsible for differences between the assemblages on benthic and floating seaweeds. Additionally, the amphipod *Gammarus locusta* occurred predominantly on floating *Sargassum* but was less common on benthic seaweeds (Table 3).

Samples from benthic thalli of the two algal hosts also differed for sessile epibiota (Fig. 4c; Table 2); the epiphytes *E. fucicola* and *Ectocarpales* as well as *H. panicea* were the main discriminating species (Table 3). However, sessile assemblages did not differ between conspecific benthic and floating thalli. Similarly, assemblages on floating patches did not differ between the two algal species.

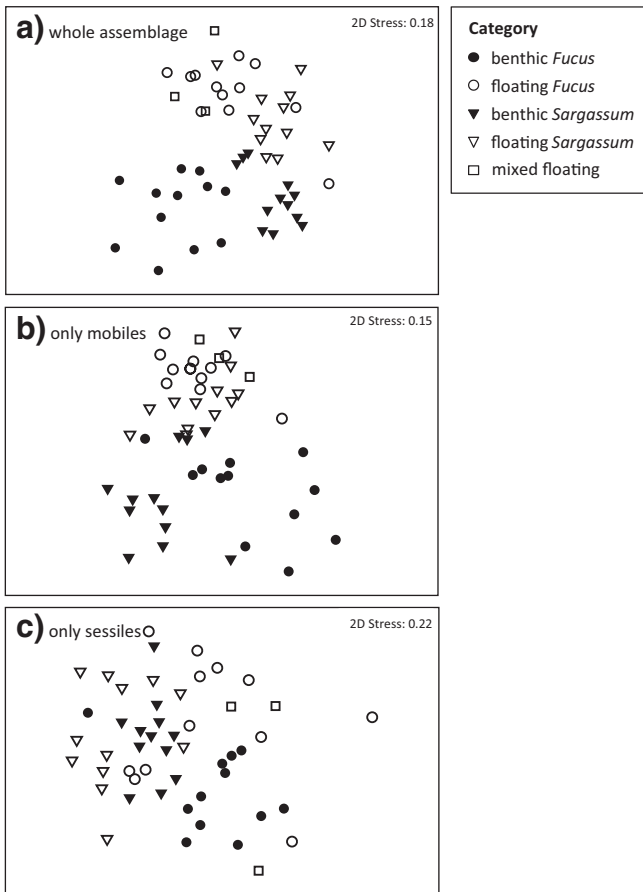
Our data set showed no nestedness for the entire epibiota (Fig. 5;  $z = -1.85$ ;  $p = 0.13$ ), nor for the mobile ( $z = -0.01$ ;  $p = 0.82$ ) and the sessile ( $z = -1.13$ ;  $p = 0.25$ ) epibiota. Accordingly, the species-poor assemblage on *Fucus* was not a subset of the species-rich assemblage on *Sargassum*. Similarly, the rafting assemblages were not subsets of the assemblages on benthic seaweeds.

**3.3. Idotea assemblage on floating seaweeds**

Isopods of the genus *Idotea* were abundant on floating seaweeds. A total of 3943 idoteid isopods were collected from the floating patches, of which 2344 individuals could be identified to species level. The *Idotea* assemblage was dominated by the species *Idotea baltica* which contributed 94% of all individuals (Fig. 6). The average ( $\pm$ SD) densities of *I. baltica* were  $51.8 \pm 47.2$  and  $28.7 \pm 63.6$  ind.  $100\text{ g}^{-1}$  on floating patches of *Fucus* and *Sargassum*, respectively. *Idotea linearis*, *Idotea chelipes* and *Idotea emarginata* occurred regularly on floating algal patches with average densities ranging from 0.5 to 2.8 ind.  $100\text{ g}^{-1}$ . *Idotea neglecta* and *I. metallica* occurred only sporadically in samples. *Idotea pelagica*, which is found on flotsam in offshore waters of the German Bight (Franke et al., 1999), was absent from our Wadden Sea samples. Densities of *Idotea* species were similar on floating patches of *Fucus* and *Sargassum*.

