Epiphytes and associated fauna on the brown alga *Fucus vesiculosus* in the Baltic and the North Seas in relation to different abiotic and biotic variables

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**Introduction**

Epiphytism and competition for a substrate is a widespread phenomenon in marine communities, especially in the rocky intertidal zone (Paine 1990; Kraberg & Norton 2007). Many algal species can grow on some host species or even are obligatory epiphytes (Pavia & Åberg 1999) providing potential for mutualistic interspecific associations (Stachowicz & Whitlatch 2005).

Fucoids are widely distributed perennial brown macroalgae in the intertidal Northeastern Atlantic with an important role in structuring intertidal communities (Lüning 1990). They can also extend to brackish non-tidal Baltic waters. *Fucus vesiculosus* L. is an important habitat-forming macroalga both in the saline and high diverse North Sea and the diluted and low diversity Baltic Sea (Kiirikki 1996a; Berger *et al.* 2004; Torn *et al.* 2006; Rohde *et al.* 2008). *Fucus vesiculosus* hosts a large variety of macroalgal species (Rindi & Guiry 2004), which provide suitable habitat for sessile invertebrates (Johnson & Scheibling 1987) and associated invertebrates, mainly grazers (Orav-Kotta & Kotta 2004; Råberg & Kautsky 2007). Despite its importance, comparisons of the spatial patterns of its epiphytes have rarely been reported (Rindi & Guiry 2004; Fraschetti *et al.* 2005).

Epiphytic organisms, such as micro- and macroalgae, invertebrates and bacteria, are often present on the thallus of perennial macroalgae. Their abundance is largely determined by abiotic factors, e.g. water motion and nutrient availability. The ability of epiphytes to tolerate regular desiccation during low tides determines their spatial distribution (Molina-Montenegro *et al.* 2005). Elevated

**Abstract**

*Fucus vesiculosus* L. is an important habitat-forming macroalga both in the saline and high diverse North Sea and the diluted and low diversity Baltic Sea. Despite its importance, comparisons of the spatial patterns of its epiphytes have rarely been reported. In this study we examined the species composition and density of macro-epiphytes and mobile fauna on the canopy-forming macroalga *F. vesiculosus* inhabiting different regimes of wave exposure in the North and Baltic Seas. The North and Baltic Seas had distinct epiphyte and mobile faunal communities. Wave exposure and segments of host fronds significantly contributed to the variability in species composition and dominance structure of epiphytes on *F. vesiculosus* in the North Sea and Baltic Sea. The study indicated that there is no clear spatial scale where environmental variables best predicted epiphytic and mobile faunal communities, and the formation of epiphytic and faunal communities is an interplay of factors operating through micro- to regional scales.

**Keywords**
Community composition; dominance structure; epibionts; fucoids; host frond; marine benthos; mobile invertebrates; seaweeds; spatial variability; wave exposure.

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nutrient loading is expected to increase both the number of epiphytic algae and invertebrates. However, the relationship varies among regions and is modulated by a number of other environmental variables, e.g. wave exposure, regional species pool, characteristics of the host plant and herbivory (Kotta et al. 2000; Worm et al. 2002; Kotta & Witman 2009). Among biotic interactions, intra-specific competition for space and light and the presence of adequate food resources for invertebrates are important (Lobban & Harrison 2000).

The ability of host algae to resist and avoid epibionts has great importance (Honkanen & Jormalainen 2005), affecting the photosynthetic rate and growth of host algae (Korpinen et al. 2007). The position within the thallus of seaweeds is important factor structuring epiphyte communities (Lobban & Baxter 1983; Cardinal & Lesage 1992; Longtin et al. 2009). Large epiphytes are associated with the basal disk; ephemeral epiphytes appearing on the tips of the host fucoxid fronds (Arrontes 1990). The cover of epiphytes often increases with the age of algae.

