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Relationship between *Fucus* coverage and algal diversity in the northern Baltic Sea

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ABSTRACT

The canopy-forming brown macroalgae *Fucus vesiculosus* and *Fucus radicans* (*Fucus*) are the largest habitat-building species on rocky shores of the northern Baltic Sea. While their role on the diversity of invertebrate fauna is well documented, there is little information on their importance for the diversity of associated macroalgal species. We used comprehensive mapping data from the Finnish marine area (divided into four sea areas) to test the relationship between *Fucus* coverage and algal biodiversity (number of taxonomic units, Shannon-Wiener diversity index H' and Pielou's evenness J'). To account for environmental variation, depth, wave exposure, Secchi depth and salinity were included as covariates. Examination of the algal communities highlighted a similar pool of taxonomic units across sea areas in shallow (0–4 m) rocky shores, with the two filamentous algal species *Pylaiella littoralis* and *Ectocarpus siliculosus* combined as one unit being the most common taxon. The Shannon-Wiener diversity index was highest in sites with *Fucus* coverage between 25% and 75%, while evenness increased with *Fucus* coverage. We did not detect any effects of *Fucus* coverage on the number of taxonomic units, which was rather affected by environmental parameters (depth, Secchi depth and salinity). The results show that *Fucus*, depending on its coverage, both competes with and facilitates the macroalgal community. Based on extensive data, we show how *Fucus* coverage relates to the diversity of the surrounding algal communities, further improving our understanding of factors that control biodiversity on shallow rocky shores in the northern Baltic Sea.

1. Introduction

Canopy-forming macroalgae, such as kelps and fucoids, are important foundation species in coastal marine areas as they create unique and complex habitats on rocky substrates (Hughes, 2010; Thomsen and South, 2019; Lamy et al., 2020) and increase biodiversity (Christie et al., 2009). Despite their positive effects on consumer biodiversity (Wikström and Kautsky, 2007), these canopy-forming species can also limit the settlement of other algal species through effects of shadowing and reduced light (Arenas et al., 2006) or by the so-called whiplash effect where thallus movements mechanically remove other species (Kiirikki, 1996a). Experimental manipulations of canopy-forming fucoid coverage have demonstrated their importance on the diversity of benthic fauna and algal species, with reductions causing decreased species richness (Pocklington et al., 2018) or promoting more unstable and less diverse algal communities (Schiel and Lilley, 2007). However, it has been shown that the habitat created by canopy-forming fucoids can be lost, with no other similar species compensating for it (Thomsen et al., 2021).

Understanding the role of fucoids in supporting biodiversity has become increasingly valuable, as coastal ecosystems today face many anthropogenic pressures (Crossland and Kremer, 2001; HELCOM, 2018) that also threaten canopy-forming algae (Moy and Christie, 2012; Jonsson et al., 2018).

The main canopy-forming macroalgae in the northern Baltic Sea are *Fucus vesiculosus* and *F. radicans*, which share many morphological traits, and thus offer comparable roles in the ecosystem (Råberg and Kautsky, 2007). Both species occur in the Bothnian Sea and the Kvarken area, although *F. radicans* is more abundant further north (Bergström et al., 2005; Johannesson et al., 2011; Rinne et al., 2018). Only *F. vesiculosus* has been observed along the southern parts of the Finnish coastline (Rinne et al., 2018, but see Ardehed et al., 2016 for unassigned *Fucus* populations in the Gulf of Finland). The upper limit of the *Fucus*-belts is affected by ice scraping in winter (Kiirikki and Ruuskanen, 1996), and consequently, fast-growing opportunistic filamentous green and brown algae typically occupy rocky substrates near the surface. The depth of the *Fucus*-belt varies between areas, but generally reaches 1–6 m depths

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(Snickars et al., 2014; Rinne and Salovius-Laurén, 2020).

In the non-tidal brackish-water Baltic Sea, the macroalgal diversity decreases northwards towards lower salinities (Schubert et al., 2011). Thus, the northern Baltic Sea hosts a distinct algal community with a low number of species (Nielsen et al., 1995), often approximately ten algal species per site (Schubert et al., 2011). On a local scale, macroalgal species coverage and vertical range are affected by wave exposure and Secchi depth (Kautsky and Kautsky, 1989; Eriksson and Bergström, 2005; Krause-Jensen et al., 2009).

Fucus vesiculosus has been studied extensively in the Baltic Sea, especially after its disappearance from many areas in the late 1970's (Kangas et al., 1982; Rönneberg et al., 1985; Kautsky et al., 1986). Eutrophication is considered to be the main reason for this decline, as high sedimentation and water turbidity have rendered some coastal areas unsuitable for *F. vesiculosus* (Kautsky et al., 1986; Rinne et al., 2011). Due to the decreased depth distribution (Törn et al., 2006; Rinne and Salovius-Laurén, 2020), the potential areas for *Fucus* growth have decreased markedly (Lappalainen et al., 2019). The increase in filamentous algae with proceeding eutrophication has also been a critical factor worsening the conditions for *F. vesiculosus* reproduction, growth and survival (Berger et al., 2003). Further, high densities of the isopod

grazer *Idotea balthica* may have contributed to the loss of *F. vesiculosus* (Kangas et al., 1982; Engkvist et al., 2000). In this generally low diversity system, the loss of a foundation species such as *Fucus* spp. could result in the loss of the habitat its structure creates.

The consequences of the disappearance of *F. vesiculosus* on faunal communities have been studied to some extent (Kraufvelin and Salovius, 2004; Wikström and Kautsky, 2007) but have still to be explored for algal communities. In addition, these studies have taken a binary presence or absence approach, comparing sites with or completely without *Fucus*. Studies focusing on macroalgal diversity within *F. vesiculosus* belts, and the possible effects of fine-scale variation in *F. vesiculosus* coverage, are lacking.

In this study, we aim to test the impact of the foundation species *F. vesiculosus* and *F. radicans* (hereafter *Fucus*) on the macroalgal diversity. We use algal species inventory data to test the relationship between *Fucus* coverage and algal species diversity in the northern Baltic Sea. The data encompasses the Bothnian Sea, Åland, the Southwest Archipelago and the Gulf of Finland. As spatial and temporal variation of the environment affects algal communities, environmental parameters are included as covariates in our models. The results will add to the knowledge of the role of *Fucus* as a foundation species for associated