**4. Discussion**

Marine organisms experience different environmental conditions in benthic and floating habitats that likely result in contrasting epibiotic assemblages on benthic and floating seaweeds. In the German Wadden Sea, we found clear differences between epibiotic assemblages on benthic *F. vesiculosus* and *S. muticum*. By contrast, similar assemblages



**Fig. 4.** nMDS-plots visualizing similarity of epibiotic assemblages on benthic thalli and floating patches of *Fucus vesiculosus* and *Sargassum muticum* collected in the northern Wadden Sea. nMDS was based on Simpson’s dissimilarity index calculated from presence/absence data. (a) Whole epibiotic assemblage; (b) mobile epibionts only; (c) sessile epibionts only.

**Table 2**

Results of the analysis of similarity (ANOSIM) comparing epibiotic assemblages on benthic thalli and floating patches of *Fucus vesiculosus* and *Sargassum muticum*. We compared entire epibiotic assemblages as well as assemblages of mobile and sessile species separately. The analysis was based on Simpson’s dissimilarity index calculated from presence/absence data (N = 12).

Substrata compared	R-statistics	p-Value
<b>All species</b>		
Benthic <i>Fucus</i> –floating <i>Fucus</i>	0.65	<0.01
Benthic <i>Fucus</i> –benthic <i>Sargassum</i>	0.66	<0.01
Floating <i>Fucus</i> –floating <i>Sargassum</i>	–0.01	0.53
Benthic <i>Sargassum</i> –floating <i>Sargassum</i>	0.43	<0.01
<b>Mobile species only</b>		
Benthic <i>Fucus</i> –floating <i>Fucus</i>	0.60	<0.01
Benthic <i>Fucus</i> –benthic <i>Sargassum</i>	0.48	<0.01
Floating <i>Fucus</i> –floating <i>Sargassum</i>	0.04	0.23
Benthic <i>Sargassum</i> –floating <i>Sargassum</i>	0.57	<0.01
<b>Sessile species only</b>		
Benthic <i>Fucus</i> –floating <i>Fucus</i>	0.07	0.11
Benthic <i>Fucus</i> –benthic <i>Sargassum</i>	0.46	<0.01
Floating <i>Fucus</i> –floating <i>Sargassum</i>	0.06	0.15
Benthic <i>Sargassum</i> –floating <i>Sargassum</i>	0.04	0.15

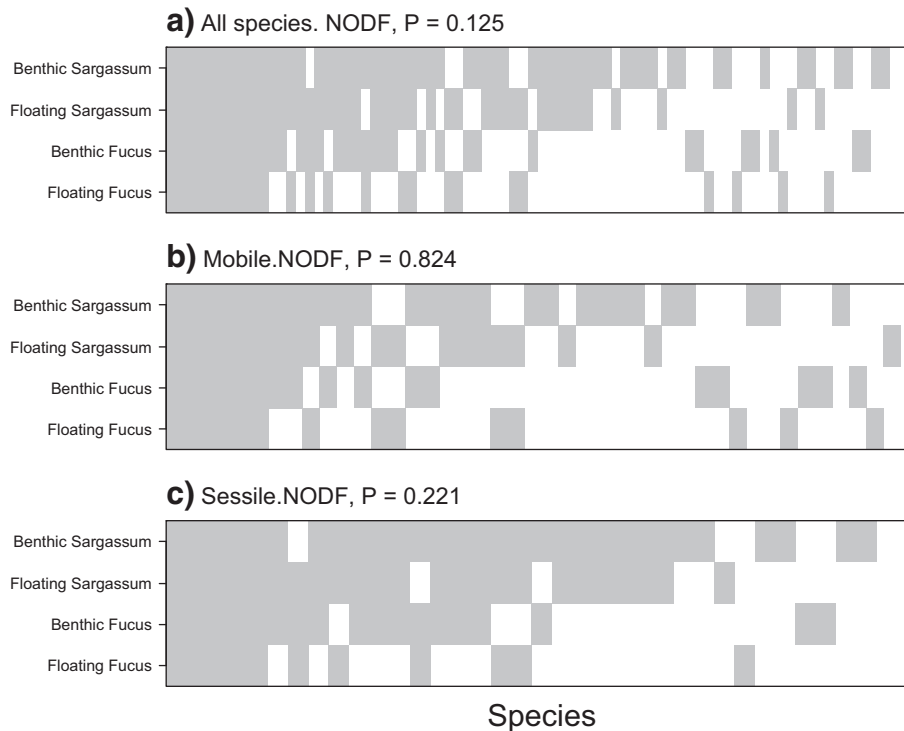
**Table 3**  
Species that contributed most to differences between epibiotic assemblages on benthic thalli and floating patches of *Fucus vesiculosus* and *Sargassum muticum* collected in the northern Wadden Sea. SIMPER was based on Simpson's dissimilarity index calculated from presence/absence data. Numbers give the specific contribution of each species to differences. Numbers in parentheses give frequencies of occurrence (%) on the respective host category (N = 12).