The objective of this study was to examine the species composition and density of epiphytes and mobile fauna on the canopy-forming macroalga *F. vesiculosus* inhabiting at different regimes of wave exposure in the North and Baltic Seas. We considered epiphytes hereafter as organism-on-a-plant concept (sensu Wahl 2009; Steel & Wilson 2003, references therein). Thus, epiphytes in this report comprise any macroalgae and sessile invertebrates on the host algae. Mobile fauna is defined here as motile macroinvertebrates associated with the host macroalgae.

We tested the following hypotheses:
1. The occurrence and cover of epiphytes are specific to the frond segment of host macroalgae.
2. The occurrence and cover of epiphytes are related to the wave exposure of the site.
3. The relationship between abiotic (exposure), biotic factors (frond segment) and epiphytes (species composition, cover) varies among different marine regions (North versus Baltic Seas).

**Material and Methods**

**Study area**

The study was performed in the North Sea and the Baltic Sea. In each region we selected three sites differing in exposure level. The used exposure levels according to the EUNIS classification were as follows: sheltered, moderately exposed and exposed. In the North Sea the sampling was done on the southwest coast of Norway in Raunefjord and Korsfjord in summer 2007 (Fig. 1). The North Sea study area contains numerous small and large islands separated by wide or narrow sounds. The bottom relief of the area is steep and very uneven. Espegren Marine Biological Station (N1; 60.273°N, 5.218°E) represented sheltered, Løholmen (N2; 60.266°N, 5.211°E) moderately exposed and Store Kalsøy (N3; 60.113°N, 5.069°E) exposed areas. During sampling, salinity ranged between 30 and 33 psu and tidal range was c. 1 m in the sampling area.

In the Baltic Sea, samples were collected from the Gulf of Riga and the Baltic Proper in summer 2008 (Fig. 1).
The Gulf of Riga is a wide, shallow, semi-enclosed brackish water ecosystem. In general, the bottom relief of the area is quite flat, with gentle slopes towards deeps. The northern part of the Gulf is characterized by a wide coastal zone with diverse bottom topography and extensive reaches of boulders. The coasts of the Baltic Proper are very exposed, hydrodynamically active and characterized by a steep coastline. The inner part of Kõigute Bay, the Gulf of Riga (B1; 58.374°N, 22.972°E) represented a sheltered area, the outer part of Kõiguste Bay (B2; 58.370°N, 22.982°E) a moderately exposed area, and Kûdema Bay, the Baltic Proper (B3; 58.568°N, 22.302°E) an exposed area. During sampling, salinity ranged between 4 and 7 psu. The Baltic Sea is nearly tideless, with an average daily tidal component of 15 cm (Schiwzer 2008). The water level fluctuations in the area are mainly caused by the meteorological forcing with a seasonal sea level mean range of 30 cm (e.g. Suursaar & Sooaāri 2007).

Sampling

In the North Sea, samples were taken at low tide on the upper littoral zone in the middle of F. vesiculosus belt. In the Baltic Sea samples were collected by a diver from a Fucus vesiculosus belt at 0.5–1 m depth. Four replicates of host algae were collected randomly with the aid of a rope that was placed along the shore and marked at every metre. Four marks were randomly selected and host plants were collected nearest to the respective marks on the rope. Samples were transported in plastic bags to the laboratory for the further analyses within 24 h. Mobile fauna were removed from host thalli, counted and identified to the lowest taxonomic level possible using a dissecting microscope (magnification 4–10×). The cover of epiphytes were estimated on a six-grade scale (0 – absence, 1 – from 1 to 20%, 2 – from 21 to 40%, 3 – from 41 to 60%, 4 – from 61 to 80% and 5 – from 81 to 100% of cover on host plant) separately on basal, middle and distal segments of each host frond (Rindi & Guiry 2004) (Fig. 2).

Data analysis

All multivariate analyses were conducted using PRIMER 6 software (Clarke & Gorley 2006). Hierarchical permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008) was used separately for epiphytes and mobile fauna to examine differences in the patterns of variation in composition, cover and abundance between regions (fixed factor), wave exposure (nested in region, fixed factor) and frond segment of host macroalgae (nested in region and wave exposure, fixed factor). Due to the mobility of organisms, frond segment was not considered an important factor for mobile or associated fauna. Therefore, 2-factor PERMANOVA was used to determine the abundances of mobile invertebrates.

