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Published in:
Estuarine, Coastal and Shelf Science

DOI:
10.1016/j.ecss.2023.108411

Published: 01/01/2023

Document Version
Final published version

Estuarine, Coastal and Shelf Science 290 (2023) 108411

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Environment- and scale-dependent changes in the functioning of invertebrate communities associated with *Fucus vesiculosus*

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ARTICLE INFO

Keywords:
Baltic sea
Body size
Eutrophication
Exposure
Trait
Macrofauna

ABSTRACT

The functional trait approach focuses on the diversity of species characteristics, and can reveal much more about community functioning and trophic structure, compared to classical biodiversity concepts. In this study, we assessed large- and small-scale patterns in the functional traits of invertebrate communities associated with the marine macroalga *Fucus vesiculosus*. Large-scale comparisons were done across coastal areas representing different water quality (good, moderate, and poor) and small-scale comparisons across communities from sites with different exposures (sheltered, exposed) within the areas. Functional richness differed between areas of different water quality, with higher richness generally observed in areas with clearer waters. On a smaller scale, functional richness and dispersion were highest at sheltered sites, whereas the effect of exposure on functional divergence varied between study areas. Community trait composition differed among areas of different water quality with opportunistic traits becoming more prevalent in areas in poorer state. For example, community-weighted body sizes differed between areas and the smallest body sizes were observed in areas with moderate or poor water quality. The results illustrate how faunal traits within the same habitat type can differ geographically and how the functioning of communities may change due to anthropogenic pressures and natural drivers at different scales.

1. Introduction

Species traits, or the morphological, physiological, and phenological characteristics of species, constitute a fundamental part of descriptions of biodiversity (Loreau et al., 2001; Violle et al., 2007). Traits are important determinants of how species and communities respond to changes in the environment (*response traits*) (Suding et al., 2008; Gladstone-Gallagher et al., 2019), and further govern how the organisms in a community influence their environment (*effect traits*) (Díaz and Cabido, 2001; Suding et al., 2008), as well as how they interact with other species (*matching traits*) (Eklöf et al., 2013). In coastal ecosystems, the trait-based diversity of faunal assemblages varies among different structural habitats (Törnroos et al., 2013; Weigel et al., 2016; Henseler et al., 2019), highlighting functional differences in community composition across the larger seascape. In addition, faunal trait composition and expression may also differ within habitats, indicating e.g. responses to fragmentation of habitats or other small-scale variations in environmental conditions (Boström et al., 2010; Törnroos et al., 2013).

Coastal ecosystems are affected by a wide range of environmental factors across different spatial scales. For example, at large, regional scale, changes in salinity directly influence community composition by selecting species based on their tolerance to high or low salinities (Giberto et al., 2004; Schubert et al., 2011), while topography will determine the direction and strength of currents, impacting flows of nutrients and organism dispersal (Boehlert and Genin, 1987; Miettunen et al., 2020). In addition, community composition and diversity may relate to the eutrophication status of the area (Rinne et al., 2022). On a smaller, island-scale, variations in wave exposure (Page-Albins et al., 2012; Wallin et al., 2011), depth (Eriksson and Bergström, 2005), or substrate composition, create an assortment of habitat patches that form distinct ecosystems. Lastly, at a within-habitat scale, smaller spatial features like crevices or canopies provided by either vascular plants or

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https://doi.org/10.1016/j.ecss.2023.108411
Received 9 February 2023; Received in revised form 6 June 2023; Accepted 14 June 2023
Available online 15 June 2023

algae (Archambault and Bourget, 1996; Wikström and Kautsky, 2007) add yet another layer of complexity in the chain of factors and scale influencing the biodiversity of a given coastal ecosystem.

Ecological, evolutionary and physiological responses to environmental change can shift community trait composition and trait expression (Hairston et al., 2005; Enquist et al., 2015). Considering body size, evolutionary responses to environmental change may result in smaller-sized individuals within a species (Atkinson, 1994; Kingsolver and Huey, 2008), while species turnover may result in smaller or larger community body size (Salo et al., 2020), depending on the driving factor. As body size is one of the most important traits determining e.g. process rates, community and ecosystem functions and stability (Brown et al., 2004; Norkko et al., 2013; Brose et al., 2017), changes in body size at the population and community level may modify ecosystem functioning. In addition to the metabolic demand of an organism (Brown et al., 2004), body size can determine e.g. what sized prey consumers feed on, thus determining interaction strengths (Brose et al., 2017). Changes in community body size can even define food web responses to disturbances (Antiqueira et al., 2022) and persistence of species in food webs (Binzer et al., 2016). Trait changes can thus have a multitude of effects on community and ecosystem functioning. As modified environmental conditions can alter traits in many ways, there is a need to assess how community traits respond to environmental and anthropogenic pressures. For comprehensive assessments, multiple complementary facets of functional diversity should be described.