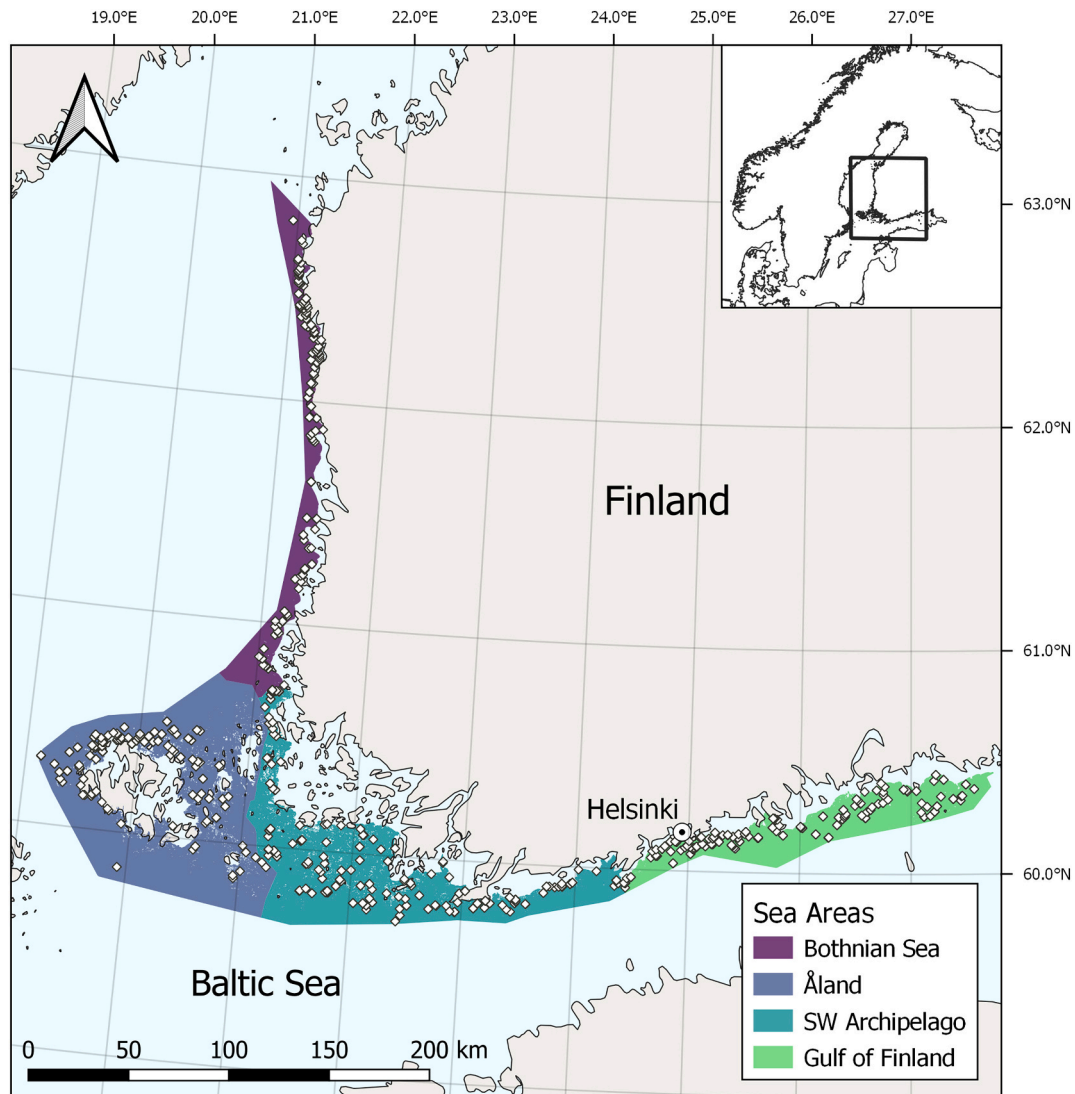


Fig. 1. Geographic extent of the study area in the northern Baltic Sea, distribution of the study points and division into the four sea areas (Bothnian Sea, Åland, Southwest Archipelago and Gulf of Finland).

algal biodiversity in the northern Baltic Sea. They will also provide new knowledge about algal diversity and distribution patterns on a large geographic scale in the northern Baltic Sea.

2. Materials and methods

2.1. Study area

The data were collected within the Finnish marine sea area in the northern Baltic Sea (Fig. 1). The coastline is scattered with numerous islands and larger archipelago areas, creating a buffer between the fluvial discharge from the coast and the open sea. This also gives rise to several environmental gradients such as wave exposure, salinity, nutrients and Secchi depth (water clarity). All of these decrease towards the mainland, except for nutrient-related parameters, which are generally highest near the mainland and decrease further out at sea.

Because *Fucus* occurs much more frequently in the outer than inner sea areas (Rinne and Salovius-Laurén, 2020), we focused the study only on the outer archipelago areas. The division into inner and outer archipelago was based on work related to the Water Framework Directive in Finland (Rantajärvi et al., 2020). We divided the study area into four sea areas: the Bothnian Sea, Åland, Southwest (hereafter SW) Archipelago and the Gulf of Finland, as these areas were significantly different from each other regarding exposure, Secchi depth and salinity (see Table A for the detailed non-parametric tests between sea areas). The Bothnian Sea had more exposed sites, while the SW Archipelago had the most sheltered ones, with Åland and the Gulf of Finland featuring intermediate exposure values. The Secchi depth was highest in Åland and lowest in the Gulf of Finland. Lastly, the salinity was highest in the SW Archipelago and lowest in the Gulf of Finland.

2.2. Algal data

In the Bothnian Sea, the SW Archipelago and the Gulf of Finland, the algal species data were collected within the national Finnish Inventory Programme for Underwater Marine Diversity (VELMU) in 2004–2019. The data from Åland were obtained during various mapping projects at Husö Biological Station, Åbo Akademi University, between 2004 and 2019 (e.g. Kiviluoto, 2013; Engström, 2018; Rinne et al., 2019; Valkonen, 2020). Data were gathered from dive transects. The 100-m long dive transects started from the shore and continued outwards perpendicular to the shoreline (Anonymous, 2015). The observations (hereafter “study points”) were spaced with either 10-m horizontal intervals or 1-m vertical intervals when the transects were steeper. This made it possible to compare communities from similar depths that would have been missed if only considering horizontal distance. Each study point consisted of observations of the substrate type and the coverage of each macroalgal taxonomic unit species recorded on a continuous scale (0% to 100%) over an area of 4-m², in Åland 2-m². To test if this difference between Åland and other areas affected the detection of algal taxonomic units, rarefaction curves were drawn for each sea area using the Rarefy R package (Thouverai et al., 2021). No clear difference was observed between the four sea areas (see Fig. A), suggesting that the smaller sampling area in Åland did not affect the sampling effort required to detect rare algal taxonomic units compared to the other three sea areas. In further analyses, only study points with at least 1% coverage of *Fucus* were used. Due to the differences in environmental conditions between the sea areas (see Table A), the models only compared data within each sea area.

As *Fucus* requires hard substrates to settle, we focused our study on rocky shores, and only study points with over 75% hard substrate were included. Hard substrates consisted of bedrock to smaller stones (>6 cm), following the 11-level substrate classification used in VELMU, modified from Wentworth (1922). Only the study points between 0-m and 4-m depth were used, as this is the depth interval where *Fucus* is most frequent across the study area. Although *Fucus* has been reported

deeper in the northern Baltic Sea (Torn et al., 2006; Snickars et al., 2014; Rinne and Salovius-Laurén, 2020), the recordings are relatively sparse, and both coverage and prevalence values drop in deeper waters.

Due to seasonal variation in the occurrence of annual algal species (Kiirikki and Lehvo, 1997), we only used data collected during July and August to make data comparable. After data filtering, the final dataset featured 1578 study points belonging to 531 transects (see Table 1 for division of study points/sea area).

2.3. Environmental data

Modelled environmental data were used to account for environmental variation between the study points. The exposure values for each study point were obtained from the Simplified Wave Exposure Model (Isaeus, 2004), hereafter SWM, calculated for the Finnish marine area with a resolution of 25-m and log-transformed. The SWM used a combination of a biological index in vertical lichen zonation, a fetch model and wind data (Isaeus, 2004). Secchi depth values were obtained from models covering the Finnish marine area based on data from MERIS satellites (average values for June–August 2003–2011), with a resolution of 300-m (Virtanen et al., 2018; Lappalainen et al., 2019). Surface salinity was modelled (to 20-m resolution) based on water quality measurements from June–August 2004–2015, accounting for the average flow rates of the 52 largest rivers (Lappalainen et al., 2019). Depth was measured on site, and the values were corrected to the water level of the sampling period. The number of study points, *Fucus* coverage and environmental variation within and between the sea areas are presented in Table 1.