Prior to analysis, a Bray–Curtis similarity matrix was calculated using raw data (untransformed) and presence/absence transformation to detect whether the potential differences between the assemblages of the epibionts were due to differences in relative abundances or species composition (Clarke & Warwick 2001).

When a factor with more than two levels (i.e. wave exposure and host frond segment) was identified as significant (P < 0.05), post-hoc PERMANOVA pair-wise tests were conducted to detect which levels were responsible for significant interactions. Taxa responsible for observed differences were identified by similarity percentages (SIMPER), where the cut-off percentage was set to 90. Non-metric multidimensional scaling (nMDS) was used to present visual images of the differences in composition of epiphytic and mobile faunal assemblages in distinct marine regions, exposure levels and frond segment of the host.

Results

A total of 27 epiphytic and mobile faunal taxa were recorded on the fronds of Fucus vesiculosus in the studied areas: 8 taxa of macroalgae, 5 taxa of sessile invertebrates (i.e. suspension-feeders) and 14 taxa of mobile invertebrates (mainly herbivores) (Table 1).

All investigated factors significantly contributed to the variability in species composition and coverage of epiphytic and mobile faunal communities on F. vesiculosus (PERMANOVA, Table 2). Epiphytic and mobile fauna communities were clearly differentiated in species

Fig. 2. Examined frond segments of the host Fucus vesiculosus.
composition and dominance structure between the North and Baltic Seas (Table 2, PERMANOVA: P = 0.001). The epiphytes and mobile fauna taxa contributing most to the regional variability were the brown algae *Pylaiella littoralis*, *Elachista fucicola*, the tube-building polychaete *Spirorbis spirorbis*, and the herbivorous snail *Theodoxus fluviatilis* (Supporting Information Tables S1–S4).

The species composition of epiphytic community (presence/absence transformed data) on their host was significantly different between every level of wave exposure in both the North and Baltic Seas (P < 0.05), except for moderately exposed versus sheltered sites in the North Sea (PERMANOVA pair-wise test: P = 0.092). Dissimilarities between different exposure levels were mostly due to *Elachista fucicola* and *Pylaiella littoralis* (Supporting Information Table S5).

Similarly, the dominance structure of epiphytic community (untransformed data) on their host was significantly different between every level of wave exposure in both the North and Baltic Seas (P < 0.05), except for moderately exposed versus sheltered sites in the North Sea (PERMANOVA pair-wise test: P = 0.078). Dissimilarities between different exposure levels were mostly due to *E. fucicola* and *P. littoralis* (Supporting Information Table S6).

The species composition (presence/absence data) and dominance structure (untransformed data) of mobile fauna community differed significantly for every exposure level in the North and Baltic Seas (PERMANOVA pair-wise test: P < 0.05). Dissimilarities between different exposure levels were mainly due to *Gammarus* spp.,

### Table 1. Recorded epiphytes and mobile fauna on the host *Fucus vesiculosus* at three study sites in the North (NS) and Baltic Sea (BS).

