Research Article

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Vegetation of the supralittoral and upper sublittoral zones of the Western German Baltic Sea coast: a phytosociological study

Abstract: Supralittoral and shallow water seaweed communities are particularly exposed to impacts such as climate change and disturbance by humans. Therefore, their classification, the study of composition, and the monitoring of their structural changes are particularly important. A phytosociological survey of the supralittoral and upper sublittoral vegetation of the South West Baltic Sea revealed eight phytobenthos communities with two variants comprising 35 taxa of macrophytes (18 taxa of Chlorophyta, 13 taxa of Rhodophyta and four taxa of Phaeophyceae, Ochrophyta). Five of the eight communities were dominated by Ulvales (*Ulva intestinalis*, *Kornmannia leptoderma*, and three *Blidingia* species), the other three by *Fucus vesiculosus*. Most *Fucus vesiculosus*-dominated communities contained *U. intestinalis* and *U. linza* as subdominants. Only one of the communities had until now been described as an association (***Ulvetum intestinalis*** Feldman 1937). The syntaxonomic composition of the investigated vegetation includes both phytocenoses with the domination of green algae (***Ulvetum intestinalis*** Feldman 1937 and communities of *Blidingia marginata*, unidentified *Blidingia* spp. and

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Kornmannia leptoderma), as well as a number of communities dominated by *Fucus vesiculosus*. Mainly boreal Atlantic species and cosmopolitans make up the bulk of the species in these associations.

Keywords: communities; macrophytobenthos; phytosociology; syntaxonomy; Ulvales.

1 Introduction

Marine phytobenthic communities in the supralittoral and uppermost sublittoral zones, located at the interface between land, water and air, are dynamic and structurally diverse. Past phytosociological classifications of such communities have been mainly limited to France, Italy, and Spain, referring mainly to the syntaxonomy of Mediterranean Sea bottom vegetation (Ballesteros 1992; Berner 1931; Boudouresque 1971; Feldmann 1937; Giaccone et al. 1993). In recent years, the European Commission and European Environment Agency have initiated projects that would underpin the continent's habitat classification schemes by applying the syntaxonomic system of the EuroVegChecklist, based on the floristic Braun-Blanquet approach, including the revision of the EUNIS system of European habitat types (Mucina et al. 2016). The data on syntaxonomy of marine macroalgal communities were summarized by Bültmann et al. (2015) and Mucina et al. (2016). The highly ranked syntaxa of algae have been compiled for the first Euro-VegChecklist, including four classes for marine algal vegetation (Mucina et al. 2016). These reports focus on Atlantic and Mediterranean sytaxa and provide no information about Baltic Sea communities.

However, the marine vegetation of the Baltic Sea has also been studied, especially in Gdansk Bay in Poland (Kornaś and Medwecka-Kornaś 1950; Kornaś et al. 1960). Using the methods of the Zurich-Montpellier phytosociological approach, the following five associations were distinguished and described in this study region: 1. ***Fuceto-Furcellarietum*** in water depths of 2.5–4 m, 2. ***Chareto-Tolypelletum*** in water depths of 2–3 m, 3.

Cladophora glaucescens community in water depth of 60 cm, 4. *Ulva linza-Spirulina subsalsa* community in water depths up to 5 m, and 5. *Ulvetum compressae* close to the surface (0–0.2 m depths) (Kornaś and Medwecka-Kornaś 1950; Kornaś et al. 1960). In Sweden and Eastern Germany, phytosociological approaches were used to study marine communities with the aim of conservation, especially in bays and inlets dominated by vascular aquatic plants (Kautsky 1990; Künzenbach 1955/56; Overbeck 1964; Pankow et al. 1967). These Baltic communities belong to two classes (cl.): *Zosteretea* Pignatti 1953 and *Ruppietea maritimae* J.Tx. 1960 (Golub and Sokoloff 1998). Another class of vegetation mentioned for Swedish coasts is *Enteromorphetea* (Waern 1952). Many of the Baltic Sea syntaxa described are characterized by domination of different Ulvales, that could not have been reliably distinguished until recently as DNA barcoding approaches became available (Steinhagen et al. 2019a). Therefore, a review of the validity of these syntaxa described more than 30 years ago seems necessary.

Moreover, phytosociological studies are lacking for the Western German Baltic Coast, in which large sections are exposed to higher salinities and therefore harbors a more diverse algal flora than the Eastern German or Polish Coasts. Although the composition of macroalgal communities at various sites along the coast of Schleswig-Holstein has been regularly monitored by the Schleswig-Holstein State Office for the Environment and Rural Areas (LLUR) for several decades, these data have not yet been evaluated from a phytosociological perspective (Dr. Rolf Karez, LLUR, pers. comm.).

The composition of algal populations is basically determined by the abiotic and biotic conditions in their habitat. These are unusual in the Baltic Sea in several respects, making it a unique environment for studying phytosociological patterns (Weinberger et al. 2020). The salinity of the Baltic Sea has changed drastically several times since its formation after the last ice age. It is now characterized by a gradient from 33 (Danish area of the Kattegat) to 4 (Northeastern Baltic Sea) (Cato and Kjellin 1992). Moreover, while the Sea does not exhibit significant tides, it features irregular variations on the surface level determined by wind and atmospheric pressure (Rönnbäck et al. 2007). A third important factor in the Southwestern Baltic Sea is the limited availability of hard substrata (Eriksson and Johansson 2003; Weinberger et al. 2020). These specific characteristics influence algal community composition along with other common factors, such as seasonally varying light availability and temperature, water movement (Sheperd and Womersley 1981), and wave exposure (Hurd 2000; Schanz et al. 2002).

Like other habitats, however, the Baltic Sea is not a static environment, and human activities in particular have already led to significant changes in the occurrence of algal species. Such processes of marine community transformation need to be studied, but this is not possible without classification of the vegetation. An important anthropogenic factor in this context is the relatively high eutrophication of the Baltic Sea, which has favored increased growth of filamentous and opportunistic annual algae in particular during the last 60 years (Cederwall and Elmgren 1990; Weinberger et al. 2020). Climate change, which has been ongoing for several decades, may also affect macrophytes in the supralittoral and upper sublittoral because it leads to less frequent ice formation in winter and more frequent heat waves in summer (Reusch et al. 2018). A third important anthropogenic factor is invasions by alien species, which are also increasingly observed in the Baltic Sea and may transform existing associations (Thomsen et al. 2007).