2.4. Taxonomic rank of the algal data used in the analyses

In the large dataset, some algae were only reported at the genus level, or in some cases as groups that shared morphological similarities. Such study points could have biased species richness values. Furthermore, some taxonomic units were reported more frequently as genus, while others were mainly recorded as species. All observations of filamentous brown algae *Pylaiella littoralis* and *Ectocarpus siliculosus* were merged, as they are challenging to differentiate and were frequently reported as a single group by divers. Although the filamentous red alga *Rhodochorton* sp. and crustose red alga *Hildenbrandia* sp. were sometimes reported at the genus level, there is only one marine species belonging to each genus that has been observed in Finland, *Rhodochorton purpureum* and *Hildenbrandia rubra* respectively (FinBIF, 2022), thus the species level was used. For some taxonomic units, both species-level (e.g.

Table 1

Total number of study points (and number per depth intervals), mean and variation in *Fucus* coverage % and environmental parameters (Log exposure, Secchi depth, depth and salinity) in the four sea areas, mean (SD). Min-max values are also presented for log exposure, Secchi depth and salinity.

	Bothnian Sea	Åland	SW Archipelago	Gulf of Finland
Number of study points	407	378	399	394
(0-1 m/1-2 m/2-3 m/3-4 m)	(54/110/126/117)	(117/120/74/64)	(170/126/59/44)	(84/117/97/96)
<i>Fucus</i> coverage %	30.9 (27.4)	42.5 (32.9)	33.3 (29.4)	30.8 (27.5)
Log Exposure	13.1 (0.7), 10.0–13.8	11.7 (1.2), 8.3–13.3	10.6 (1.5), 5.8–13.6	12.0 (0.8), 8.3–13.4
Secchi depth (m)	3.9 (0.6), 2.3–5.0	5.4 (0.4), 4.5–6.6	4.4 (0.5), 2.6–5.5	3.0 (0.3), 2.0–3.7
Depth (m)	2.2 (1.1), 5.2 (0.2), 4.5–5.7	1.7 (1.1), 5.6 (0.2), 5.4–6.1	1.3 (0.9), 5.8 (0.2), 4.9–6.2	2.0 (1.1), 4.6 (0.5), 2.9–5.4
Salinity				

Table 2

Prevalence (% of all study points) of the algal taxonomic units in the four sea areas. Taxonomic units at the genus level (e.g. *Ceramium* spp.) were not counted in the total number of taxonomic units if data at the species level was available.

Algal taxonomic units used in the analysis	Prevalence (% of all study points)			
	Bothnian Sea	Åland	SW Archipelago	Gulf of Finland
Rhodophyceae				
<i>Aglaothamnion roseum</i> (Roth) Maggs & L'Hardy-Halos	0.2	0	0	0
<i>Ceramium</i> spp. Roth	6.6	0	0	0.3
<i>Ceramium tenuicorne</i> (Kützting) Waern	28.3	30.2	34.1	55.6
<i>Ceramium virgatum</i> Roth	0	0.3	0	0.3
<i>Coccolytus truncatus</i> (Pallas) Wynne & Heine / <i>Phyllophora pseudoceranoides</i> (Gmelin) Newroth & Taylor ex Dixon & Irvine	1.7	3.4	1.0	3.6
<i>Furcellaria lumbricalis</i> (Hudson) Lamouroux	48.9	15.6	19.3	11.7
<i>Grania efflorescens</i> (Agardh) Kylin	0.2	0	0	0
<i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini	36.4	32.8	39.6	42.4
<i>Polysiphonia</i> spp. Greville	11.1	0.3	2.3	0.3
<i>Leptosiphonia fibrillosa</i> (Agardh) Savoie & Saunders	3.9	2.4	2.3	3.3
<i>Vertebrata fucoides</i> (Hudson) Kuntze	29.2	1.3	4.0	3.6
<i>Rhodochorton purpureum</i> (Lightfoot) Rosenvinge	17.2	5.0	0.8	2.8
<i>Rhodomela confervoides</i> (Hudson) Silva	0.2	0	0.5	0.5
Chlorophyceae				
<i>Acrosiphonia arcta</i> (Dillwyn) Gain	0.7	0.3	0.5	0
<i>Aegagropila linnaei</i> Kützting	0	2.1	0.3	18.5
<i>Cladophora</i> spp. Kützting	2.0	0	1.8	1.5
<i>Cladophora fracta</i> (Müller ex Vahl) Kützting	0.5	0	2.8	1.0
<i>Cladophora glomerata</i> (Linnaeus)	53.3	45.8	45.1	65.2
<i>Cladophora rupestris</i> (Linnaeus) Kützting	28.5	25.4	9.5	38.1
<i>Monostroma</i> spp. Thuret	0	0	0.5	0
<i>Monostroma balticum</i> Wittrock	0	0	0.3	0
<i>Monostroma grevillei</i> (Thuret) Wittrock	0	0	0.3	0
<i>Mougeotia</i> spp. Agardh	0	0	0	0.3
<i>Spirogyra</i> spp. Link	1.7	0.5	14.3	0.8
<i>Spongomorpha aeruginosa</i> (Linnaeus) Hoek	0	7.1	0	0.5
<i>Ulothrix zonata</i> (Weber & Mohr) Kützting	0	0	0.3	0
<i>Ulva</i> spp. Linnaeus	5.2	4.5	15.8	23.6
<i>Ulva intestinalis</i> Linnaeus	1.5	9.8	4.3	0.3
<i>Ulva prolifera</i> Müller	0	0.5	0	0
<i>Zygnema</i> spp. Agardh	0	0	0	0.3
Phaeophyceae				
<i>Chorda filum</i> (Linnaeus) Stackhouse	16.7	18.5	33.6	21.3
<i>Dictyosiphon foeniculaceus</i> (Hudson) Greville / <i>Stictyosiphon tortilis</i> (Gobi) Reinke	10.6	4.5	5.3	6.3
<i>Dictyosiphon</i> spp. Greville	0.2	1.3	1.8	0
<i>Dictyosiphon chordaria</i> Areschoug	0	5.3	1.0	0
<i>Dictyosiphon foeniculaceus</i> (Hudson) Greville	16.7	12.4	26.1	16.2
<i>Ectocarpus confervoides</i> Harvey	0	2.1	0	0.3
<i>Elachista fucicola</i> (Vellay) Areschoug	13.5	7.7	8.5	14.7
<i>Eudesme virescens</i> (Carmichael ex Berkeley) Agardh	2.2	7.4	3.8	1.5
<i>Halosiphon tomentosus</i> (Lyngbye) Jaasund	3.2	0	0	0
<i>Lithoderma</i> spp. Areschoug	0.2	0.3	0	1.3
<i>Pseudolithoderma</i> spp. Svedelius	8.4	0.5	5.5	16.8
<i>Pylaiella littoralis</i> (Linnaeus) Kjellman / <i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye	89.9	69.0	64.9	81.0
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	0	0	1.3	0
<i>Sphacelaria</i> spp. Lyngbye	2.2	0	0	0
<i>Battersia arctica</i> (Harvey) Draisma, Prud'homme & Kawai	11.1	0.8	0.8	5.3
<i>Protohalopteris radicans</i> Draisma, Prud'homme & Kawai	0	0.5	0	0
<i>Stictyosiphon tortilis</i> (Gobi) Reinke	1.0	7.7	1.8	6.1
Total number of taxonomic units	26	28	29	28
Number of taxonomic units per study point mean (SD), min-max	4.6 (2.1), 0–10	3.3 (1.7), 0–9	3.6 (2.0), 0–11	4.5(2.1), 0–11

Ceramium tenuicorne) and genus-level (e.g. *Ceramium* spp.) data were recorded in the same sea area (e.g. the Bothnian Sea). However, most of the study points featured only one species per study point when the species level of precision was available (see Table B). Therefore, all cases with genus level data at a study point were counted as only one taxon. Although this leads to a slight underestimation of diversity metrics, the proportion of study points possibly affected remained small (3.2% at most, except for *Cladophora* spp. and *Polysiphonia* spp.) in relation to the size of the overall dataset (see Table B for percentages of data affected).