Fucus vesiculosus (L.) (bladderwrack, henceforth *Fucus*) is a perennial, habitat-forming marine macroalga. Due to its major role in providing a range of ecosystem functions and services, it is a key species in the Baltic Sea. For example, *Fucus* offers food and refuge for many invertebrate and fish communities in coastal rocky areas (Kautsky et al., 1992; Wikström and Kautsky, 2007; Henseler et al., 2019). *Fucus*-associated invertebrate communities in the Northern Baltic Sea consist largely of different gastropods, bivalves, amphipods, isopods and insect larvae (Rinne et al., 2022), i.e., free-living selection-, suspension- and surface feeders, which move by crawling, rafting or swimming. The reproduction in these communities is often annual and takes place over an extended period, and the fauna is either short-lived (<1 year), or rather long-lived (5–10 years) (Henseler et al., 2019). The low salinity of the northern Baltic Sea is the main environmental factor limiting *Fucus* distribution, but within its distribution area, the eutrophication of the Baltic Sea has severely deteriorated the living conditions of *Fucus* (Kautsky et al., 1986, Berger et al., 2004). Eutrophication resulted in the disappearance of *Fucus* from many areas in the 1980s (Kangas et al., 1982; Rönnberg et al., 1985) and an overall decrease in depth penetration (Torn et al., 2006; Rinne and Salovius-Laurén, 2020) leading to substantially lower total spatial coverage of *Fucus* (Lappalainen et al., 2019). Although eutrophication effects on the occurrence of *Fucus* are well known (Rinne et al., 2022, Snickars et al., 2014; Rinne and Salovius-Laurén, 2020), information on the variation of *Fucus*-associated fauna across geographic and environmental gradients is limited. However, existing studies indicate that water quality modifies the species composition and diversity of invertebrate communities (Rinne et al., 2022). With such changes in biodiversity at the taxa level, it is likely that environmental change also modifies the community and ecosystem functioning.

In this study, we examined the variation in functional traits of *Fucus*-associated invertebrates. We assessed traits across both large and small scales, where large-scale geographical comparisons were done across areas with different water quality (good, moderate, poor). To assess small-scale variation, we compared communities between different exposures (sheltered, exposed) within each area. We expected the community trait composition to vary between areas with different water quality, and that community trait diversity is highest in the areas with the highest water quality and decreases towards the areas with poorer water quality. We expected community traits to differ depending on the exposure, but that the effect may depend on the water quality. In more detail, we expected trait diversity to be highest in sheltered locations in areas with higher water quality and contrastingly lowest in sheltered locations in areas with poorer water quality. Finally, we determined whether population or community level processes were driving community body size patterns across the study scales.

2. Materials and methods

2.1. Study area

This study builds on the data set on invertebrate abundances and biomasses in Rinne et al. (2022), with additional trait measurements (see 2.3 Laboratory analyses). The study was carried out along the southern coast of Finland in the non-tidal, brackish-water northern Baltic Sea (Fig. 1). The area is characterised by large archipelagos, influenced by Baltic Sea-wide eutrophication. Nutrient concentrations and turbidity increase towards the mainland and are especially high close to river discharge areas (Bonsdorff et al., 1997; Carstensen et al., 2020), whereas salinity and exposure increase towards the open sea.

Seven distinct geographical areas with varying water quality were chosen for the study (Fig. 1): Outer Archipelago Sea (hereafter AS-good, with the end of the abbreviation reflecting the water quality in the area), Eastern Åland (EÅ-good), Central Archipelago Sea (AS-moderate), Uusikaupunki (UKI-moderate), Western Åland (WÅ-moderate), Inner Archipelago Sea (AS-poor), and Helsinki-Espoo (HE-poor). The water quality of the sea areas was defined using long-term Secchi depth (water clarity) as a proxy. The division of areas into good, moderate and poor status was based on Secchi depth threshold values used in the status assessments related to the Water Framework Directive (WFD; Aroviita et al., 2012). As our study comprised six WFD assessment regions, with region-specific, slightly different threshold values for status classes (Aroviita et al., 2012), we used their averages to have the same criteria for classification across the study area, namely; <2.9 m Secchi depth for poor status, 2.9–4.6 m for moderate status and >4.6 m for good status. To obtain Secchi depth for the study areas, we used a Secchi depth model based on MERIS satellite data (raster with 300 m resolution) produced within the Finnish Inventory Programme for the Underwater Marine Environment, VELMU (Lappalainen et al., 2019). The model presents an average for June–August Secchi depth values for the years 2003–2011.

Within each of the seven study areas, ten treeless small skerries were randomly selected as sampling locations. To assess small-scale variation, six replicate *Fucus* individuals with associated invertebrates were sampled at each location: three replicates from the exposed side, and three replicates from the more sheltered side of the skerry. Locations with similar exposure were selected to reduce the environmental variation not related to anthropogenic pressures. Exposure was determined using the Simplified Wave Exposure Model, hereafter SWM (Isaeus, 2004). The locations that were chosen resided in moderately exposed areas (SWM 10 000–50 000).