In this paper, we present results on the classification of the current macrophytobenthos communities from the supralittoral and upper sublittoral zone of the southwestern Baltic Sea coast in Germany based on floristic criteria. Our study represents the first phytosociological study within the study area, building on a recent revision of its inventory of Ulvales species, which are a very important component of the communities studied (Steinhagen et al. 2019a, 2021; Weinberger et al. 2018). It therefore provides a baseline required for the study of further transformations of the macrophytobenthos of the SW Baltic Sea.

2 Materials and methods

2.1 Sampling areas

Our study area was located in the SW Baltic Sea. The coast of Schleswig-Holstein (ca. 260 km long) is mainly composed of stones, gravel and sand (Rönnbäck et al. 2007) with the annual mean salinity ranging from approximately 18 to 12 (Gräwe et al. 2014), although freshwater inflow and local seasonal fluctuations generate notably steeper gradients. The SW Baltic Sea is generally influenced strongly by anthropogenic factors and suffers from eutrophication due to past and present excessive inputs of nitrogen and phosphorus (HELCOM 2018).

Along the western part of the Baltic Sea coast, 54 sampling sites were visited between July and August 2013 (Figure 1). These locations were throughout the German states of Schleswig-Holstein and Mecklenburg-Vorpommern, ranged over a distance of 452 km from Flensburg to Rerik and differed in their salinity and exposure. Additionally, locations in the western part of the Kiel Bay were visited between July and August 2019.
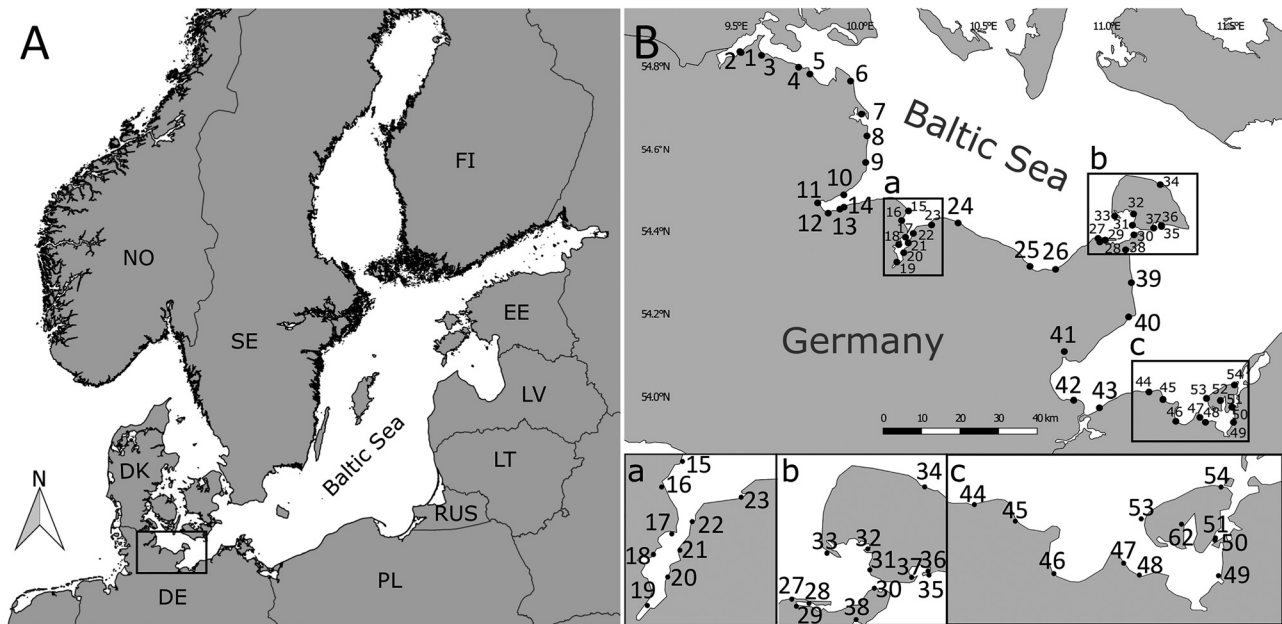
Figure 1: Map of sampling sites in Northern Germany. Insets (a–c) provide higher resolution. Sampling areas: 1 – Glücksburg; 2 – Glücksburg Estuary; 3 – Bockholmwik; 4 – Neukirchen; 5 – Norgaardholz; 6 – Falshoft; 7 – Maasholm, Schlei; 8 – Schönhagen; 9 – Fischleger; 10 – Karlsminde; 11 – Eckernförde, port; 12 – Eckernförde, Kiekut; 13 – Aschau, sea; 14 – Aschau, lagoon; 15 – Kiel-Bülk; 16 – Kiel-Schilksee, marina; 17 – Kiel-Friedrichsort; 18 – Kiel-Holtenau, Tonnenhof; 19 – Kiel-Düsternbrook; 20 – Kiel-Mönkeberg; 21 – Kiel-Heikendorf, Hafen; 22 – Kiel-Laboe; 23 – Kiel-Marina Wendtorf; 24 – Kiel-Brasilien; 25 – Hohwacht; 26 – Weissenhäuser Strand; 27 – Heiligenhafen, sea; 28 – Heiligenhafen, Binnensee; 29 – Heiligenhafen, marina; 30 – Grossenbroderfahre; 31 – Strukkamphuk, Fehmarn; 32 – Westerberg, Fehmarn; 33 – Flügge, Orther Bucht, Fehmarn; 34 – Gruner Brink, Fehmarn; 35 – Burgtiefe, Fehmarn; 36 – Burger Binnensee, Fehmarn; 37 – Wulfen, Fehmarn; 38 – Marina Grossenbrode; 39 – Süssau; 40 – Kellenhusen; 41 – Neustadt, Binnenwasser; 42 – Brodtener Ufer; 43 – Rosenhagen; 44 – Steinbeck; 45 – Boltenhagen; 46 – Wohlenberg; 47 – Hohen-Wieschendorf; 48 – Zierow; 49 – Redentin; 50 – Bridge to Poel, S side; 51 – Bridge to Poel, N side; 52 – Kirchdorf; 53 – Timmendorf, Poel; 54 – Gollwitz, Poel.

2.2 Measurement of abiotic factors

Salinity was measured at each site using a calibrated hand-held refractometer with automatic temperature compensation (Euromex, Arnhem/NL).

A visual substrata classification was carried out in accordance with an approximation to the Wentworth grade classification (Buchanan 1985). Additionally, wood and artificial concrete structures were identified and the exposure of the habitat was assessed visually. Four grades of exposure were distinguished: open, semi-open, semi-closed and closed water areas. The latter included small natural or artificial coastal lagoons.