<table>
<thead>
<tr>
<th>No.</th>
<th>Taxon</th>
<th>Region</th>
<th>Wave exposure</th>
<th>Frond segment of host</th>
<th>NS: Mean cover/abun ± SE</th>
<th>BS: Mean cover/abun ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Electra crustulenta</em> (Pallas, 1766)</td>
<td>BS</td>
<td>S, ME</td>
<td>B, M, D</td>
<td>0</td>
<td>0.25 ± 0.07</td>
</tr>
<tr>
<td>2</td>
<td><em>Electra pilosa</em> (L.)</td>
<td>NS</td>
<td>S, ME</td>
<td>B, M, D</td>
<td>0.47 ± 0.14</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td><em>Spirorbis spirorbis</em> (Linnaeus, 1758)</td>
<td>NS</td>
<td>S, ME</td>
<td>B, M, D</td>
<td>1.03 ± 0.18</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td><em>Balanus improvisus</em> Darwin, 1854</td>
<td>BS</td>
<td>E</td>
<td>M</td>
<td>0.33 ± 0.26</td>
<td>6.5 ± 2.21</td>
</tr>
<tr>
<td>5</td>
<td><em>Gammarus</em> spp.</td>
<td>BS, NS</td>
<td>S, ME</td>
<td>E, –</td>
<td>1.5 ± 0.4</td>
<td>6.17 ± 1.60</td>
</tr>
<tr>
<td>6</td>
<td><em>Idotea balthica</em> (Pallas, 1772)</td>
<td>BS, NS</td>
<td>S, ME</td>
<td>E, –</td>
<td>1.5 ± 0.4</td>
<td>6.17 ± 1.60</td>
</tr>
<tr>
<td>7</td>
<td><em>Jaera chelipes</em> (Pallas, 1766)</td>
<td>BS, NS</td>
<td>S, ME</td>
<td>E, –</td>
<td>1.5 ± 0.4</td>
<td>6.17 ± 1.60</td>
</tr>
<tr>
<td>8</td>
<td><em>Jaera albifrons</em> Leach, 1814</td>
<td>BS</td>
<td>ME</td>
<td>–</td>
<td>0</td>
<td>0.25 ± 0.25</td>
</tr>
<tr>
<td>9</td>
<td><em>Cyanophthalma obscura</em> (Schultze)</td>
<td>BS</td>
<td>E</td>
<td>–</td>
<td>0</td>
<td>0.08 ± 0.08</td>
</tr>
<tr>
<td>10</td>
<td><em>Gibbula cineraria</em> (L.)</td>
<td>NS</td>
<td>ME</td>
<td>–</td>
<td>0.08 ± 0.08</td>
<td>0</td>
</tr>
<tr>
<td>11</td>
<td><em>Hydrobia</em> spp.</td>
<td>BS</td>
<td>S, ME</td>
<td>E, –</td>
<td>14.92 ± 6.24</td>
<td>6.5 ± 2.21</td>
</tr>
<tr>
<td>12</td>
<td><em>Lacuna vinca</em> (Montag)</td>
<td>NS</td>
<td>E</td>
<td>–</td>
<td>0.17 ± 0.11</td>
<td>0</td>
</tr>
<tr>
<td>13</td>
<td><em>Littorina littorea</em> (L.)</td>
<td>NS</td>
<td>S, ME</td>
<td>E, –</td>
<td>7.17 ± 1.62</td>
<td>0</td>
</tr>
<tr>
<td>14</td>
<td><em>Littorina obtusata</em> (L.)</td>
<td>NS</td>
<td>S, ME</td>
<td>E, –</td>
<td>7.17 ± 1.62</td>
<td>0</td>
</tr>
<tr>
<td>15</td>
<td><em>Lymnaea peregra</em> (Müller)</td>
<td>BS</td>
<td>ME</td>
<td>E, –</td>
<td>0</td>
<td>0.42 ± 0.26</td>
</tr>
<tr>
<td>16</td>
<td><em>Mytilus edulis</em> L.</td>
<td>NS</td>
<td>S</td>
<td>–</td>
<td>0.17 ± 0.17</td>
<td>0</td>
</tr>
<tr>
<td>17</td>
<td><em>Mytilus trossulus</em> Gould</td>
<td>BS</td>
<td>E</td>
<td>–</td>
<td>0</td>
<td>0.42 ± 0.29</td>
</tr>
<tr>
<td>18</td>
<td><em>Theodoxus fluviatilis</em> (L.)</td>
<td>BS</td>
<td>S, ME</td>
<td>E, –</td>
<td>0</td>
<td>39.17 ± 6.47</td>
</tr>
</tbody>
</table>

S, Sheltered; ME, moderately exposed; E, exposed site. B, basal; M, middle; D, distal segment of host alga.