Species	Benthic <i>Fucus</i> /benthic <i>Sargassum</i>	Benthic <i>Fucus</i> /floating <i>Fucus</i>	Benthic <i>Sargassum</i> /floating <i>Sargassum</i>
All species			
<i>Balanus crenatus</i>			1.5 (92/8)
Bivalvia		4.3 (92/0)	
<i>Caprella</i> sp.			1.3 (83/8)
Ectocarpales	1.9 (0/100)		
<i>Elachista fucicola</i>	1.8 (100/8)	4.2 (100/17)	
<i>Halichondria panicea</i>	1.8 (0/92)		
<i>Idotea</i> spp.		4.0 (17/92)	1.4 (25/100)
Mobile species only			
<i>Apohyale prevostii</i>		6.6 (50/0)	
<i>Caprella</i> sp.	5.2 (0/83)		4.2 (83/8)
<i>Gammarus locusta</i>			4.0 (25/92)
<i>Idotea</i> spp.		7.8 (17/92)	4.4 (25/100)
<i>Littorina littorea</i>	4.1 (75/17)	6.8 (75/0)	
<i>Microprotopus maculatus</i>	5.2 (17/100)		
Sessile species only			
Ectocarpales	2.4 (0/100)		
<i>Elachista fucicola</i>	2.3 (100/8)		
<i>Halichondria panicea</i>	2.2 (0/92)		

inhabited floating seaweed patches consisting of different host species. Our results indicate that the homogenization of rafting assemblages is primarily driven by mobile epibionts moving among floating seaweed patches. We suggest that increasing population densities of mobile rafters, as well as rapid decomposition of floating algal patches, lead to habitat scarcity and frequent migration of mobile rafters among available rafts. The resultant high turnover in the mobile rafter assemblage likely homogenizes rafting epibiota over different floating seaweed hosts.

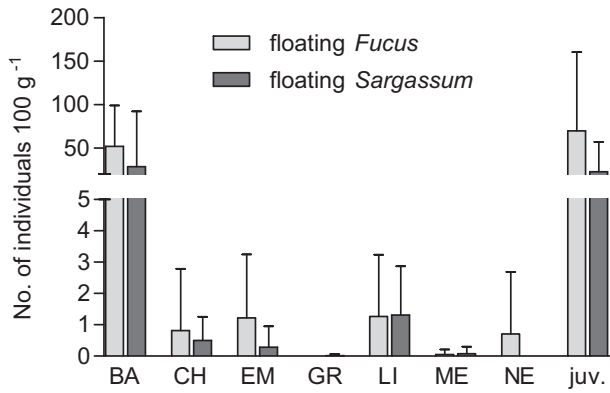
#### 4.1. Epibionts on benthic seaweeds

Benthic *Fucus* and *Sargassum* in the northern Wadden Sea were colonized by different epibiotic assemblages, with *Sargassum* hosting almost twice as many species as *Fucus*. Our results confirm previous studies that also showed differences in composition and diversity of epibiotic assemblages on these two seaweed species (Buschbaum et al., 2006; Viejo, 1999; Whithers et al., 1975). Previous studies attribute high epibiont diversity on *Sargassum* to the morphological