2.3 Description of communities

Numerous plots (77 in 2013 and 5 in 2019) that represented typical supralittoral and upper sublittoral phytocenoses in <1 m depth were designated on the sites, representing habitats with homogeneous vegetation and environmental conditions (Abdullin et al. 2017; Mirkin et al. 2000). All the different habitats (marine, estuarine, overflow basins etc.) and types of substrata (stones, gravel, concrete, wood, mud with mollusk shells) present in the study region were included and described. Accordingly, the sites were chosen to describe the communities of all these diverse habitats.

At each site, before describing the communities, the maximum and minimum depths were recorded, the macrophytobenthos distributions were assessed visually and the abiotic parameters were evaluated. Then a homogeneous area of vegetation was selected within the boundaries of each type of habitat. The described plot was randomly placed within this homogeneous vegetation area. The communities of macroalgae were described in quadrats of 0.01 m² (10 × 10 cm) for supralittoral zones and 0.0625 m² (25 × 25 cm) or 0.25 m² (50 × 50 cm) for upper sublittoral zones (Abdullin et al. 2017; Minicheva et al. 2014). The percentage of macrophyte coverage in each of the plots, as well as the abundance of each species, were recorded. Before collecting, all sites and plots were photographed.

Each macrophyte sample was placed in a plastic or gauze bag with a label containing the details about sampling place and conditions. Samples were then stored in a chilled container (~10 °C) and transported to the laboratory for more precise analysis and identification of small or cryptic species. After handling, all samples were frozen for long term storage. Some macrophytes were stored as herbarium sheets.

To estimate the abundance of each species, a modified Braun-Blanquet scale was used: r – rare, + – few individuals, 1 – total projected cover of a species up to 5%, 2 – cover 6–15%, 3 – cover 16–25%, 4 – cover 26–50%, 5 – cover >51%.

When compiling synoptic tables, a species frequency scale was used: r – 0–5%; + – 6–10%; I – 11–20%; II – 21–40%; III – 41–60%; IV – 61–80%; V – 81–100%. The frequency of species was determined using the formula: $F = a/A*100\%$, where: a – the number of plots in which the species was recorded, A – the total number of plots.

Analysis of the collected data was carried out following Braun-Blanquet (1964). The selection and diagnosis of new syntaxa followed the International Code of Phytosociological Nomenclature (Theurillat et al. 2020). According to the Code, we used the term "association" (ass.) for communities which were validly published previously. All other phytocenoses, which currently do not have a clear syntaxonomic rank, are described here as "communities".

Lists of macroalgal species with an indication of their phytogeographic characteristics (Cormaci et al. 1982; Kalugina-Gutnik 1975; Zinova 1962) were used for phytogeographical analysis of the communities. These sources still represent the most complete lists of macroalgal species from European seas according to their phytogeographic characteristics. Realizing that these sources date from before accurate species identifications were based on genetics, we continue to use them until the appearance of new reports on the phytogeography of marine macroalgae, whose distribution has been confirmed by genetic studies.

2.4 Species identification

2.4.1 Morphological analysis: Most of the macrophytes present in the investigated quadrats were identified based on their morphology, either observed directly in the field or after microscopic examination of representative samples in the laboratory. To identify species using light microscopy, the collected samples were stored in a chilled container (~10 °C) and transported to the laboratory. Identification was based on typical morphological characters using identification keys (Brodie et al. 2007; Kornmann and Sahling 1989; Pankow 1990). Some species of *Acrochaetium, Cladophora, Ceramium* and *Polysiphonia* could not be identified confidently and were marked as *Acrochaetium* sp., *Cladophora* sp., *Ceramium* sp. and *Polysiphonia* sp. One species of brown algae was recognized just as "Ectocarpales".

2.4.2 Molecular analysis: Due to the predominant role of Ulvales in the composition of the shallow water zone communities and because some specimens could not be unambiguously identified based upon morphological characteristics, they were identified by DNA barcoding. First, morphological identification of Ulvales was carried out for each sample. Then, a few specimens of each species from each sample were taken for genetic analysis and additionally conserved as herbarium vouchers. In total, 70 samples of Ulvales were genetically analyzed. Genetic tests were repeated for samples where the first genetic test was at variance with the morphological identification. Subsequent to morphological analysis, epiphyte-free pieces of thallus tissue (1 cm^2) or complete smaller thalli were either frozen and lyophilized or dried in silica gel for further molecular analysis. Total genomic DNA was extracted from the thallus tissue, using the Invisorb Spin Plant Mini Kit (Stratec, Birkenfeld, Germany), following the manufacturer´s instructions. DNA-barcode fragments of the plastid encoded elongation factor Tu (*tuf*A) were amplified by polymerase chain reaction (PCR), using the primers tufGF4 (Saunders and Kucera 2010) and tufAR (Famà et al. 2002). For amplification, the following temperature profile was used: initial denaturation 4 min at 94 °C, 38 cycles of 94 °C for 1 min, 55 °C for 30 s, 72 °C for 1 min, final extension for 7 min at 72 °C. PCR products were Sanger-sequenced in both directions by GATC biotech (Konstanz, Germany). Forward and reverse sequences of each gene were assembled and reciprocally edited with Sequencher (v. 4.1.4, Gene Codes Corporation, Ann Arbor, MI). Representative barcodes of each detected species were deposited in GenBank (accession numbers: KT207466 and KT290271 to KT290281).

To strengthen the robustness of the phylogenetic analysis, reference sequences from GenBank were included in the analysis, with preference given to annotated (origin, collection date, collector etc.) sequences published in peer-reviewed articles. The *tuf*A sequences were aligned with the reference sequences downloaded from GenBank and used for further phylogenetic analysis. The models that best fit our data were found under the Akaike information criterion by employing MrModeltest v.2.2 (Nylander 2004). The optimal substitution model was determined and found to be GTR + Γ + I. Maximum likelihood (ML) analyses were then carried out using RAxML v.8 (Stamatakis 2014), employing the chosen substitution model with 1000 bootstrap replicates.

3 Results

Altogether, 35 taxa of algal macrophytes were detected in this study; among them were 18 taxa of Chlorophyta, 13 taxa of Rhodophyta and 4 taxa of Phaeophyceae, Ochrophyta.

Green algal species of the genera *Ulva, Blidingia* and *Kornmannia* were molecularly identified by DNA barcoding and phylogenetic analysis (Figure 2). In addition to *Blidingia marginata*, which is known to occur in this area, two other *Blidingia* species that could be genetically distinguished were detected, but could not be clearly identified at the species level, so we refer to them as *Blidingia* sp. 3 and *Blidingia* sp. 4. Notably, the taxonomy of the genus *Blidingia* is not resolved in detail yet, thus we go over the identity of the species encountered here in the Discussion. Besides these three *Blidingia*-species, *Ulva intestinalis* and *Ulothrix flacca* were also detected in the supralittoral zone. All other species occurred only in the upper sublittoral zone.