Means and standard errors were calculated from untransformed coverage and abundance data.
Littorina spp. and Theodoxus fluviatilis (Supporting Information Tables S7 and S8).

Different segments of host fronds had significantly different species composition of epiphytic communities at the moderately exposed site in the North Sea (between middle and distal segments; P = 0.033) and at exposed (between middle and distal segments; P = 0.03) and sheltered sites in the Baltic Sea (between basal and distal segments; P = 0.031). Different segments of host fronds had significantly different dominance structure of epiphytic communities (untransformed data) at the sheltered site in the North Sea (between basal and middle segments; P = 0.026) and at exposed (between middle and distal segments; P = 0.023) and sheltered sites in the Baltic Sea (between basal and distal segments; P = 0.03). The differences in species composition and dominance structure were mainly caused by E. fucicola and P. littoralis (Supporting Information Tables S9 and S10).

According to nMDS ordination, the epiphytic community composition and structure on host macroalgae clearly differed between sea regions in epiphyte coverage and also in mobile fauna abundance. It is also possible to detect a separate effect of wave exposure on epiphytic and mobile faunal community composition and structure within the two sea regions. However, the distinctions are larger for regions than for exposure levels. Nevertheless, in some instances the differences were very clear, e.g. epiphytes were totally absent at the exposed site of the North Sea (Fig. 3).

Discussion

We predicted that the occurrence and cover of epiphytes would be specific to the frond segments of host macroalgae. The results agreed with the hypothesis as different parts of host seaweeds had different epiphytic and mobile fauna species composition and dominance structure. The distal segment of host frond had the lowest coverage and the lowest species richness of epiphytes. This pattern is due to the high metabolic activity of apical (new) parts of Fucus vesiculosus thallus where the host alga produces allelopathic compounds such as phlorotannins (Wikström & Pavia 2003). Also, the topmost parts of fucoid algae have an anti-fouling strategy of periodically shedding surface cell layers (Kiirikki 1996b), which reduces the probability of epibionts settling and becoming established on the host plant. A similar strategy of mechanical defence has been observed in red algal hosts (Nylund & Pavia 2005).

We also predicted that the occurrence and cover of epiphytes would be related to the wave exposure of the site.

Table 2. Main results of PERMANOVA analyses on the effect of region, wave exposure, and frond segment to species composition and dominance structure of epiphytic and mobile faunal assemblages on Fucus vesiculosus.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P(perm)</th>
<th>Unique perms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epiphytic coverage</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Presence/absence transformed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Region</td>
<td>1</td>
<td>15,498</td>
<td>15,498</td>
<td>41.016</td>
<td>0.001</td>
<td>998</td>
</tr>
<tr>
<td>Wave exposure (Region)</td>
<td>4</td>
<td>36,967</td>
<td>9241.6</td>
<td>24.459</td>
<td>0.001</td>
<td>997</td>
</tr>
<tr>
<td>Frond segment (Wave exposure (Region))</td>
<td>12</td>
<td>13,869</td>
<td>1155.7</td>
<td>3.0588</td>
<td>0.001</td>
<td>999</td>
</tr>
<tr>
<td>Res</td>
<td>54</td>
<td>20,403</td>
<td>377.84</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>71</td>
<td>86,736</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Untransformed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Region</td>
<td>1</td>
<td>18,220</td>
<td>18,220</td>
<td>33.454</td>
<td>0.001</td>
<td>998</td>
</tr>
<tr>
<td>Wave exposure (Region)</td>
<td>4</td>
<td>50,430</td>
<td>12,607</td>
<td>23.149</td>
<td>0.001</td>
<td>997</td>
</tr>
<tr>
<td>Frond segment (Wave exposure (Region))</td>
<td>12</td>
<td>19,143</td>
<td>1595.2</td>
<td>2.929</td>
<td>0.001</td>
<td>996</td>
</tr>
<tr>
<td>Res</td>
<td>54</td>
<td>29,410</td>
<td>544.63</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>71</td>
<td>117,200</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mobile faunal abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Presence/absence transformed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Region</td>
<td>1</td>
<td>42,429</td>
<td>42,429</td>
<td>123.9</td>
<td>0.001</td>
<td>999</td>
</tr>
<tr>
<td>Wave exposure (Region)</td>
<td>4</td>
<td>9522.1</td>
<td>2380.5</td>
<td>6.9515</td>
<td>0.001</td>
<td>999</td>
</tr>
<tr>
<td>Res</td>
<td>66</td>
<td>22,601</td>
<td>342.45</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>71</td>
<td>74,553</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Untransformed</td>
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<td></td>
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<tr>
<td>Region</td>
<td>1</td>
<td>109,390</td>
<td>109,390</td>
<td>12.33</td>
<td>0.001</td>
<td>997</td>
</tr>
<tr>
<td>Wave exposure (Region)</td>
<td>4</td>
<td>35,212</td>
<td>8803</td>
<td>10.408</td>
<td>0.001</td>
<td>996</td>
</tr>
<tr>
<td>Res</td>
<td>66</td>
<td>55,825</td>
<td>845.83</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Total</td>
<td>71</td>
<td>200,430</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Res, Residual.
Some epiphytic (e.g. *Spirorbis spirorbis*, Bryozoa, *Cladophora glomerata*, *Pylaiella littoralis*) and mobile faunal species (e.g. *Jaera albifrons*) were not observed at exposed study sites, suggesting that occurrence and cover/abundance are related to the exposure level of a site. This pattern is explained by the high hydrodynamic pressure on the thallus of *F. vesiculosus* at highly exposed sites, which removes epiphytic algae and prevents benthic suspension feeders from settling on the algae.