The final list of taxonomic units and their prevalence in each sea area is presented in Table 2.

2.5. Data analysis

To estimate the diversity of the algal community among *Fucus*-belts, the number of taxonomic units, the Shannon-Wiener Diversity index (H') and Pielou's evenness (J') were calculated for each study point. As the aim was to investigate the algal diversity associated with the foundation

species, *Fucus* was excluded from the diversity metrics in the analyses. As the algae may occur as “layers” (with epiphytes or canopy-forming algae and algae growing under them), the total coverage could exceed 100%. For this reason, relative coverage was calculated based on the total summed coverage of all taxonomic units instead of using the raw field coverage values. The Shannon-Wiener Diversity index was calculated using the relative coverage of each taxonomic unit (Rad et al., 2009; Vahdati et al., 2017).

Several data points used were recorded along the same transects. As the benefits of using all the data points along transects when analysing phytobenthic data have been shown to be higher than the negative effects of potential autocorrelation (Sandman et al., 2008), all study points meeting our selection criteria along the dive transects were used. To avoid overestimating the effects of *Fucus* coverage and environmental covariates, we used mixed models with transects included as a random factor.

Poisson regression was applied to test the relationship between *Fucus* coverage and the number of algal taxonomic units, using the generalized mixed-effect models function in R (Bates et al., 2015). The goodness of fit was estimated with the conditional R² using the trigamma estimate (Barton, 2020) (Table 3). The relationship between *Fucus* coverage and both the Shannon-Wiener diversity index and Pielou’s evenness were analysed using mixed-effect models in R (Bates et al., 2015).

To account for the possibility of the relationship being non-linear, linear models were compared to non-linear models featuring an additional term of squared *Fucus* coverage.

As environmental factors may explain some of the variation between study points, exposure, Secchi depth and depth were included as covariates. Salinity was a fourth covariate in the Gulf of Finland, as it was the only area where salinity varied to some extent (Table 1). The variance inflation factor (VIF) was used to diagnose potential collinearity. In all four study areas (Åland, Gulf of Finland, Bothnian Sea and SW Archipelago), the VIF values of the environmental covariates were under 5, meaning that no collinearity occurred, and thus, all environmental covariates could be kept in the models if significant. Models with and without these covariates were compared with F tests. When the F-test was not significant, the most parsimonious model was kept. Because the covariates included were on different measurement scales, either PSU, log exposure or meters (Table 1), the standardized beta coefficients were calculated. Standardized beta coefficients β* were calculated using the following method (1), with β the unstandardized coefficient, s_y the standard deviation of the dependent variable and s_x the standard deviation of the independent variable (Menard, 2004). This allowed us to compare the relative strength of the effects of *Fucus* coverage and the environmental covariates on the diversity metrics on the same scale.

$$\beta^* = \beta * (s_x / s_y) \tag{1}$$

Table 3

Generalized linear models on the effects of *Fucus* coverage, *Fucus* coverage squared (*Fucus* cov.²) and environmental covariates (depth, Secchi depth, exposure and salinity) on the number of algal taxonomic units per study point. Only environmental variables with significant effects on the model are presented in the table. Salinity was included in the model only in GoF.

Sea area	Independent variables	p value	Standardized beta coefficients	Conditional R ²
Bothnian Sea	<i>Fucus</i> coverage	0.119	0.061	0.293
	<i>Fucus</i> cov. ²	0.114	−0.044	
	Depth	<0.001 ***	0.134	
Åland	<i>Fucus</i> coverage	0.339	−0.037	0.274
	Depth	0.034 *	0.076	
SW Archipelago	<i>Fucus</i> coverage	0.878	0.005	0.301
	Secchi depth	<0.001 ***	0.166	
Gulf of Finland	<i>Fucus</i> coverage	0.492	0.020	0.231
	Depth	0.004 **	0.079	
	Salinity	<0.001 ***	−0.131	

2.6. Algal taxonomic units per sea area and depth

The taxonomic composition of *Fucus*-belts was described with each different sea area divided into four depth ranges (0–1-m, 1–2-m, 2–3-m and 3–4-m). The percentage of study points where each algal taxonomic unit occurred was calculated for each subset to determine their prevalence among *Fucus*-belts. The average coverage and standard deviation of the five most common taxonomic units in each subset were also calculated.

3. Results

3.1. Number of algal taxonomic units within *Fucus*-belts

The total number of algal taxonomic units within the *Fucus*-belts per study point was similar across the four sea areas. The number of taxonomic units per study point was on average higher in the Bothnian Sea and the Gulf of Finland (4.6 and 4.4) than in Åland and the SW Archipelago (3.3 and 3.6) (Table 2).

The algal taxonomic units were generally the same within *Fucus*-belts (0–4-m depths) across the study area. Of all the 39 taxonomic units (ignoring taxonomic units at the spp. level when data at the species level was available), 28 were recorded in at least two of four study areas, with 19 recorded in all four study areas (Table 2). The area with the highest number of unique species was the SW Archipelago, with four species (*Monostroma grevillei*, *M. balticum*, *Ulothrix zonata* and *Scytosiphon lomentaria*) not reported in any other area. No relationship was detected between the coverage of *Fucus* and the total number of algal taxonomic units (Table 3). Instead, environmental covariates had significant effects. The algal richness increased with depth in the Bothnian Sea, Åland and the Gulf of Finland. In the Gulf of Finland, the number of algal taxonomic units decreased with increased salinity. This decrease did not correspond to the loss of any specific algal taxonomic unit or group. The number of taxonomic units in the SW Archipelago increased with Secchi depth. The standardized beta coefficients show that while the results were significant, the effects of the different environmental variables on the number of algal taxonomic units were low.

Table 4

Comparison between linear and quadratic models for the Shannon-Wiener diversity index (H') in relation to *Fucus* coverage.

Sea area	p value (F test)	AIC	
		Linear	Quadratic
Bothnian Sea	0.002 **	414.9	406.9
Åland	0.005 **	305.5	299.6
SW Archipelago	0.323	312.2	313.2
Gulf of Finland	0.009 **	377.1	372.4