According to the field observations and support from molecular analysis, the most abundant species among green algae were *U. intestinalis* and *U. linza*. The latter was detected both in its partly sheet-like "*linza*" and its tube-like "*procera*" (or "*ahlneriana*") morphologies.

Altogether, 10 syntaxa (eight communities of macrophyte algae with two variants) were identified in our study area. Five of them are communities dominated by different Ulvales species, while three are dominated by *Fucus vesiculosus* (Table 1, Supplementary Table S1).

3.1 Characteristics of the syntaxa

Ass. ***Ulvetum intestinalis*** Feldmann 1937

Diagnostic species: *Ulva intestinalis*

Communities of this association are the most common in the investigated part of the Baltic Sea. They occupied various horizontally and vertically oriented solid surfaces (boulders, cobbles, concrete and wooden structures) in a zone between 0.15 m above and 0.6 m below the mean
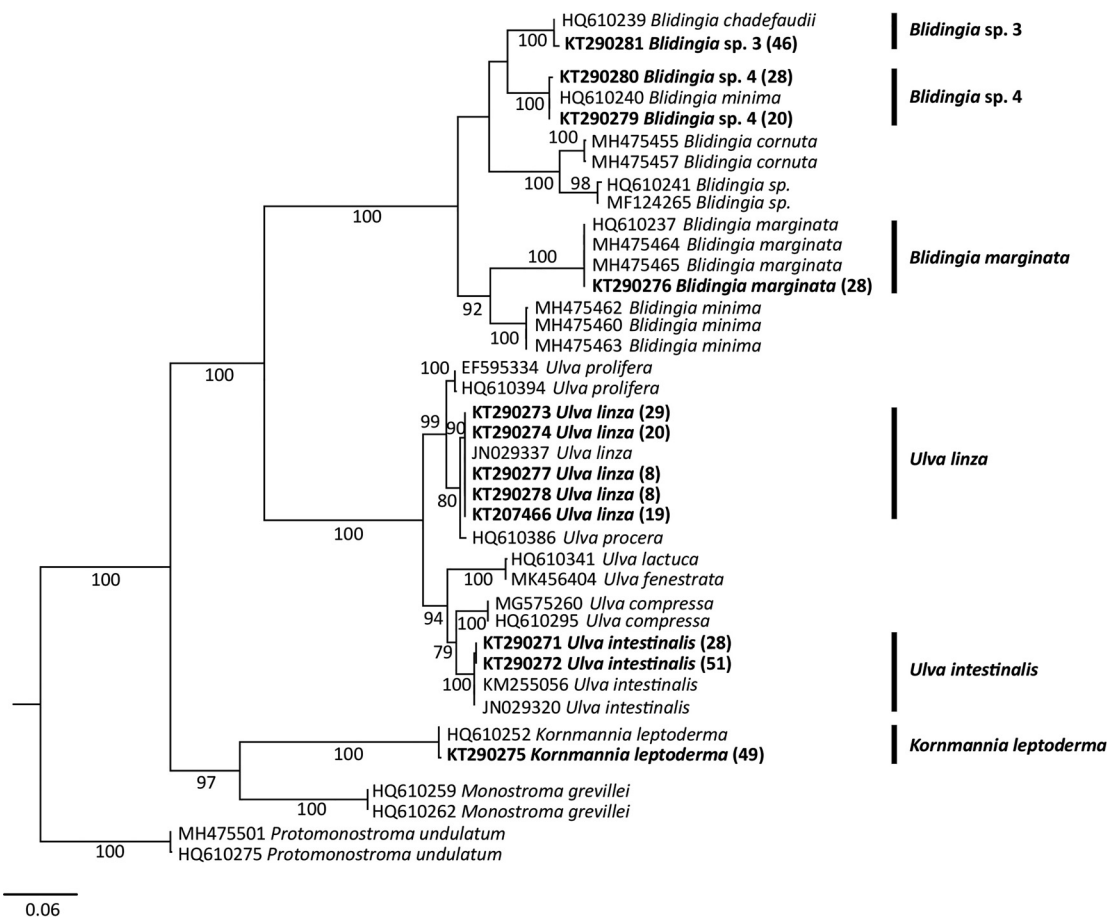
Figure 2: Maximum likelihood phylogram based on *tuf*A sequence data, showing the phylogenetic relationships of 12 Ulvales samples from the Baltic Sea (bold) identified in this study. Numbers after species names indicate collection sites (see Figure 1). Numbers below branches are bootstrap values; poorly supported nodes (>0.70) are not labelled. Branch lengths are proportional to sequence divergence.

water surface level (Supplementary Figure S1). This association occurred in a wide range of salinities ranging from 15 to near freshwater conditions (estuaries, overflow basins, and water inlets).

The floristic core of the association includes only the diagnostic species; other species occurred with low constancy. The number of species in the plots ranged from 1 to 6, but a total of 19 taxa were detected in communities of this association. The total percentage covered by phytocenoses belonging to this ass. varied from 25 to 100%, at an average of 69%.

Community **Fucus vesiculosus–Ulva intestinalis**

Diagnostic species: *Fucus vesiculosus, Ulva intestinalis*

This is one of the most abundant communities along the western coast of the German Baltic Sea. The community was detected at depths ranging from 0 to 0.5 m and at salinities between 9 and 15. It may occur near open shores but only in environments with low exposure (e.g., the inner part of the area between breakwaters). This community develops on boulders, cobbles and pebbles, but rarely on silty bottoms (in this case, algae attach to the shells of mollusks).

Phytocenoses belonging to this community are dominated by *F. vesiculosus*. Among all the species of the community, only *F. vesiculosus* and *U. intestinalis* occurred with high constancy (Supplementary Figure S2). The average number of taxa in the plots was 4 (range 2–7), but 14 taxa have been identified in this community. The total coverage of the community ranged from 30 to 100% and averaged 73%.

The **Fucus vesiculosus–Ulva intestinalis** community has a variant, **Fucus vesiculosus–Ulva intestinalis var. Elachista fucicola**, with *Elachista fucicola* as an additional diagnostic species. This occupied the same depths as the main community, but occurred more frequently in habitats with higher exposure. All diagnostic species occurred here with a very high constancy, and the same was true for *Ceramium tenuicorne, Polysiphonia stricta* and different *Cladophora* species, especially of the *Cladophora vagabunda* complex. This is the one of the most diverse

Table 1: Occurrence, abundance and preferred habitat of the dominant and diagnostic species of the Baltic Sea macrophyte communities.