2.2. Field sampling

The field sampling was conducted between July 8th and 30th, 2020. *Fucus* and faunal samples were collected at 0.8–1 m depth (sublittoral zone) in areas of 10 × 5 m by snorkelling. The samples were collected by covering individual algal thalli of ca 30 ± 10 cm (length) with a mesh bag (mesh size 0.5 mm) and loosening them from the substrate. The invertebrate macrofauna (≥0.5 mm) was separated from the algae and preserved in 70% EtOH. The wet weight (WW) of each *Fucus* individual was quantified. The dry weight (DW) of ten randomly selected *Fucus* individuals was measured (48h at 60 °C) to obtain the WW:DW ratio. This ratio was used to estimate the DW of all sampled *Fucus* individuals.

2.3. Laboratory analyses

Invertebrate taxa were identified to the lowest possible level. Due to the difficulties with identifying small individuals, some taxa were

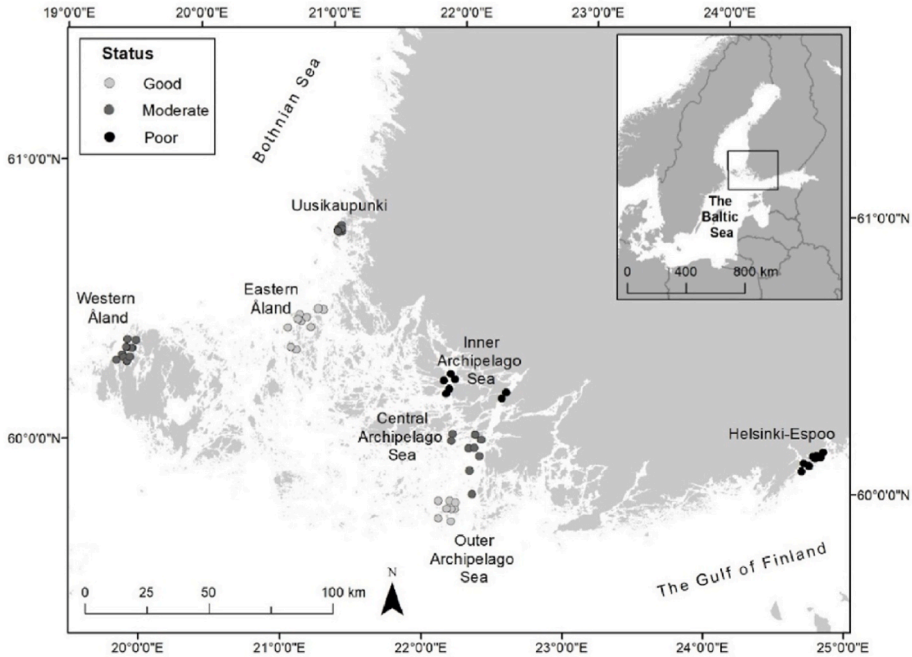

Fig. 1. Sampling locations in the different areas and status classes describing water quality. Light grey indicates good status, dark grey moderate status and black poor status. From Rinne et al. (2022).

pooled to the following groups: hydrobiid snails (*Hydrobia* spp. and *Potamopyrgus antipodarum*), *Parvicardium/Cerastoderma* (*Parvicardium* and *Cerastoderma* bivalves), *Chironomus* spp. (chironomid larvae), *Gammarus* spp. (gammarid amphipods), and lymnaeids (*Physa*, *Radix* and *Lymnaea* gastropods). The abundance of each taxon was determined and standardised by *Fucus* dry weight (ind. g^{-1} *Fucus* DW).

The body size of individuals was estimated to the nearest mm, except for amphipods, where size classes of ≤2, 3–4, 5–6, 7–9, 10–20 and > 20 mm were used. Chironomids and isopods sized ≤2 mm were pooled into one size class each. Body size was estimated as the maximum length from anterior to posterior; gastropods from the shell apex to the bottom, bivalves from the opening to the umbo, and decapods from the rostrum to the telson. All measurements excluded any antennae and legs. Amphipods and *Palaemon* spp. were measured in their naturally curved position. When abundances were high (i.e., >80 individuals for one taxon), body sizes were noted for a subsample of at least 40 randomly chosen individuals.

2.4. Traits

Functional traits can be defined as morpho-physio-phenological traits which affect individual fitness (Violle et al., 2007). Thus, we identified fundamental trait information, i.e., traits linked to surviving, feeding, and reproduction for each taxon: size (average body size in mm), longevity (very short [<1 year], short [1–2 years], long [2–5 years], very long [5–10 years]), reproductive frequency (semelparous, annual episodic, annual protracted), feeding position (suspension feeder, surface feeder, selection feeder, miner, parasite), feeding habit (detrivore, omnivore, herbivore, carnivore, scavenger, parasite), and movement type (swimmer, rafter/drifter, crawler, byssus, tube builder, burrower). These traits are commonly used to assess community functioning (e.g., Henseler et al., 2019; Pecuchet et al., 2020) and can be affected by environmental changes (such as eutrophication) (Pecuchet et al., 2020).