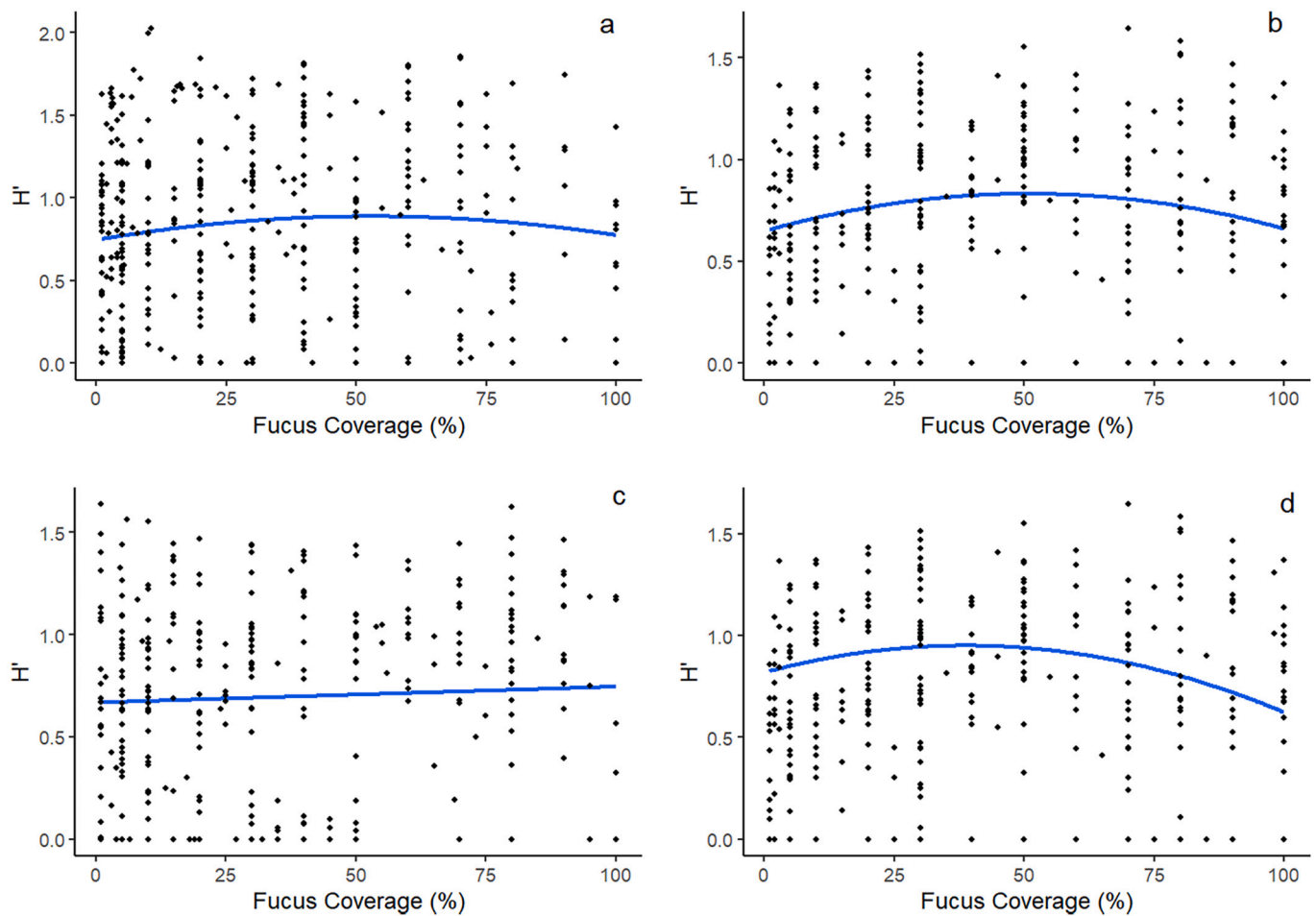


Fig. 2. Modelled (LMM) relation between the Shannon-Wiener diversity index (H') and *Fucus* coverage in the Bothnian Sea (a), Åland (b), and the Gulf of Finland (d). The SW Archipelago (c) is a linear relation, as F-tests showed that a linear model was the best fit, while a non-linear model was a better fit for the other three areas. The curves are model predictions, with the environmental variables included in the model kept constant at their mean.

Table 5

Linear mixed models showing the effects of *Fucus* coverage and environmental covariates (depth, Secchi depth, exposure and salinity) on the Shannon-Wiener diversity index (H') of the algal communities. Only environmental variables with significant effects on the model are presented in the table.

Sea area	Independent variables	p value	Standardized beta coefficients	Conditional R ²
Bothnian Sea	<i>Fucus</i> coverage	0.0214 *	0.291	0.641
	<i>Fucus</i> cov. ²	0.0416 *	-0.247	
	Depth	<0.001 ***	0.249	
Åland	<i>Fucus</i> coverage	0.005 **	0.534	0.418
	<i>Fucus</i> cov. ²	0.005 **	-0.528	
SW Archipelago	<i>Fucus</i> coverage	0.380	0.041	0.627
	Secchi depth	<0.001 ***	0.240	
Gulf of Finland	<i>Fucus</i> coverage	0.010 *	0.408	0.484
	<i>Fucus</i> cov. ²	0.003 **	-0.466	
	Depth	<0.001 ***	0.172	
	Salinity	<0.001 ***	-0.293	

Shannon-Wiener diversity (H') of macroalgae among *Fucus*-belts.

In Åland, the Bothnian Sea and the Gulf of Finland, F tests confirmed that adding of a quadratic term for *Fucus* coverage improved the models testing the relationship between *Fucus* coverage, environmental covariates and the Shannon-Wiener diversity (H') (Table 4). In the SW Archipelago, this addition did not significantly improve the model, so the original linear equation was kept (Fig. 2).

In all areas where the quadratic model was an improvement over the linear model, a significant relationship between *Fucus* coverage and the diversity index was detected (Table 5). In the SW Archipelago, no

significant impact of *Fucus* coverage on taxonomic diversity was observed. In the areas where *Fucus* coverage correlated with diversity, the coefficient of the quadratic term was negative (Table 5), indicating a convex relationship. The resulting curves showed that the diversity was at its highest between 25% and 75% coverage and decreased towards either low or high coverage values (Fig. 2). The variability of the values of H' was mainly due to differences between transects rather than within each transects. Including this parameter as a random factor in the linear mixed models helped remove some of this variability, explaining the comparatively high conditional R² (Table 5).

Table 6

Linear mixed models on the effects of *Fucus* coverage, *Fucus* coverage squared (*Fucus cov.*²) and environmental covariates (depth, Secchi depth, exposure and salinity) on Pielou's evenness (*J'*) of the algal communities. Only environmental variables with significant effects on the model are presented in the table.

Sea area	Independent variables	p value	Standardized beta coefficients	Conditional R ²
Bothnian Sea	<i>Fucus</i> coverage	0.585	-0.028	0.552
	Depth	0.015 *	0.115	
Åland	<i>Fucus</i> coverage	0.003 **	0.186	0.214
	Depth	0.012 *	-0.155	
SW Archipelago	<i>Fucus</i> coverage	0.039 *	0.121	0.370
Gulf of Finland	<i>Fucus</i> coverage	0.010 *	0.474	0.334
	<i>Fucus cov.</i> ²	0.003 **	-0.506	
	Salinity	<0.001 ***	-0.166	

The significance of environmental covariates on the Shannon diversity index (*H'*) followed similar patterns as the ones observed in relation to the number of taxonomic units (compare Table 3 and Table 5). The only difference was the lack of significance for depth as covariate in Åland (Table 5). *Fucus* coverage showed a comparable standardized beta coefficient to depth in the Bothnian Sea and was the only significant factor for *H'* in Åland. In the Gulf of Finland, *Fucus* coverage had a stronger coefficient than the environmental covariates, with depth having the weakest (Table 5).

Pielou's evenness of macroalgal communities among *Fucus*.

The coverage of *Fucus* had a positive impact on Pielou's evenness in Åland, the SW Archipelago and the Gulf of Finland (Table 6). The quadratic model was a better fit only in the Gulf of Finland. Depth had a significant effect on evenness both in the Bothnian Sea and in Åland, but the direction of the effect varied between the areas. The evenness increased with depth in the Bothnian Sea but decreased with depth in

Åland. In the Gulf of Finland, salinity had a significant negative impact on evenness. In the SW Archipelago, none of the environmental covariates had significant effects.

3.2. Algal taxonomic units within *Fucus*-belts

The average *Fucus* coverage increased with depth from 0 to 1-m to 1–2-m in every area aside from the SW Archipelago (Fig. 3), where it only decreased with depth. It increased continuously with depth below 2 m in Åland, while it decreased below 3-m in the Bothnian Sea and the Gulf of Finland. The average coverage was highest in Åland, the only area where it was above 40% for every depth aside from the upmost 0–1-m.