Syntaxa*	1	2	3	4	5	6	7	8	9	10
Sampling areas: see Figure 1	1, 4, 6, 7, 9, 12, 19, 24–26, 28, 32, 35, 37, 39, 40, 42–47, 49, 51, 52	2, 7, 17, 23, 24, 28, 33, 47, 50, 51, 53	1, 12, 22, 25, 27, 36, 42, 53	1, 3, 4, 8, 10, 15, 22, 42	18, 20, 21, 54	5, 11, 16, 29	15, 20, 35, 44, 53	24, 45, 46	28, 48	49, 54
Substrata**	b, c, p, w, cn	b, c, p	b	b, c	b, c	c, ss, cn	b	cn, b, w	cn, b	b, c
Salinity	5–15	9–15	9–15	14–15	10–15	11–15	9–15	9–14	5–12	10–13
Average number of species	2.3	4.0	6.6	4.1	3.5	6.1	1.0	1.0	1.5	2.0
Number of descriptions	31	11	8	8	4	8	5	3	2	2
Ulva intestinalis L.	V***	V	V							
Fucus vesiculosus L.		V	V	V	V	V				
Elachista fucicola (Velley) Areschoug			V	V	V					
Ulva linza L.	+	+	II		V	V				
Blidingia sp. 4							V			
Blidingia sp. 3								V		
Blidingia marginata (J.Ag.) P.J.L.Dangeard *ex* Bliding									V	
Kornmannia leptoderma (Kjellman) Bliding						I				V

*Syntaxa are: 1 – **Ulvetum intestinalis** Feldmann 1937; 2 – **Fucus vesiculosus–Ulva intestinalis**; 3 – **Fucus vesiculosus–Ulva intestinalis var. Elachista fucicola**; 4 – **Fucus vesiculosus–Elachista fucicola**; 5 – **Fucus vesiculosus–Elachista fucicola var. Ulva linza**; 6 – **Fucus vesiculosus–Ulva linza**; 7 – **Blidingia sp. 4**; 8 – **Blidingia sp. 3**; 9 – **Blidingia marginata**; 10 – **Kornmannia leptoderma**. **Substrata are: cn – concrete; b – boulder; c – cobble; p – pebble; ss – shells on silt; w – wood. ***Frequencies of species are indicated as follows: + – 6–10%; I – 11–20%; II – 21–40%; III – 41–60%; IV – 61–80%; V – 81–100%.

communities – the average number of taxa in the description was about 7 and a total of 20 taxa contributed to these phytocenoses. The total coverage of this community was relatively high, ranging from 55 to 100%, with an average of 78%.

The floristic composition of this variant is obviously transitional between **Fucus vesiculosus–Ulva intestinalis** and **Fucus vesiculosus–Elachista fucicola** communities**.** Its environmental preferences differ from the last one by being confined to waters that are visually less clean and with lower salinity (Supplementary Figure S3).

Community **Fucus vesiculosus–Elachista fucicola**

Diagnostic species: *Fucus vesiculosus, Elachista fucicola*

This community is located on boulders and cobbles at depths ranging from 0 to 0.9 m. It develops in habitats with high exposure, facing toward the open sea. It was found in environments with salinity >14. The community occurs more commonly along open coasts and in the seaward oriented parts of bays and fjords.

The diagnostic species of the community is *F. vesiculosus*, whose thalli are covered with epiphytes: *E. fucicola* with high constancy, *Acrochaetium* sp., *Ceramium tenuicorne, Ceramium deslongchampsii, Polysiphonia stricta* with lower constancy (Supplementary Figure S4).

The average number of taxa in the community was 4. The number of detected taxa was 13. The total coverage of the community ranged from 50 to 100%, on average 70%.

In this community we also distinguish a variant, **Fucus vesiculosus–Elachista fucicola var. Ulva linza**, with the additional diagnostic species of *U. linza*. This variant grows mostly in the middle parts of bays and fjords on cobbles and boulders at the same depths, while more frequently in habitats with high exposure and relatively high salinity (10–15). Apparently, its environmental preferences differ from the **Fucus vesiculosus-Elachista fucicola** community by being confined to less visually clean and less salty waters (Supplementary Figure S5).

Community **Fucus vesiculosus–Ulva linza**

Diagnostic species: *Fucus vesiculosus, Ulva linza*

The community was predominantly observed in enclosed parts of bays, harbors and fjords on cobbles, concrete structures and mollusks shells at depths ranging from 0 to 0.9 m. Surf in such habitats is obviously much weaker. The substratum is often heavily silted and phenomena such as temporary hypoxia, negative substratum redox potential or acidification are possible. The range of salinities in areas where the community was identified was

11–15. Phytocenoses of this community seem to be tolerant of low water transparency (Supplementary Figure S6).

The community is dominated by *F. vesiculosus*, whose thalli are covered with a lot of epiphytic micro- and macroalgae: *U. linza* (*procera* (*ahlneriana*) morphology), many diatoms (including tubular *Navicula* spp., which formed macroscopic "bushes" on the surface of *F. vesiculosus*) and other (mainly) green algae.

The average number of species observed in this community was 6 (ranging from 4 to 8). Altogether, 10 species have been identified in these phytocenoses. The total coverage of the community varies from 30 to 100%, on average 88%.

Community *Kornmannia leptoderma*

Diagnostic species: *Kornmannia leptoderma*

This community develops mainly on semi-open beaches, particularly on cobbles and boulders below the water edge at a depth of 0–0.2 m with a salinity range of 10–13 (Supplementary Figure S7).

Phytocenoses of this community contain only a few species and are dominated by *K. leptoderma*. The average number of species in the description was 2. The total coverage of the community varied from 40 to 60%, on average 51%.

Community *Blidingia marginata*

Diagnostic species: *Blidingia marginata*

This community consisted of dense populations of *B. marginata,* which develop above the water edge up to 0.15 m above the water level on sites with a wide range of exposure and different types of substrata (mainly boulders and concrete). The salinity varies from near freshwater up to 12 (Figures S8 and S9).

Phytocenoses belonging to this community are monodominant, often composed of a single species. At the community level, apart from *B. marginata*, only *Ulothrix flacca* has been detected. The total coverage of the community ranged from 55 to 90%, on average 68%.

Community *Blidingia* sp. 3

Diagnostic species: *Blidingia* sp. 3

The community developed above the water edge up to 0.15 m above the water level. Communities were most dominantly found on sites with low wave exposure, on boulders and artificial constructions (concrete, wood pillars) at salinities ranging from 9 to 14 (Figures S10 and S11).