Categorical body size (i.e., a single size class for all individuals within a species) is commonly used in trait-based evaluations (see Törnroos and Bonsdorff, 2012 and references therein), which allows assessing the impact of species turnover on community body size. However, assessing actual values of body size provides more information of ecological, evolutionary, and eco-evolutionary processes. Thus, size was determined as a continuous variable and calculated as the average size of individuals for each taxon in each sample. When fauna (amphipods) were divided into size categories, the average of the size class was used in the calculations (e.g. individuals in the 3–4 mm size class were estimated as 3.5 mm). All other traits were categorical and determined from the literature. Traits for most of the taxa were accessed from Törnroos and Bonsdorff (2012). The same categorical traits were assigned to each species within the genera *Idotea* spp., *Palaemon* spp., and *Praunus* spp., respectively, while *Echinogammarus* sp. were assigned the same traits as *Gammarus* spp. Categorical traits for *Rhithropanopeus harrisii* were from Aarnio et al. (2015) and Jormalainen et al. (2016), and *Sinelobus vanhaareni* from Gagnon et al. (2022). *Palaemon* spp. and dytiscidae traits were accessed from invasions.si/edu/nemesis/ (assessed Sept. 7th, 2022). Each taxon was assigned one or when appropriate several trait categories. Traits were scored as either 0 (trait absent) or 1 (trait present). All trait categories were divided by the number of categories in each trait so that the sum of categories for each trait was 1.

2.5. Data analyses

2.5.1. Functional diversity

The FD package (v. 1.0–12.1; Laliberté and Legendre, 2010; Laliberté et al., 2022) in R was used to calculate trait biodiversity indices for each community. We calculated four complementary functional diversity indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis) (Villéger et al., 2008; Mouchet et al., 2010). Functional richness indicates the number of functions (i.e., the traits and/or modalities) and the amount of trait space that the taxa in a community occupy (Mouchet et al., 2010). Functional evenness describes how evenly distributed the taxa in a community are in the trait space (Mouchet et al., 2010). High values indicate that the niche space is evenly used (Mason et al., 2005). The functional divergence indicates how far the taxa in a community are from the centre of the trait space. It gains a low value when the taxa with the most individuals has traits that are close to the middle of the trait

space (Villéger et al., 2008). The functional dispersion indicates the average distance from all taxa to the weighted centroid of the trait space (Villéger et al., 2008).

To calculate FD, ≥3 individual taxa are required in each community. As communities from nine *Fucus* individuals (replicates) did not fulfil this requirement, we used the average of the three replicates from each exposure within a location for all calculations. Thus, each location had two values for FRic, FEve, FDiv, and FDis, one from the sheltered and one from the exposed side of the location (n = 1 per exposure within location). Differences in trait biodiversity between areas were analysed in the PERMANOVA+ package in PRIMER 6.1.13 separately for each trait diversity index. Factors included area and exposure, with exposure nested under area. Resemblance matrices were based on Euclidean distance. PERMANOVA analyses were run with 9999 permutations using type III SS. The data dispersions for all analyses were inspected with PERMDISP and with nMDS plots, and when necessary data were transformed (4th root) to reach homogenous dispersions among data groups (Table 1).

2.5.2. Community-weighted means

The FD package (Laliberté et al., 2022) in R was also used to calculate community-weighted means (CWM) for each trait and invertebrate community (n = 3 per exposure within a location). CWM values for traits were used to assess multivariate differences in traits between different areas. Prior to analyses, CWM values were normalised (each trait varied between −1 and 1, with an average of 0) to decrease the weight of the continuous variable (size of organisms). Differences in CWM traits between areas and exposures were analysed with nonmetric multidimensional scaling (nMDS), ANOSIM and SIMPER in PRIMER. The nested structure of the data was ignored in ANOSIM and SIMPER analyses due to the technical limitations of the analyses. Ignoring the nested structure may underestimate the variation between samples. However, the faunal communities at sheltered and exposed sites of skerries were relatively different (Rinne et al., 2022), which should increase the variation in the data.

In addition to including the continuous trait size of organisms in the multivariate CWM analyses, variation in CWM size across areas and exposure were also analysed in a separate PERMANOVA analysis (n = 3 per exposure within a location). In addition, to estimate how much of the variation in size across areas and exposures was due to community (species turnover) and population (intraspecific trait variability) level processes, or their interaction, we used the partitioning method by Lepš et al. (2011). In this method, CWM is calculated for each sample i) by using specific size values for each taxon in each sample, and ii) by using average values across samples. The former gives the specific (or local) average and the latter the fixed (or global) average. Intraspecific trait variability is then calculated by subtracting the fixed average from the specific average. Three separate PERMANOVAs were run with these data to get the sum of squares (SS) for area, exposure (nested under area), residual and total SS. The SS's were then used to calculate the proportion of variability explained by species turnover, intraspecific trait variability, and the covariation between these (Lepš et al., 2011).