**Fig. 5.** Distribution of species within epibiotic assemblages on benthic thalli and floating patches of *Fucus vesiculosus* and *Sargassum muticum* collected in the northern Wadden Sea and results of the nestedness analysis. We did not observe nestedness among epibiotic assemblages from different host categories. (a) Entire epibiotic assemblage; (b) mobile epibionts only; (c) sessile epibionts only.





**Fig. 6.** Mean ( $\pm$ SD) densities of *Idotea* species on floating patches of *Fucus vesiculosus* and *Sargassum muticum* collected in the northern Wadden Sea. juv. refers to juvenile individuals that could not be identified to species level. BA = *Idotea baltica*, CH = *I. chelipes*, EM = *I. emarginata*, GR = *I. granulosa*, LI = *I. linearis*, ME = *I. metallica*, NE = *I. neglecta*; N = 12.

complexity of this seaweed species, which provides diverse microhabitats for a great variety of associated species (Cacabelos et al., 2010).

Epiphytes contribute substantially to seaweed structural complexity (Pavia et al., 1999). They provide shelter from predators and food for mobile herbivores (Boström and Mattila, 1999) and are, thus, crucial in shaping the assemblages of mobile associates on benthic seaweeds (Norton and Benson, 1983; Viejo, 1999). The epiphyte *E. fucicula* occurred exclusively on *Fucus* whereas other ectocarpalean brown algae and the sponge *H. panacea* occurred primarily on *Sargassum*. These sessile epibionts contributed most to differences in epibiotic assemblages. Accordingly, compositional differences between the epibiotic assemblages of the two seaweed species were primarily attributable to host specificity of sessile species whereas mobile species might choose their algal host mainly for the associated epiphytes. Herbivores can efficiently control the densities of epiphytes on seaweeds (Duffy, 1990). Accordingly, mobile species migrate frequently among seaweeds in search of epiphytic food thereby causing rapid turnover in mobile epifauna (Taylor, 1998). This turnover ultimately leads to the specific distributional patterns of epifaunal organisms in diverse benthic seaweed canopies (Coyer, 1984; Taylor and Cole, 1994).

#### 4.2. Epibionts on floating seaweeds

The epibiotic assemblages on *Fucus* and *Sargassum* clearly differed between benthic and floating seaweeds. Some species are lost from floating seaweeds early during the rafting journey because they cannot hold onto floating substrata (Edgar, 1987; Gutow et al., 2009; Kingsford and Choat, 1985). In later successional stages, biological interactions primarily shape the rafting assemblage (Thiel, 2003; Thiel and Gutow, 2005). In our study, the loss of species during the rafting journey reduced species richness on floating seaweeds. However, no pattern of nestedness was evident among species-rich and species-poor epibiotic assemblages, indicating that the rafting assemblage was not just an impoverished subset of the epibionts on benthic seaweeds but supported species that were uncommon or even absent in benthic samples. A substantial shift in the epibiotic assemblage from benthic to floating seaweeds was evident for mobile but not for sessile epibionts, indicating that high species turnover in the mobile associates in the assemblage explained the compositional changes of the epibionts from benthic to floating seaweeds. Clarkin et al. (2012b) observed a similar shift for mobile epibionts for associated idoteid isopods in the Irish Sea.