Phytocenoses consisted only of *Blidingia* sp. 3. The total coverage of the community varied from 35 to 90%, on average 69%.

Community *Blidingia* sp. 4

Diagnostic species: *Blidingia* sp. 4

This community may be observed at exposed and semi exposed sites, on boulders, above the water edge up to 0.2 m above the water level. The community of this species occurred at salinities of up to 15, and it furthermore tolerated freshwater inflows. It was, for example, often observed in the vicinity of rain water drainage (Figures S12 and S13).

Phytocenoses of this community were monodominant and consisted only of *Blidingia* sp. 4. The total coverage of the community ranged from 30 to 95%, on average 60%.

Our results highlighted two separated belts within the investigated zones: the vegetation of the supralittoral zone and the vegetation of the upper sublittoral. The communities of **Blidingia marginata, Blidingia sp. 3** and **Blidingia sp. 4** were found only above the water edge of the supralittoral zone. Communities from this zone were mainly single-species phytocenoses and did not form any transient communities with other species.

Most of the communities dominated by *Fucus vesiculosus* were identified in the sublittoral zone. Only two communities (association **Ulvetum intestinalis** Feldmann 1937 and community **Fucus vesiculosus-Ulva intestinalis var. Elachista fucicola**) were found above and below the mean sea surface level.

The investigated communities show different affinities to exposure (Figure 3). The **Blidingia sp. 4** and **Kornmannia leptoderma** communities were only detected in exposed and semiexposed habitats. Other communities of *Blidingia* spp. developed in habitats with different exposures, including sheltered ones. Decreasing exposure leads to a change of the sublittoral communities in the following order: **Fucus vesiculosus-Elachista fucicola – Fucus vesiculosus-Elachista fucicola var. Ulva linza – Fucus vesiculosus-Ulva intestinalis var. Elachista fucicola – Fucus vesiculosus-Ulva intestinalis** – association (ass.) **Ulvetum intestinalis** Feldmann 1937 – **Fucus vesiculosus-Ulva linza**. Interestingly, *Ulva linza* appears in distinct morphology in different communities. In the variant **Fucus vesiculosus–Elachista fucicola var. Ulva linza**, which is found primarily in open shores and develops in relatively intensive wave conditions, *U. linza* is present in its "*linza*" morphology, exhibiting a sheet-like thallus with undulating margins. In contrast, in the community **Fucus vesiculosus–Ulva linza**, which is found in enclosed waterbodies without surf, *U. linza* exhibits the distinct "*procera*" (or "*ahlneriana*") morphology, which is characterized by a branched tubular thallus. According to *tuf*A marker gene barcoding, these morphotypes are indistinguishable from each other at the genetic level.

The species of the ass. **Ulvetum intestinalis** Feldmann 1937 and of the communities **Fucus vesiculosus–Ulva intestinalis** are mainly cosmopolitan and annual (Figure 4).

Communities dominated by *F. vesiculosus* have a more diverse composition than communities of the supralittoral
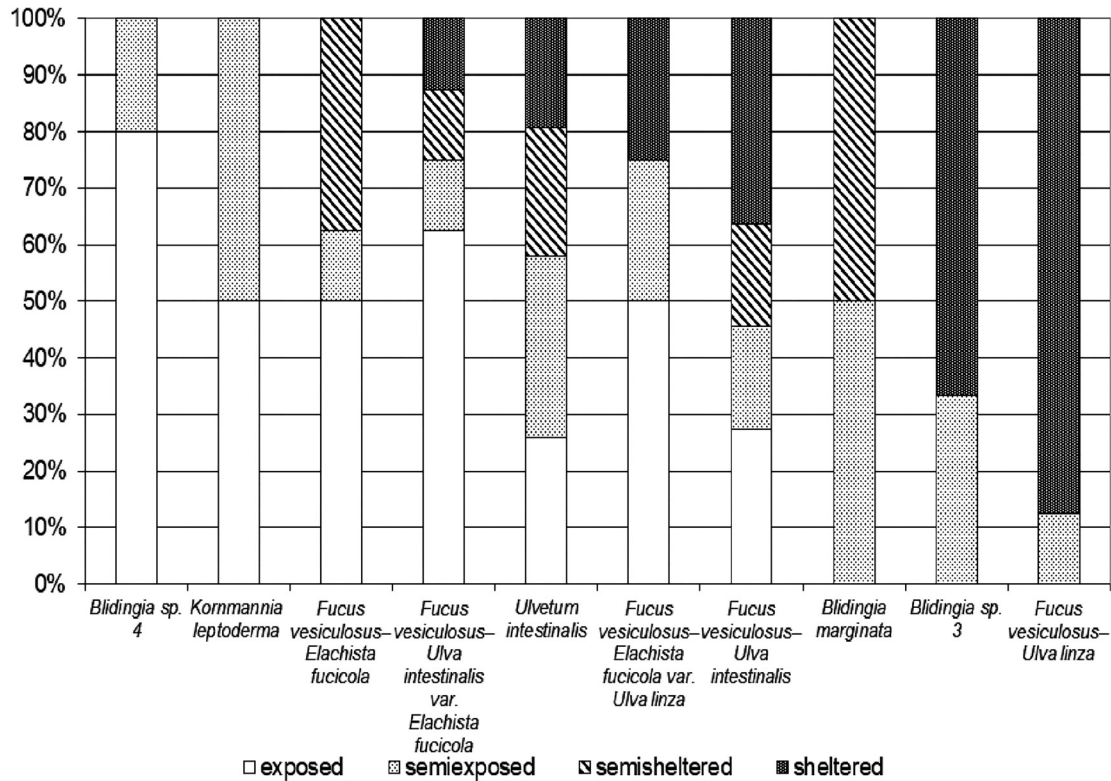
Figure 3: Distribution of the macrophyte communities of the SW Baltic Sea in habitats with different exposure. The *y*-axis shows the proportion of habitats with different exposure grades in which the different communities were found.
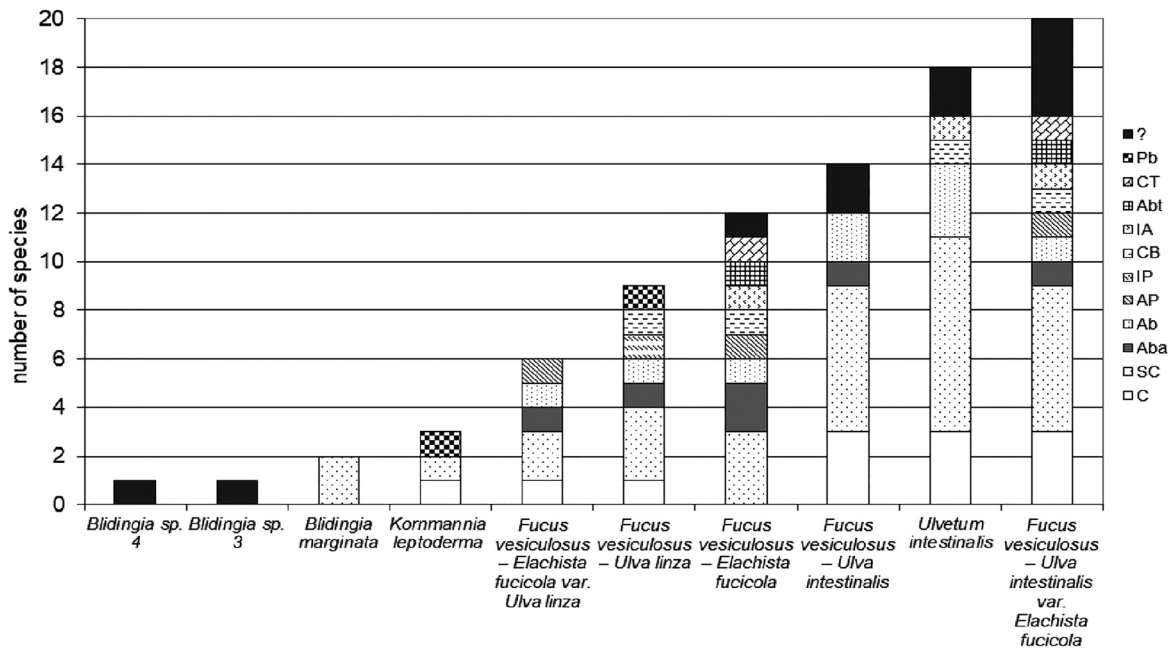