Table 1
Variation between areas and exposures in the functional indices (FRic = functional richness, FEve = evenness, FDiv = divergence and FDis = dispersion) and community-weighted mean (CWM) body size of organisms. The multivariate trait data is based on CWM. Results from PERMANOVA. Significant results are indicated with italics. Body size data were 4th root transformed.

	df	SS	Pseudo-F	P(perm)
FRic				
area	6	3443.80	5.30	*0.041*
exposure(area)	7	764.37	2.29	*0.034*
residual	93	4436.50		
FEve				
area	6	0.19	1.27	0.393
exposure(area)	7	0.17	0.82	0.578
residual	93	2.81		
FDiv				
area	6	0.36	2.29	0.150
exposure(area)	7	0.19	2.43	*0.026*
residual	93	1.02		
FDis				
area	6	20.93	2.48	0.124
exposure(area)	7	9.93	2.22	*0.045*
residual	93	59.34		
CMW body size (4th root)				
area	6	0.57	11.74	*0.003*
exposure(area)	7	0.06	1.51	0.178
residual	93	0.50		

3. Results

3.1. Functional trait indices

Analyses on trait diversity revealed that functional richness differed between areas (Fig. 2a, Table 1). Richness was highest in the WÅ-moderate, EÅ-good and UKI-moderate areas, and lowest in the AS-poor, HE-poor and AS-moderate areas (Fig. 2a). However, none of the pairwise comparisons were significant. Data dispersion was significantly different among the areas due to the low variation in WÅ-moderate compared to other areas. Exposure affected functional richness (Table 1), with generally higher richness at sheltered sites (Fig. 2a).

Functional evenness was similar across all areas and exposures (Table 1, Fig. 2b), indicating that taxa were distributed to different trait categories in comparable ways in the studied communities, independent of area or exposure. Functional divergence was similar across all areas (Fig. 2c, Table 1), indicating a similar level of niche differentiation in faunal communities. It differed between exposures (Fig. 2c, Table 1), but the impact of exposure depended on the area (Fig. 2c). Functional dispersion was similar across all areas but differed between exposures. It was higher at the sheltered sites compared to exposed sites (Fig. 2d), suggesting that in less exposed conditions some traits become more abundant while exposure may reduce variability in trait expression.

3.2. Community trait composition

CWM trait composition differed between areas (Fig. 3, ANOSIM Global R: 0.297, p = 0.001), but not between exposures (ANOSIM Global R: 0.006, p = 0.25). In general, surface feeder, crawler, scavenger, larger body size and rafter/drifter were commonly observed traits in areas with high (good) water quality, whereas omnivore, swimmer, very short lifespan, tube-builder and sub-surface feeder, among others, were traits common in areas with poor water quality (Fig. 3).

Pairwise comparisons (ANOSIM) indicated that the differences in CMW trait composition were largest between AS-poor and EÅ-good, AS-good and UKI-moderate, AS-poor and AS-good, and AS-poor and WÅ-moderate (Table 2). No significant differences in CMW trait composition were observed between the two areas with high water quality (EÅ-good and AS-good) and UKI-moderate and AS-poor areas (Table 2). There were generally shorter longevity, more omnivores, parasites and smaller body sizes in areas with poor water quality compared to areas with high water quality (Fig. 3). As an example, SIMPER analyses indicated that in the Archipelago Sea, where areas with differing water quality were geographically relatively close to each other, differences between AS-poor and AS-good were mainly due to fewer surface feeders, herbivores, semelparous taxa and taxa with short longevity, and more carnivores, tube-builders, miners, taxa with very short longevity and parasites in the AS-poor area (Fig. 3).

3.3. Body size

CWM body size (4th root transformed) differed significantly between areas (Fig. 4a, Table 1). CMW body size was largest in EÅ-good, AS-