Pylaiella littoralis/Ectocarpus siliculosus (filamentous brown algae) was the taxon with the highest average coverage in almost all sea areas and at all depths, except for the 0–1-m range in Åland, the SW

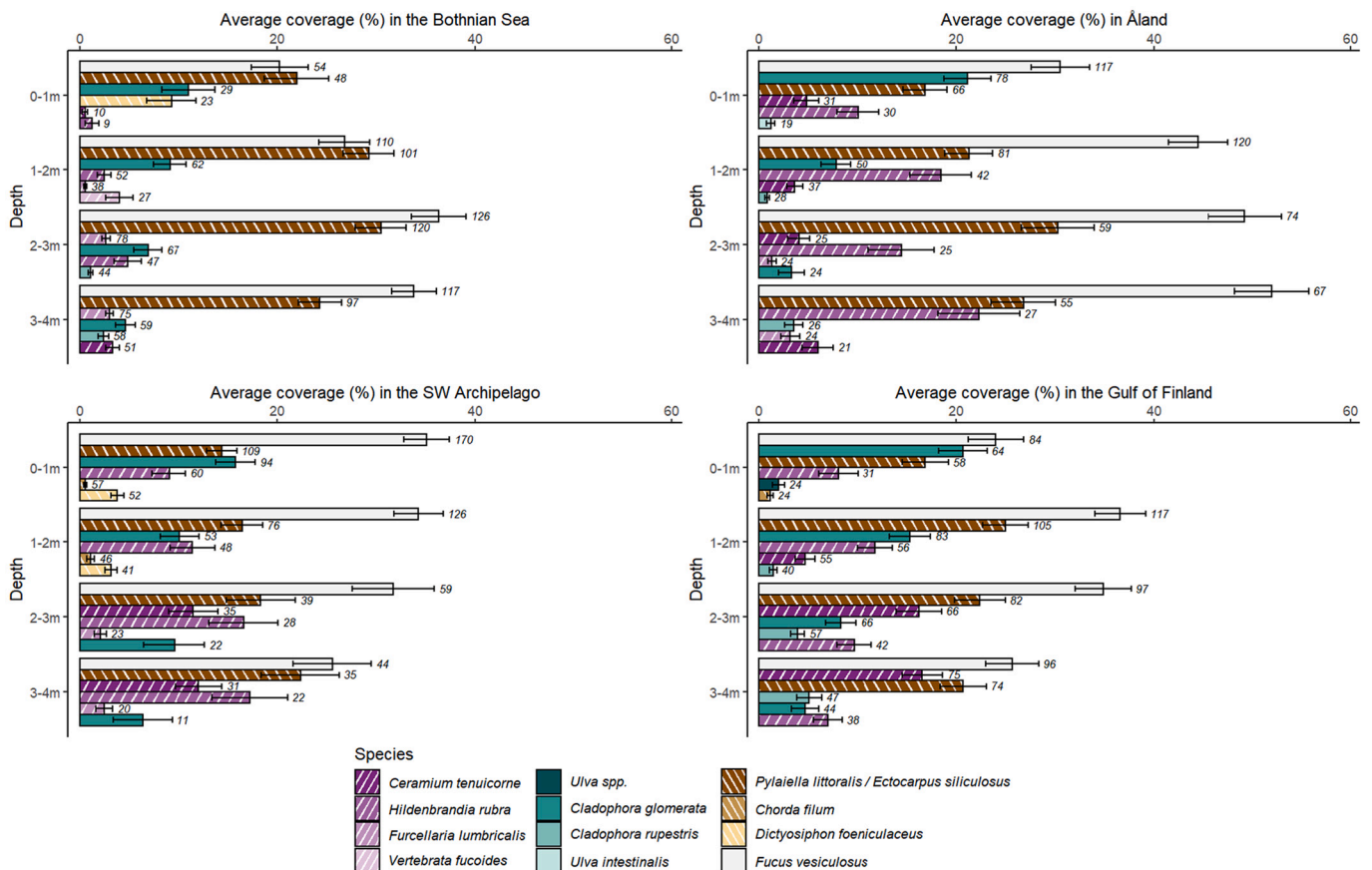


Fig. 3. Average coverage of the five most frequently observed algal taxonomic units at different depths (0–4 m) in each sea area. The error bars represent the standard error. The number of study points where the species was found is indicated to the right of each bar. Because the study points were selected to always have *Fucus* spp. present, the number of study points with *Fucus* spp. is also the total number of study points for each subset.

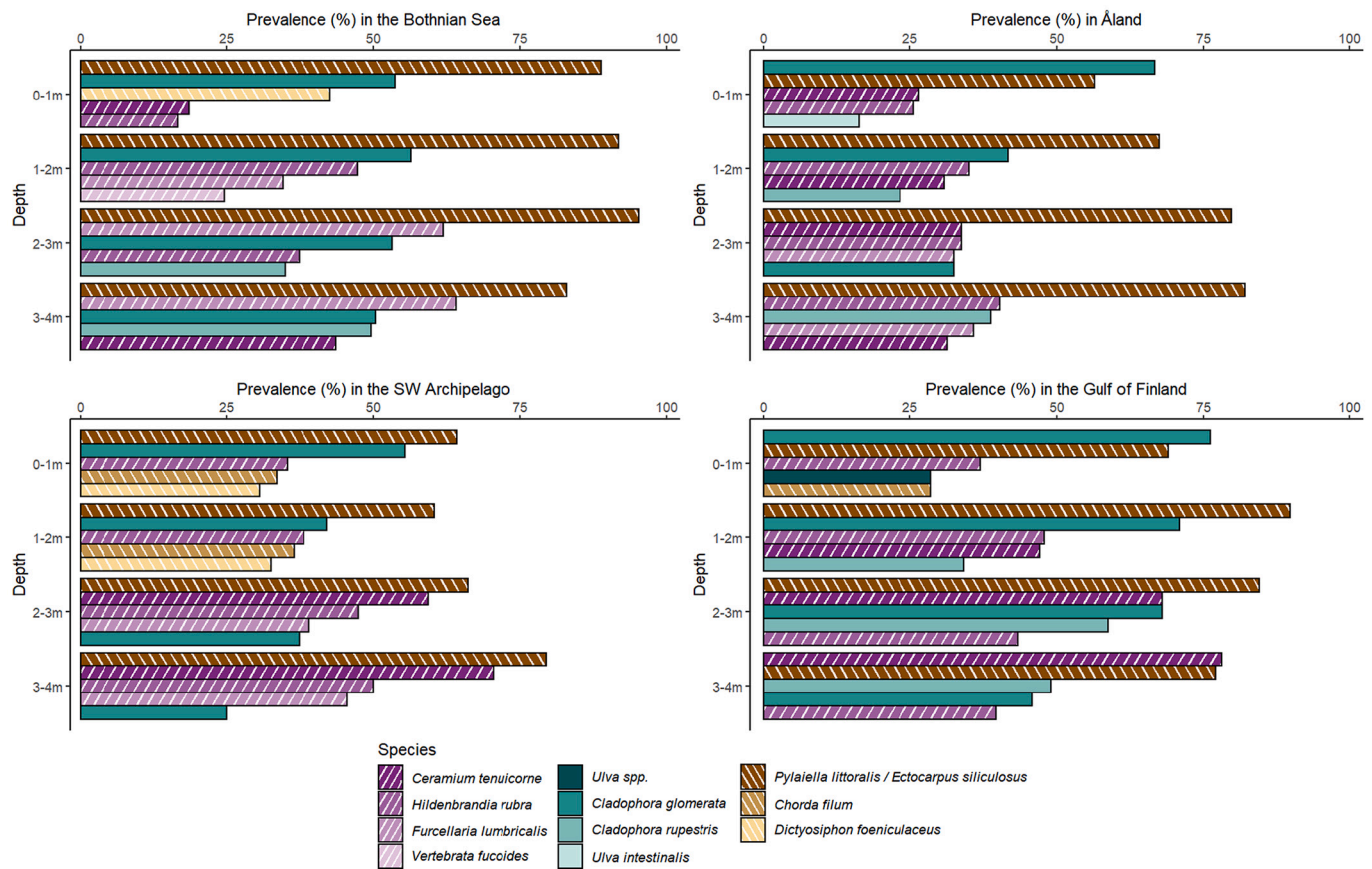


Fig. 4. Prevalence of the five most frequently observed algal taxonomic units at different depths (0–4 m) in each sea area.