Previous studies indicate that the rafting assemblage is dependent on characteristics of the raft, such as the taxonomic identity of the floating seaweed host (Stoner and Greening, 1984; Vandendriessche et al.,

2006) as well as size and age of the raft (Clarkin et al., 2012a; Hobday, 2000; Ingólfsson, 1998; Tsikhon-Lukanina et al., 2001; Vandendriessche et al., 2006). Similarly, floating duration and distance from the shore have been proposed as key factors in defining the rafting assemblage (Edgar, 1987; Ingólfsson, 1995). We found a positive correlation between raft size and species richness of the rafting assemblage, with higher species richness on *Sargassum* than on *Fucus*. By contrast, Vandendriessche et al. (2006) reported a higher number of rafting species on *Fucus* than on *Sargassum*, indicating that factors other than structural thallus complexity also influence epibiotic species richness on floating seaweeds. Despite these differences in species richness, multivariate analyses could not distinguish the epibiotic assemblages on floating *Fucus* and *Sargassum*. Clarkin et al. (2012a) observed similar rafting assemblages on different host species in the Irish Sea and concluded that environmental parameters (e.g., temperature) define rafting assemblages rather than characteristics of the algal rafts. They suggested that continuous breakup and coalescence of algal rafts (Ingólfsson, 1998) homogenize rafting assemblages. Vandendriessche et al. (2006) pointed at the “obligate opportunistic nature of the associated macrofaunal species” that colonize any floating item available and may thus distribute randomly over available rafts. Both processes, incidental aggregation of floating algal patches and exchange of rafters among rafts, inevitably lead to homogenization of rafting assemblages.

Our comparison of the epifaunal assemblages on benthic and floating seaweeds provides more detailed insights into the processes responsible for homogenizing rafting assemblages. The most prominent difference between the epibiont assemblages on benthic and floating seaweeds was the high number of idoteid isopods on floating seaweeds. The almost complete absence of *Idotea* spp. from benthic seaweeds suggests that they are restricted to floating habitats in the Wadden Sea or that they immigrate into the area from distant populations by rafting. The distant origin of some rafters and their algal hosts was corroborated by the occurrence of the oceanic seaweed *H. elongata* in our floating samples. The flow of oceanic waters from the British Channel along the Dutch and German coasts defines the dominant current system (Pohlmann, 2006), and thus the major rafting route, in the southeastern North Sea. Conspicuous accumulations of *Idotea* spp. on floating seaweeds are common in the N Atlantic (Table 4) and in other parts of the world's oceans (Hobday, 2000), indicating the high potential of this genus for colonizing floating algal patches (Clarkin et al., 2012b) and for rafting dispersal.

Some *Idotea* species reached extremely high densities on floating seaweeds in the German Wadden Sea compared to other samples from the N Atlantic region (Table 4). The high abundances, especially of *I. baltica* and young indeterminate *Idotea* spp., suggest an accumulation of isopods during the rafting journey along the North Sea coast resulting from (1) continuous reproduction of the isopods on the rafts, and (2) accelerated loss of algal rafts caused by the enhanced consumption of the seaweed host by these voracious herbivores (Gutow, 2003; Vandendriessche et al., 2007). High densities of mobile rafters may, therefore, result from severe habitat limitation and the need to colonize any available algal patch irrespective of the identity of the floating algal host. Abundant herbivores, many of which preferentially consume epiphytic algae (Karez et al., 2000), likely deplete epiphyte assemblages on the algal raft and thereby contribute to the homogenization of the sessile rafting assemblage on different floating seaweed species. In conclusion, the accumulation of successful mobile rafters, their high turnover among ephemeral floating seaweed patches, and their consumption of structuring epiphytes are most likely responsible for homogenizing rafting assemblages among different floating seaweed species. Additionally, enhanced rates of raft destruction caused by intense herbivory likely force associated rafters to abandon the sea surface and descend to benthic habitats when available. This process may substantially intensify exchange processes between the pelagic and the benthic environment, thereby fuelling benthic populations with individuals from distant populations and contributing to successful dispersal. These

**Table 4**  
Average densities (ind. · 100 g<sup>-1</sup>) of *Idotea* species on floating seaweeds in different regions of the NE Atlantic. Units were transformed to ind. · 100 g<sup>-1</sup> if they were reported in different units in the original publication. Data in parentheses give range of densities if available.