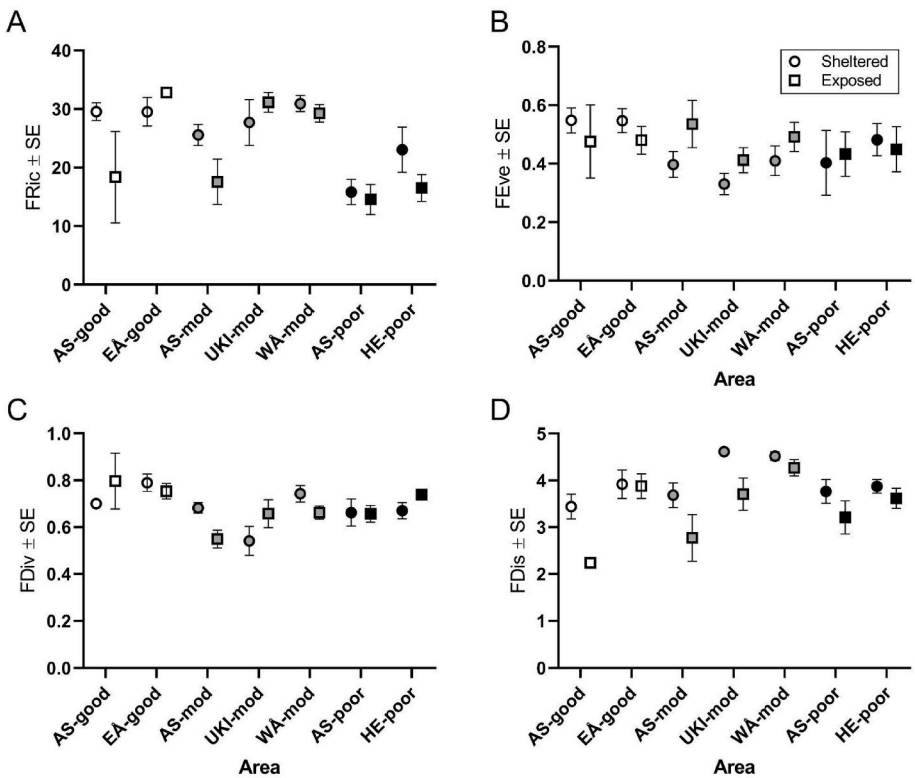

Fig. 2. Average ± SE trait diversity in different areas and exposures. (A) trait richness, (B) trait evenness, (C) trait divergence, and (D) trait dispersion. The shade of the symbol indicates water quality (clear: good, grey: moderate, black: poor) while the shape indicates exposure (circles: sheltered, squares: exposed).

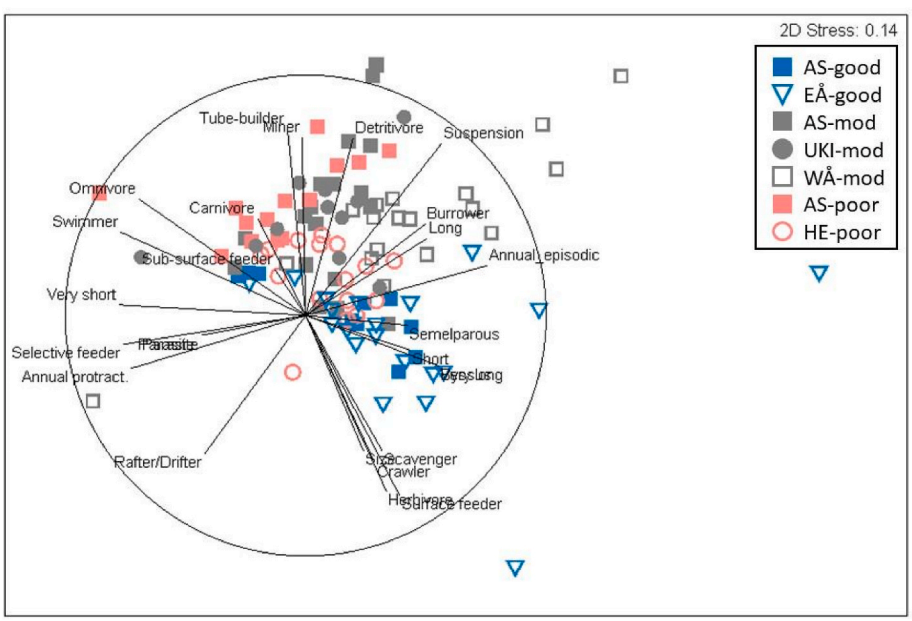

Fig. 3. nMDS on CWM traits in different areas (different symbols). Water quality of the areas is indicated by colours: blue – good, grey – moderate, red – poor. Vector overlay indicates traits with >0.2 correlation and traits included are size, longevity (very short, short, long, very long), reproductive frequency (semelparous, annual episodic, annual protracted), feeding position (suspension feeder, surface feeder, selection feeder, miner, parasite), feeding habit (detrivore, omnivore, herbivore, carnivore, scavenger, parasite), and movement type (swimmer, rafter/drifter, crawler, byssus, tube builder, burrower).

good, and AS-moderate, and lowest in WÅ-moderate, UKI-moderate and the two poor status class areas in AS and HE (Fig. 4a). Variation in CWM body size between areas was mainly explained by species turnover (19.3%) and covariation between species turnover and intraspecific trait variation (19.0%), while intraspecific trait variation contributed less to the observed variation (8.4%, Fig. 4b). CWM body size did not differ between sheltered and exposed locations (Table 1, Fig. 4a,c).