We also predicted that the relationship between abiotic (exposure), biotic factors (host frond segment) and epiphytes (species composition, cover) would vary among different marine regions (North versus Baltic Seas). Indeed, our study showed that the North and Baltic Seas had different epiphytic and mobile faunal species compositions and dominance structures. The epiphytic and mobile faunal taxa contributing most to the dissimilarity between North and Baltic Sea communities were the brown alga *P. littoralis* and the herbivore *Theodoxus fluviatilis*, respectively. Both species have a strong degree of tolerance to lowered salinity which consequently enables them to thrive in the low salinity environment. This suggests that salinity determines interregional differences in epiphyte communities between North and Baltic Seas (Kangas & Skoog 1978; Russell 1994; Snoeijs 1999). *Theodoxus fluviatilis* was consistently absent in the North Sea study sites, causing high dissimilarities in abundance among regions.

This study also showed a higher variability of epiphytes and mobile faunal community structure in the Baltic Sea than in the North Sea. It has been proposed that processes affect ecosystems simultaneously at various spatial and temporal scales (Denny et al. 2004; Fraschetti et al. 2005; Kotta et al. 2008). The relative importance of small- and large-scale processes on the formation of marine communities is little known and it is likely the patterns vary among regions (e.g. Hewitt et al. 2007; Kotta & Witman 2009). Our study indicates that large-scale factors mostly determine the distribution patterns of epiphytes in the North Sea and within these patterns, processes operating at microscale (e.g. due to frond segment) further modify the epiphyte communities. On the other hand,

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**Fig 3.** Non-metric multidimensional scaling (nMDS) plots showing the effect of sea region and wave exposure (E = exposed; M = moderately exposed and S = sheltered sites) on epiphytic (coverage) and mobile faunal (abundance) community composition and structure. Lefthand plots are composed from presence/absence transformed data, righthand plots from untransformed data. Some marks are overlapped on the figure because epiphytes and mobile fauna were absent in these samples, thus representing 100% similarity.
large-, meso- and microscale processes are all equally important in determining the distribution patterns of epiphytes in the Baltic Sea.

In general, associated faunal community composition was different between all levels of wave exposure in both marine regions, whereas epiphytic composition and structure did not significantly differ between moderately exposed and sheltered sites in the North Sea. This indicates that epiphytic algae inhabiting the North Sea tolerate a larger range of exposure than those inhabiting the Baltic Sea.