Region	<i>I. baltica</i>	<i>I. chelipes</i>	<i>I. emarginata</i>	<i>I. granulosa</i>	<i>I. linearis</i>	<i>I. metallica</i>	<i>I. neglecta</i>	<i>I. pelagica</i>	<i>Idotea</i> spp.	Reference
Iceland, N Atlantic	<0.1		<0.1	<0.1			<0.1	<0.1		Ingólfsson (1995)
W Ireland, Galway Bay, Celtic Sea			0.4	0.4			1.7		9.6	Clarkin et al. (2012a)
NE Ireland, Irish Sea	0.3		<0.1	<0.1			<0.1	<0.1		Clarkin et al. (2012b) <sup>a</sup>
Ireland, NE Atlantic, Galway Bay	6.0 (0.4–25.0)		12.0 (0.5–62.0)				9.7 (10.0–59.5)		46.0 (0.5–488.5)	Tully and Ó Céidigh (1986)
Belgium, North Sea	10								3	Vandriessche et al. (2006)
German Bight, North Sea	5.0 (3.4–8.5)	0.1 (0.1–0.6)	0.2 (0.0–0.9)	0.1 (0.0–0.5)	0.2 (0.0–0.7)	<0.1 (0.0–0.7)	0.1 (0.1–0.8)	<0.1 (0.0–0.5)	46.2 (0.0–257.4)	Franke et al. (1999)
German Wadden Sea, North Sea	40.2 (0.0–217.3)	0.7 (0.0–6.6)	0.8 (0.0–6.9)	<0.1 (0.0–0.2)	1.3 (0.0–6.3)	0.1 (0.0–0.8)	0.4 (0.0–6.9)			this study <sup>b</sup>

<sup>a</sup> Densities estimated from column graphs.

<sup>b</sup> Densities were given as ind. · L<sup>-1</sup> seaweed; for the estimation of densities we assumed 1 L = 1 kg seaweed.

<sup>c</sup> Floating samples of *Fucus vesiculosus* and *Sargassum muticum* combined.

processes are probably most pronounced in down-current regions where rafting assemblages have travelled over extensive time periods.

#### 4.3. The role of floating seaweeds in the Wadden Sea

We observed a large amount of floating seaweeds in the northern Wadden Sea area. Persistent westerly winds may have contributed to exceptionally high abundances of floating seaweeds in the area. However, prevailing westerly winds in the North Sea region (Siegismund and Schrum, 2001) suggest that the elevated abundances of floating seaweeds in the Wadden Sea were probably not a unique event. To date, knowledge about retention of flotsam in the Wadden Sea and exchange processes with the open North Sea is scarce. Based on drift card observations, Neumann (1966) predicted that a substantial amount of floating objects in the southeastern North Sea ends up on beaches in the Wadden Sea. Hinojosa et al. (2010) suggested that persistent fronts at the entrance between barrier islands prevent export of flotsam to the open ocean, and thus trap floating seaweeds in the Chilean fjord system. Pulses of floating seaweeds from the open North Sea that are retained in the Wadden Sea may substantially contribute to the overall macrophyte biomass in the area, which may influence coastal food webs and increase the complexity of the pelagic environment.

The massive import of *I. baltica* into the Wadden Sea region of the List tidal basin indicates that floating seaweeds, arriving from western source regions, might also facilitate the immigration of non-indigenous species. On the one hand, the arrival of the oceanic bryozoan *Watersipora subtorquata* on floating thalli of *H. elongata* in coastal waters of the southeastern North Sea (Kuhlenkamp and Kind, 2013) illustrates the potential for rafting invasions. On the other hand, rafting on floating algae could enhance the connectivity between distant benthic populations (Nikula et al., 2010) and increase genetic diversity of recipient populations in down-current regions. Therefore, floating seaweeds likely contribute substantially to the functioning and the diversity of the Wadden Sea ecosystem where large seaweeds have traditionally been considered to be of only minor importance.

#### Acknowledgments

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