4. Discussion

4.1. Community trait diversity

The functional trait approach focuses on the diversity of species characteristics, and may be more informative compared to traditional (species) biodiversity concepts, especially when considering community functioning. This study revealed differences in functional community traits in *Fucus* (bladderwrack) associated invertebrate communities

Table 2
ANOSIM R statistics between different areas. A high value indicates a more different community trait composition and low values indicate more similar community trait composition between areas. Significant comparisons are in italics. Darker grey indicates the most different area comparisons and light grey the most similar areas.

	EÅ-good	AS-mod	UKI-mod	WÅ-mod	AS-poor	HE-poor
AS-good	0	*0.32*	*0.45*	*0.39*	*0.44*	*0.25*
EÅ-good		*0.33*	*0.35*	*0.38*	*0.47*	*0.18*
AS-mod			*0.22*	*0.33*	*0.13*	*0.20*
UKI-mod				0.33	0.06	*0.34*
WÅ-mod					*0.42*	*0.40*
AS-poor						*0.37*

across large and small geographic scales reflecting water quality and exposure, respectively. Highest trait diversities were generally found in areas with good environmental status and at the more sheltered sides of the skerries.

When the current trait diversity patterns are compared with the results from Rinne et al. (2022), who assessed species diversity in these exactly same communities, the results clearly differ. Rinne et al. (2022) observed intermediate Shannon diversity and low number of taxa in the most pristine areas compared to some of the areas with lower water quality, while contrasting patterns were observed for functional trait diversity (trait richness) in the current study. Ecosystem functioning does not always correlate with species richness, and especially ecosystems in estuarine and transitional waters often function successfully despite low species diversity (Elliott and Quintino, 2007). Accordingly, the observed discrepancy between trait (this study) and taxa diversity (Rinne et al., 2022) indicates that lower species richness is not equivalent with lower ecosystem functioning in *Fucus* habitats and emphasises that even communities with low species number may host a diverse trait composition.

Anthropogenic impacts modify communities and the mechanisms may vary from loss of sensitive species or traits to increases in non-native species, among others (Piola and Johnston, 2008; Michaud et al., 2022). Similarly, in the current study, lower functional richness was observed in the areas with poorer water quality. Shifts in species distributions can result in higher trait diversity through community processes (Frainer et al., 2021) as e.g. non-native species may bring new traits to communities (Vivó-Pons et al., 2022). However, in our study, trait diversities in areas with poor water quality were among the lowest despite more abundant non-native taxa (*Palaemon elegans, R. harrisii, S. vanhaarenii*) in these areas (Rinne et al., 2022). Further, non-native taxa were more common in the AS-poor compared to the HE-poor area (Rinne et al., 2022), while the functional trait diversity was comparably low in communities in both of these areas. This suggests that the non-native species in the study area have mainly brought redundant traits to the communities.

Both natural disturbance (i.e., higher exposure to wave activity) and anthropogenic pressure (i.e., poorer water quality) had negative effects on diversity. Elliott and Quintino (2007) described this as the Estuarine Quality Paradox, i.e. that natural and anthropogenic pressures can cause similar changes in the structure of the community or ecosystem. They suggested that functional characteristics such as traits could be more useful in detecting impacts of anthropogenic pressures instead of diversity, and that a combination of functional and structural information of the community should be used to gain more reliable estimates of ecosystem functioning (Elliott and Quintino, 2007). Our findings