Archipelago and the Gulf of Finland, where *Cladophora glomerata* (filamentous green algae) was dominating (Fig. 3). At 0–1-m depth in Åland and the Gulf of Finland, *C. glomerata* was the most commonly reported taxonomic unit, and was also very common in other sea areas and depths.

The average coverage of green algae decreased with increasing depth in all four sea areas, with *C. glomerata* being consistently more abundant than *C. rupestris* in all sea areas and depths except for 3–4 m in the Gulf of Finland.

In all four sea areas, *P. littoralis*/*E. siliculosus*, *Hildenbrandia rubra* (crustose red algae), *Ceramium tenuicorne* (filamentous red algae), and *Cladophora* spp. were among the most common taxonomic units within *Fucus*-belts although their respective ranking and prevalence varied (Fig. 4).

At the 3–4 m depth interval in the Gulf of Finland, *C. tenuicorne* was the most common taxon. It was especially common deeper (2–4 m) in the SW Archipelago and the Gulf of Finland, reaching over 50% prevalence. The red algae *Furcellaria lumbricalis* was relatively common in the Bothnian Sea (1–4 m), in Åland and SW Archipelago (2–3 m) but not in the Gulf of Finland. However, despite being reported in at least 25% of the study points in >1-m depths in the Bothnian Sea, and > 2-m depths in Åland and the SW Archipelago, *F. lumbricalis* had consistently low coverage values when present (compare Figs. 3 and 4).

P. littoralis/*E. siliculosus* was especially common, found in over 50% of the study points. It occurred at all studied depths in all sea areas and reached >75% prevalence across all depths in the Bothnian Sea (Fig. 4). Åland was the only sea area where no taxonomic unit other than *P. littoralis*/*E. siliculosus* was found in at least 50% of the sites at depths below 1 m. The average coverage of this taxonomic unit was as high as the average *Fucus* coverage in the Bothnian Sea, while all other taxonomic units had lower coverages despite their frequent occurrence in all

studied depths (compare Figs. 3 and 4).

In the Bothnian Sea, each of the four observed red algal species occurred commonly in at least one depth range. Brown algal taxonomic units were common in the SW Archipelago but in Åland, only *P. littoralis* and *E. siliculosus*, treated as one taxonomic unit, belonged to the most common taxonomic units across all depths. Of all the four green algal taxonomic units that frequently occurred across the study area, only *C. glomerata* was among the five most common in the SW Archipelago.

4. Discussion

Using extensive marine inventory data from the Finnish marine areas, we show that there exists a non-linear relationship between the coverage of the perennial canopy-forming foundation algal species *Fucus* and the diversity of associated algal communities. However, environmental parameters play an important role in defining algal diversity within *Fucus*-belts.

4.1. Effects of *Fucus* coverage on diversity

The coverage of *Fucus* did not affect the total number of taxonomic units in the studied sea areas (Table 3), but it did influence the algal diversity (Shannon-Wiener index H' and Pielou's evenness J') in the Bothnian Sea, Åland and the Gulf of Finland. In the SW Archipelago, the best-fitting model and the significant factors affecting algal diversity differed (Table 5). The modelled diversity index curves reached their highest values between 25% and 75% *Fucus* coverage and decreased in lower or higher coverages, except in the SW Archipelago, where the *Fucus* coverage did not affect H' . Because H' varies depending on the metric used to estimate it (Dickman, 1968; Wilhm, 1968), the values presented here should not be compared with studies calculating H' using

the number of individuals.

The diversity values presented in our study may be a slight underestimation of the true diversity due to the grouping of some species under more general taxonomic units. However, the proportion of study points possibly affected remained low (16.8 study points out of 1578, see Table B). Of its two main components, richness and evenness, H' is most affected by the evenness, but this effect remains small when the total richness is under 15 (Strong, 2016). As none of our study points featured more than 11 taxonomic units, we consider that our findings still represent the existing diversity with satisfying accuracy.

The differing response of the number of taxonomic units compared to H' suggests that changes in *Fucus* coverage affect the diversity of the algal community by changing the relative proportion of the taxonomic units rather than by changing the total number of taxonomic units. This is supported by the fact that J' was positively affected by *Fucus* coverage in Åland, the SW Archipelago and the Gulf of Finland (Table 6), as it quantifies how similar the proportions of the different species are (Pie-lou, 1969). Higher evenness values associated with higher *Fucus* coverages indicate that algal communities are less likely to be dominated by one very abundant species when *Fucus* coverage is higher.

There are several examples of how *Fucus* can affect the surrounding algal community. The presence of fucoids has been linked to increased algal diversity (Eriksson et al., 2006), where crust-forming algae are favoured under the shading of adult *Fucus* canopies. It has also been shown that the cover of perennial algae was positively related to the coverage of canopy-forming fucoids in other systems (Schiel and Lilley, 2007). In our study area, a beneficial effect of *Fucus* may be reflected in the high prevalence of *Furcellaria lumbricalis* in *Fucus*-belts close to the surface (Fig. 4), when the species typically only dominates the vegetation below the lower limit of *Fucus* (Kiirikki, 1996b).

The algal diversity decreased with high (> 75%) coverage of *Fucus*, which may be caused by competition for space and light. In areas with high coverage of *Fucus*, other algal species may also be controlled through the whiplash effect (Kiirikki, 1996a). On the other hand, low coverage of *Fucus* (< 25%) exerts a limited control on the algal community and may lead to the mass occurrence of a few dominant opportunistic filamentous species (*E. siliculosus*/*P. littoralis* and *C. glomerata*), limiting the ability of other species to develop. When the coverage of *Fucus* is low (< 10%), it is likely that *Fucus* is limited by the surrounding algal community, especially due to reduced germling settlement in the presence of filamentous algae (Berger et al., 2003). Sites with coverage between 25% and 75% likely reach a balance where *Fucus* is present at a high enough density to exert some control over other species without dominating the algal community entirely. The density of foundation kelp species has been shown to have both positive and negative impact on the surrounding algal communities, notably by favouring crust algae but reducing the total species richness due to increased scouring pressure when increasing in coverage (Hughes, 2010). This balance between beneficial and detrimental effects, resulting in the highest diversity being reached between 25% and 75% *Fucus* coverage, is expected to be found in systems following the intermediate disturbance hypothesis (Connell, 1978). This suggests that *Fucus* could be considered a disturbance from the perspective of other algae regarding diversity. However, further studies will be required to confirm this possibility. This highlights the importance of inventory programmes recording data on a fine scale, as such effects cannot be detected using a binary absence-presence approach.

Biotic interactions related to the invertebrate fauna associated with *Fucus* may also affect algal diversity. Invertebrate grazers may reduce *Fucus* by consuming the canopy, but they can also control mass blooms of opportunistic filamentous algal species by consuming them (Worm et al., 1999). This can further indirectly favour the occurrence of slow-growing species, such as *C. tenuicorne* (Korpinen et al., 2007) and thereby increase the algal diversity (Worm et al., 1999). As we used data from July–August when the abundance of grazers such as the isopod *Idotea balthica* is often high (Korpinen et al., 2010), it is likely that

grazing also had some effects on the algal communities, but quantifying its effect was not possible in this study.