The effect of host frond segments on the patterns of epiphytes varied among North and Baltic Seas, supporting the hypothesis that there are different factors (levels) forming different epiphytic communities on *F. vesiculosus* in the Baltic and North Sea. It seems likely that at smaller spatial scales, biotic factors (i.e. frond segment) play a more important role in epiphytic communities in the Baltic Sea, whereas abiotic factors (i.e. wave exposure) are more important in the North Sea.

Our understanding of the causes of local species diversity in marine habitats mostly originates from observations performed at small spatial scales. Comparing local and regional variability of epiphyte communities, our study clearly demonstrated that regional differences define broad patterns of species diversity and are among the most significant factors explaining population variability in these marine environments. However, our study was limited to two-region cases and further studies from multiple regions may provide us with a generic knowledge of the processes shaping epiphyte communities. Besides the spatial aspect, epiphytes are known to have a strong component of seasonal variability (Borum 1985; Vairappan 2007; Torn et al. 2010). This was not considered in the current study but may be highly relevant, as different regions are characterized by different types and intensity of seasonality.

To conclude, all investigated factors contributed significantly to the variability in species composition and coverage of epiphytes and mobile faunal communities on *F. vesiculosus*. The North and Baltic Seas each had distinct epiphyte and mobile faunal communities. Within the studied regions, wave exposure and frond segment contributed significantly to the variability in species composition and dominance structure of epiphytes on *F. vesiculosus* in the North Sea and Baltic Sea. Large-scale factors greatly determine the distribution patterns of epiphytes in the North Sea, whereas large-, meso- and microscale processes were all equally important in determining the distribution patterns of epiphytes in the Baltic Sea. The study indicated that there is no clear spatial scale where environmental variables best predicted epiphyte and mobile faunal communities. The formation of epiphytic and mobile faunal communities is an interplay of factors operating through micro- to regional scales.

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**References**


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and analysis of empirical studies of scale-dependent systems. 


Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Results of SIMPER analyses testing for differences in the species composition of epiphytic communities on *Fucus vesiculosus* between the North and Baltic Seas (presence/absence transformed data, coverage of epiphytes on host).

**Table S2.** Results of SIMPER analyses testing for differences in the dominance structure of epiphytic communities on *Fucus vesiculosus* between the North and Baltic Seas (untransformed data, coverage of epiphytes on host).

**Table S3.** Results of SIMPER analyses testing for differences in the species composition of mobile faunal communities on *Fucus vesiculosus* between the North and Baltic Seas (presence/absence transformed data, abundance of fauna on host).

**Table S4.** Results of SIMPER analyses testing for differences in the dominance structure of mobile faunal communities on *Fucus vesiculosus* between the North and Baltic Seas (untransformed data, abundance of fauna on host).

**Table S5.** Results of SIMPER analyses testing for differences in the species composition of epiphytic communities on *F. vesiculosus* between different wave exposure levels (presence/absence transformed data, coverage of epiphytes on host).

**Table S6.** Results of SIMPER analyses testing for differences in the dominance structure of epiphytic communities on *Fucus vesiculosus* between different wave exposure levels (untransformed data, coverage of epiphytes on host).

**Table S7.** Results of SIMPER analyses testing for differences in the species composition of mobile faunal communities on *Fucus vesiculosus* between different wave exposure levels (presence/absence transformed data, abundance of fauna on host).

**Table S8.** Results of SIMPER analyses testing for differences in the dominance structure of mobile faunal communities on *Fucus vesiculosus* between different wave exposure levels (untransformed, abundance of fauna on host).

**Table S9.** Results of SIMPER analyses testing for differences in the species composition of epiphytic communities on *Fucus vesiculosus* between different frond segments (presence/absence transformed data, coverage of epiphytes on host).

**Table S10.** Results of SIMPER analyses testing for differences in the dominance structure of epiphytic communities on *Fucus vesiculosus* between different frond segments (untransformed data, coverage of epiphytes on host).

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