Figure 4: Number of species from different phytogeographical elements in each macrophyte community of the SW Baltic Sea. Phytogeographical elements are indicated in accordance with Cormaci et al. (1982), supplemented by data from Zinova (1962) and Kalugina-Gutnik (1975): C – Cosmopolitan, SC – Sub-cosmopolitan, AP – Atlanto-Pacific, IP – Indo-Pacific, CB – Circumboreal, IA – Indo-Atlantic, Abt – Boreo-tropical Atlantic, CT – Circumtropical, Ab – Boreo-Atlantic, Aba – Boreo-Arctic Atlantic, Pb – Boreo-Pacific.

zone. The community ***Fucus vesiculosus-Ulva intestinalis*** has a similar phytogeographical composition to the phytocenoses of the ass. ***Ulvetum intestinalis*** Feldmann 1937. However, only the community ***Fucus vesiculosus-Elachista fucicola*** has less than 50% of cosmopolitan species. Thus, a relatively small proportion of boreal and boreal-arctic elements, as well as an absence of endemic species, provide evidence of the opportunistic character of the studied phytocenoses.

4 Discussion

Our work is a first approximation to the differentiation of macrophyte communities in the upper sublittoral of the Baltic Sea using the Braun-Blanquet approach. This approach does not involve the study of distinct algal species, but of their communities. In contrast with this approach, official assessments of the marine vegetation status in Germany and many neighboring countries, e.g. for the EU Water Framework Directive and the Marine Strategy Framework Directive, are primarily based on the observation of habitat-forming core indicator species, such as *Fucus* spp., *Chara* spp. or *Zostera* spp. (Selig et al. 2007; Zampoukas et al. 2014) and on the recording of presence or absence of neophyta (Zampoukas et al. 2014). The current methodology has several advantages, such as the availability of historical base line data (Selig et al. 2007) and the possibility of quick and relatively inexpensive implementation. However, it provides limited insight into the consequences of environmental change, as shifts in overall community compositions – for example after the loss of indicator species or after the introduction of new species – are hardly captured. In this respect, the Braun-Blanquet approach could provide a convenient additional tool for assessing the state of coastal vegetation throughout the Baltic.

Overall, the differentiation of syntaxa requires more taxonomic expertise than the observation of a few selected indicator species. Many shallow water habitats in the Baltic Sea are dominated by Ulvales. These are notoriously difficult to distinguish, but the recent and more widespread application of DNA barcoding approaches permits reliable identification. Thus, it is now possible to review formerly designated syntaxa that are dominated by Ulvales. Of the syntaxa revealed here, only one was already described in the syntaxonomic literature as an association: ass. ***Ulvetum intestinalis*** Feldman 1937. This syntaxon is frequently recorded all over the world and found on Atlantic and Mediterranean coasts (Gallardo and Perez-Cirera 1985), the Black Sea (Kalugina-Gutnik 1975), the Caspian Sea (Gromov 2010) and mineralized freshwater

bodies (Hynes 1972). *Ulva intestinalis* is one of the few Ulvales that can be relatively reliably identified based on morphology (Blomster et al. 1998; Steinhagen et al. 2019a). The older findings of ass. ***Ulvetum intestinalis*** Feldman 1937 may therefore be consistent with the current concept.

In contrast, the concept of ass. ***Blidingietum minimae*** den Hartog 1959 possibly requires take account of recently gained taxonomic insights. In addition to *Blidingia marginata,* two other *Blidingia* species were detected in our study that could not be clearly identified at the species level. Based on their tufA sequences, all three *Blidingia* species were clearly distinct from each other and formed clusters with full bootstrap support (Figure 2). While *B. marginata* was unambiguously identified at the species level by alignment with reference sequences, *Blidingia* sp. 3 was clustered with a reference sequence from New Brunswick (HQ610239; Figure 2) that was recently renamed as *Blidingia chadefaudii* (Saunders and Kucera 2010; Steinhagen et al. 2019a). Because molecular data for the type specimen of *B. chadefaudii* are lacking, and because our specimens did not show the characteristic morphological traits of *B. chadefaudii*, we refer to this entity here as *Blidingia* sp. 3 (Figure 2). Specimens of the well-supported cluster representing *Blidingia* sp. 4 were most closely related to a sequence from New Brunswick (HQ610240) identified as *Blidingia minima*. However, a recent epi-typification of *B. minima* showed that it is genetically distinct from *B. minima* (Steinhagen et al. 2021), so we refer to this cluster as *Blidingia* sp. 4 (Figure 2). Further studies would be required to determine the species affiliation of *Blidingia* sp. 3 and *Blidingia* sp. 4. However, this was not the aim of the present study. Given their large number, we were unable to obtain DNA barcodes for all *Blidingia* individuals in all plots, but found no evidence of co-occurrence of multiple *Blidingia* species in the same plot. Thus, all three species apparently form separate supralittoral communities. *Blidingia* sp. 4 appeared to be more confined to wave exposed environments, but the exact environmental factors determining the habitat preference of *Blidingia* species in our area remain to be identified. Up to now, communities of only two *Blidingia* species have been described in Europe – ass. ***Blidingietum minimae*** den Hartog 1959 and the community of ***Blidingia marginata*** (Gallardo and Perez-Cirera 1985). According to the molecular data presented here and elsewhere (Steinhagen et al. 2021), European communities of many different *Blidingia* species were probably combined under the name ass. ***Blidingietum minimae*** den Hartog 1959.