4.2. Effects of the environment on the number of algal taxonomic units and diversity

Of all the environmental variables analysed, depth (0–4 m) was the most frequent significant covariate affecting algal diversity. The number of algal taxonomic units increased in deeper sites in all study areas except the SW Archipelago (Table 3). Generally, the shallowest depths consisted of filamentous algal species with short lifecycles (Fig. 4) that can colonise the substrate rapidly (Kiirikki and Lehvo, 1997). This opportunistic life strategy is especially suited for shallow areas where ice scraping annually may clean the rocky shores from vegetation (Kiirikki and Ruuskanen, 1996). Thus, perennial species are more common in deeper and more stable environments (Eriksson and Bergström, 2005; Rinne et al., 2011), which was also found in our results, where *Furcellaria lumbricalis* and *Cladophora rupestris* became more prevalent deeper (Fig. 3). The Bothnian Sea was the only sea area where increased depth had a positive effect on all diversity metrics used (total number of taxonomic units, diversity H' and evenness J' , see Tables 3, 5 and 6). This could be due to the many red algal species that occur in the area, especially at deeper sites, but rarely become dominating due to low coverage (Rinne and Kostamo, 2022).

Global warming will likely result in milder winters and less sea ice (Snoeijis-Leijonmalm et al., 2017), allowing *Fucus* to grow closer to the surface in areas where it would otherwise be subject to ice-scraping (Kiirikki and Ruuskanen, 1996; Eveleens Maarse et al., 2020). Additionally, although the Baltic Sea is a non-tidal system, water level fluctuations can be relatively high, and low water events can kill the algae closest to the surface (Kautsky and Kautsky, 2000). This may further affect the overall structure of the shallow water algal communities of the northern Baltic Sea that are generally characterized by, often monospecific, filamentous algal belts closest to the surface (Kiirikki, 1996a).

The Gulf of Finland was the only studied sea area with a clear salinity gradient, thus salinity was included as a covariate in the analyses. Salinity had a significant effect on all three algal diversity metrics in the area. The negative effect of higher salinity on the number of taxonomic units and diversity was unexpected, as increasing salinity is known to increase the diversity of macroalgae in the Baltic Sea (Schubert et al., 2011). One explanation may be that the blue mussel *Mytilus edulis* is a competitor for space in shallow rocky sea areas with higher salinity in the Gulf of Finland (Westerbom et al., 2002; Rinne et al., 2021). Due to lower salinities in the East, *M. edulis* becomes less frequent and competition for space decreases at the local scale, offering more space for the macroalgal community to develop (i.e. more algal species can settle). This could explain the observed effect on the diversity at the scale of individual study points, despite the list of species found in the Gulf of Finland as a whole remaining comparable to the other three sea areas.

The SW Archipelago was the only area where increasing Secchi depth positively affected the number of taxonomic units and the algal diversity index. No other environmental parameters affected the diversity metrics in this area. As the area showed intermediate Secchi depth values compared to other sea areas (Table 1), exceptionally clear waters cannot explain the observed relationship. In general, the Archipelago Sea is highly affected by eutrophication, which also affects the algal communities (Rinne and Salovius-Laurén, 2020; Rinne and Kostamo, 2022). One of the consequences of eutrophication is increased sedimentation, which limits clean rocky surfaces where algal propagules can attach (Berger et al., 2003). Thus, the Secchi depth being the only variable affecting the diversity metrics in this area may be related to other eutrophication-related parameters that were not included in the models but generally negatively correlate with Secchi depth, such as sedimentation rate or nutrient (N and P) concentrations.

The level of wave exposure had no effect on any diversity metrics.

Previous studies have outlined the importance of exposure for the algal community structure, e.g. for the occurrence and lower limit of *Fucus* and other algae (Eriksson and Bergström, 2005; Rinne et al., 2011; Rinne and Kostamo, 2022). While exposure was not used to filter the data in this study, we only selected sites where *Fucus* was present. Because *Fucus* typically favours higher wave exposure, as it reduces the negative effects of sedimentation on its recruitment (Berger et al., 2003), most study points of this study were relatively exposed (SWM >50,000 or 10.82 with log transformation; Table C).

The resulting small variation in exposure values may explain why its effects were not detected. It is possible that exposure would have affected the algal diversity if more sheltered or moderately exposed study points had met our selection criteria.

4.3. Variation in *Fucus*-associated algal communities

The taxonomic units found were quite similar in the four sea areas (Table 2) and reflect the small pool of macroalgal species occurring in the Finnish marine area (Nielsen et al., 1995; Schubert et al., 2011). Despite this, the species composition of algal communities in *Fucus*-belts in the northern Baltic Sea differs locally depending on their geographical location (Rinne et al., 2011) and depth. Although limited to 0–4-m depths, our examination of species prevalence further confirms these findings, as the five most commonly reported species varied between areas, and with depth within each area (Fig. 3 and Fig. 4).

Our study focused only on the algal communities present during the summer months (late July–August), as that is the best period to study the spectrum of macroalgal species occurring in the area (Kiirikki and Lehvo, 1997). The *P. littoralis*/*E. siliculosus* group was very abundant in the majority of the study points regardless of depth or area (Fig. 4) and is thereby the most common group of macroalgae among *Fucus*-belts in shallow waters in the outer Finnish marine sea areas. As the data were collected in summer, it is likely that the *P. littoralis*/*E. siliculosus* group was mainly represented by the warm water species *E. siliculosus* and not by *P. littoralis*, which prefers colder waters (Kiirikki and Lehvo, 1997). However, when considering the most common species, if *P. littoralis* and *E. siliculosus* were identified at the species level, it is possible that *C. glomerata* would be the most common species in several cases instead. This could occur due to the coverage and prevalence values being split between the two species. The prevalence of red algae increased with depth in all sea areas except for Åland. This may result from Åland having the highest average Secchi depth (Table 1), allowing filamentous brown and green algae to remain competitive deeper compared to the other three sea areas. Red algae are generally most prevalent in the outer parts of the Finnish marine area (Rinne and Kostamo, 2022), and they were also common in our study, although in relatively low coverages (Figs. 3 and 4). The coverage of red algal species may have been higher below 4 m depth as many of them generally prefer deeper areas (Kostamo et al., 2021).

5. Conclusions

The macroalgal taxonomic units within *Fucus*-belts in different sites are quite similar, with fast-growing ephemeral algal species dominating in most depths, reflecting the widespread eutrophication in the northern Baltic Sea.

A non-linear relationship existed between the coverage of *Fucus* and algal diversity (H') and evenness (J'), with the Shannon-Wiener diversity index generally peaking at sites with *Fucus* coverage between 25% and 75%. This is likely a result of competition exerted by *Fucus*, as the presence of *Fucus* may prevent filamentous algae from dominating the surrounding community. However, when *Fucus* occurs in high coverages, it suppresses most other algae and lowers the diversity of the community. A significant relationship also existed between *Fucus* coverage and the evenness of the algal community. This may result from *Fucus* affecting the relative coverage of the algal taxonomic units rather

than the total number of algal taxonomic units at a given site. Instead, the number of algal taxonomic units was driven mainly by environmental parameters, such as depth, salinity and Secchi depth. Although the effects of foundation species *Fucus* on macroinvertebrate diversity have been extensively studied, their effects on other co-occurring algae are less known. To our knowledge, this is the first study on macroalgal diversity associated with the foundation species *Fucus* across a large geographic area in the Baltic Sea. The study further highlights the importance of ambitious large-scale inventories and the need for extensive high-quality datasets to understand species occurrence patterns in shallow benthic communities on different spatial scales.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2022.102312>.

Code availability

The R Script used is available upon request.

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Contributions

All authors contributed to the conceptualizing the study. Data analyses were performed by JFB. The manuscript was written by JFB, and HR and SS-L took an active part in its formulation. All authors have read and approved the final manuscript.

Ethics approval

No approval of research ethics committees was required to accomplish the goals of this study as it consisted of inventories of algal species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The enquiries on the data gathered during the VELMU programme should be appointed to the Finnish Environment Institute. The enquiries on the data for Åland should be made to Åbo Akademi University (authors). The data can be viewed at https://paikkatieto.ymparisto.fi/velmu/index_eng.html.

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