In our study (conducted in 2013), phytocenoses of *Kornmannia leptoderma* were encountered rarely in a restricted area near Wismar and Poel. However, the species

seems to be more frequent in the Western Baltic. *Kornmannia leptoderma* is a circumarctic boreal green macroalga and its range has recently expanded into the Baltic Sea along a 220 km long section of the German Coast, which was apparently facilitated by adaptation to higher water temperatures (Weinberger et al. 2018).

The average number of species in *F. vesiculosus*-dominated communities varied from 3.5 to 6.6, which classifies them as one of the most diverse phytocenoses of the investigated area and supports the use of *F. vesiculosus* as an indicator of biodiversity (Selig et al. 2007; Zampoukas et al. 2014). Our data on the average number of species in *F. vesiculosus* community samples are in good agreement with the data obtained from the southeastern Baltic coast of Sweden, where the average number of species varies from 5.1 to 7.4 (Wikström and Kautsky 2007). However, considerably higher numbers of up to 16–19 species were observed in association with fucoids in an area of 0.25 m^2 on the German North Sea island Helgoland (Kuhlenkamp et al. 2020), reflecting the generally higher macroalgal diversity in this non-brackish environment (Weinberger et al. 2020). In the Arctic White and Barents Seas, however, communities that are dominated by *F. vesiculosus* are characterized by floristic poverty; the average number of species there varies from 1.0 (the White Sea) to 1.9–3.8 (Barents Sea) (Abdullin et al. 2007; Golub et al. 2003).

According to the EuroVegChecklist scheme (Mucina et al. 2016), all the *Fucus vesiculosus*-dominated communities described in this paper can be tentatively assigned to the class (cl.) **Entophysalidetea deustae** Giaccone in Bültmann et al. 2015 (photophytic marine macro- and microalgal communities on hard substrata in the supra- and eulittoral zones of seashores) and the order (ord.) **Fucetalia vesiculosi** Julve in Bültmann et al. 2015 (photophytic marine macroalgal communities on hard substrata in the eulittoral zone of the Atlantic Ocean), although the eponymous species inhabits the upper sublittoral in the Baltic Sea. There are two alliances (all.) of such vegetation: communities in the upper eulittoral zone are combined into the all. **Ascophyllion nodosi** Julve in Bültmann et al. 2015 and those in the lower eulittoral zone into the all. **Fucion serrati** Julve et Manneville 2006. However, given the absence of tides and a true eulittoral in our study area, a distinction between upper and lower eulittoral seems impossible. We assume that *Fucus vesiculosus*-dominated communities in our study area can be preliminarily placed in the all. **Ascophyllion nodosi** Julve in Bültmann et al. 2015 because *Fucus vesiculosus* is indicated as a characteristic species of this particular alliance (Bültmann et al. 2015) and despite the fact that the eponymous species *Ascophyllum nodosum* is absent from the study area. The

ass. **Fucetum vesiculosi** Golub, Sokolov, Sorokin 2003 described from the White Sea was also placed in this alliance. Future research in other parts of the Baltic may reveal whether it is necessary to describe a new alliance of *Fucus vesiculosus*-dominated vegetation for the Baltic Sea.

Communities of *Blidingia* species, as well as phytocenoses of *Kornmannia leptoderma*, obviously also belong to the cl. **Entophysalidetea deustae**. Provisionally, we placed them in the ord. **Fucetalia vesiculosi** Julve in Bültmann et al. 2015, but refrained from the definition of the appropriate alliance.

According to the EuroVegChecklist (Mucina et al. 2016), ass. **Ulvetum intestinalis** Feldmann 1937 should be placed in the cl. **Cystoseiretea** Giaccone 1965 (photophytic marine macroalgal communities on hard substrata in the infralittoral and circalittoral zones of Atlantic and Mediterranean seashores), in the ord. **Ulvetalia lactucae** Molinier 1960 (photophytic marine macroalgal communities on nutrient enriched hard substrata in the [eu-] infralittoral and circalittoral zones along the Mediterranean Sea and Atlantic Ocean shores) and in the all. **Ulvion rigidae** Berner 1931 *corr.* Giaccone et al. 1994 (photophytic marine macroalgal communities on nutrient enriched, sheltered hard substrata of the lower eulittoral zone of the shores of the Mediterranean Sea and the Atlantic Ocean).

5 Conclusions

The syntaxonomic composition of the vegetation of the supralittoral and upper sublittoral zones of the SW Baltic Sea includes both phytocenoses with dominant green algae (ass. **Ulvetum intestinalis** Feldmann 1937, communities of **Blidingia marginata, Kornmannia leptoderma** and unidentified *Blidingia* species) and some communities with dominant *Fucus vesiculosus*. In the latter formation we found mainly zonal boreal Atlantic and cosmopolitan species.

Most of the shallow water associations and communities encountered in our study area corresponded with syntaxa that have been described earlier, although many of them were rich in Ulvales. Thus, the relatively high risk of misidentification of Ulvales species is seemingly not reflected in a similarly high risk of misidentification of syntaxa. One exception is **Blidingietum minimae** den Hartog 1959, which appears to be a cluster of multiple distinct communities that are adapted to similar, but still different, environments. Another possible exception could be past Baltic Sea records of **Ulvetum compressae** (Berner 1931) Giaccone 1993, given that *U. compressa* virtually

never exhibits its type morphology in the Baltic Sea (Steinhagen et al. 2019b). We did not encounter ***Ulvetum compressae*** (Berner 1931) Giaccone 1993.

Higher syntaxa described for Atlantic coasts could still be identified in our study area, despite relatively divergent salinity and tidal conditions, and lower species richness. Such homologisation with Atlantic syntaxa may possibly become more challenging in the inner Baltic Sea given its even lower salinity. Nonetheless, the Braun-Blanquet approach may become a convenient tool to universalize phytobenthos monitoring research throughout the Baltic and to complement other approaches. The establishment of such a tool would require more studies along the salinity gradient in order to facilitate comparisons between study areas and to potentially identify brackish water-specific higher order syntaxa that may be present in the Baltic Sea.

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