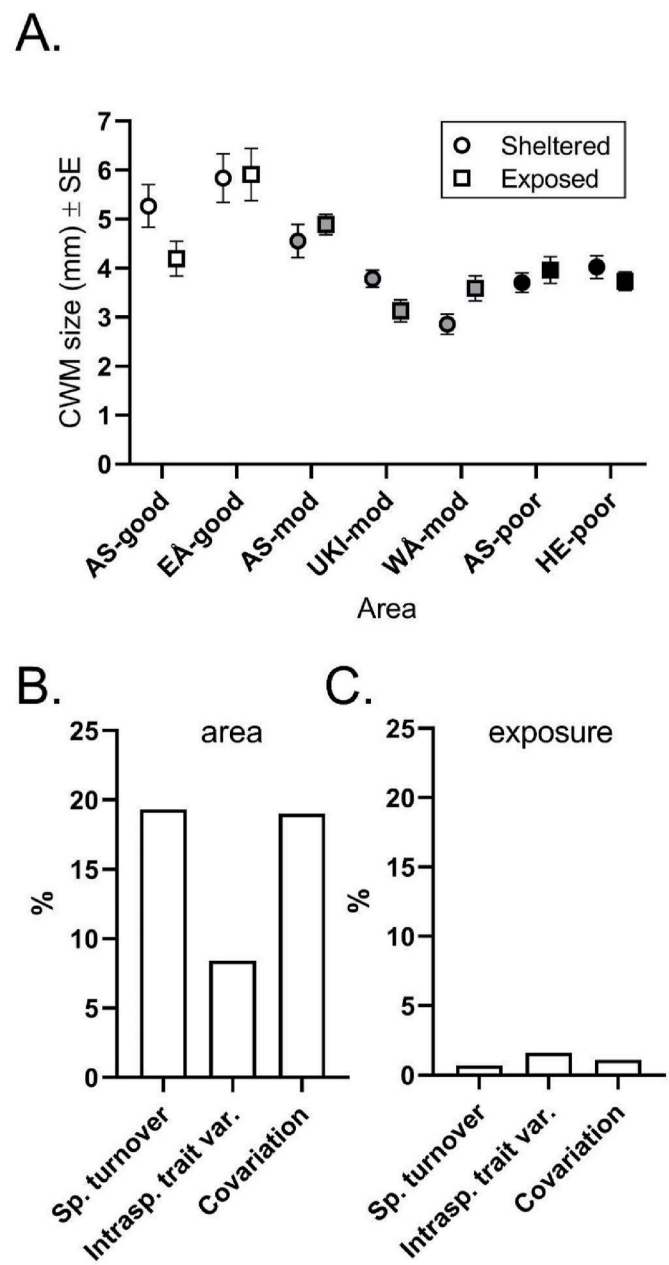

Fig. 4. (A) Average ± SE body size (community-weighted mean) in different areas and exposures. The shade of the symbol indicates water quality (clear: good, grey: moderate, black: poor) while the shape indicates exposure (circles: sheltered, squares: exposed). (B) and (C) describe how much (%) species turnover, intraspecific trait variation and covariation between these contribute to the observed differences between areas and exposures, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

support this recommendation: using functional community information revealed a pattern of lower trait diversity in areas with lower water quality (this study) compared to the structural approach (Rinne et al., 2022) where patterns in species richness or diversity were less clear in relation to water quality. Further, taxonomic diversity may fluctuate more compared to trait diversity (Henseler et al., 2019). Thus, assessing traits that often are redundant among taxa may result in more stable diversity estimates. However, considering the impact that exposure had on trait diversity in this study, collecting trait data from sites with differing exposures may result in more realistic estimates (i.e., increased variability) of community functioning, especially when scaling up and

assessing ecosystem processes, functioning and/or services on a larger scale.

4.2. Community traits

Loss of biodiversity is a non-random process and extinction risk may increase e.g. with body size (Brose et al., 2017). In our study, body size was smallest in the areas with the highest anthropogenic impact and this was mainly driven by species turnover. Thus, our results support the previous findings of non-random loss of taxa and traits due to pressures with increased extinction rates for larger individuals (e.g. Norkko et al., 2013) and taxa (e.g. Brose et al., 2017). Further, body size may correlate with ecosystem process rates and functioning (Norkko et al., 2013; Salo et al., 2018). Hence, considering the smaller size of individuals in areas with poor water quality, it is likely that the community and ecosystem functioning in *Fucus* habitats is reduced or modified in these areas compared to areas with higher water quality.

Body size may also correlate with longevity in some taxa, such as bivalves (Norkko et al., 2013). Accordingly, in addition to smaller body size, longevity was lower in communities in the areas with the lowest water quality. Fauna in these areas also tended to have more omnivorous feeding habits compared to fauna in areas with good environmental status, increasing the prevalence of opportunistic traits. Indeed, opportunistic taxa and traits often become more common with increased anthropogenic pressures (e.g. Pearson and Rosenberg, 1978; Bremner et al., 2006; Elliott and Quintino, 2007; Neumann et al., 2016). Other features that often characterise stressed communities in estuarine environments besides small body size, shorter lifespans and omnivorous feeding habits, are e.g. tolerance to low salinity and low oxygen conditions (Elliott and Quintino, 2007). However, also other pressures, such as temperature may modify community trait composition (Bremner et al., 2006; Elliott and Quintino, 2007; Salo et al., 2020). In addition, the impact of anthropogenic pressure and natural environmental variability may be difficult to separate (e.g. Pearson and Rosenberg, 1978; Elliott and Quintino, 2007; Neumann et al., 2016). For example, in our study region, gradients in salinity and exposure overlap with water quality (see section 2.1 above, Salo and Salovius-Laurén, 2022). While further studies are needed to gain a more mechanistic understanding of the relative roles of these factors, among others, the results indicate that an increase in the prevalence of opportunistic traits in invertebrates could be used as an indicator of stress in *Fucus*-associated fauna, which is in line with the Pearson-Rosenberg model (Pearson and Rosenberg, 1978).

5. Conclusions

We assessed invertebrate community traits across large and small scales in *Fucus* habitats. We observed lower trait diversity (richness) in areas with disturbances (poor water quality and higher physical disturbance). Communities in areas with lower water quality were characterised by opportunistic traits such as smaller body sizes, shorter lifespans and omnivorous feeding habits. This emphasises the severe impact that anthropogenic pressure may have on community and ecosystem functioning and highlights the importance of monitoring traits as an indicator of changes due to environmental or anthropogenic pressures.

CRediT authorship contribution statement

Tiina Salo: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Henna Rinne:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Data curation, Conceptualization. **Ellen Rancken:** Writing – review & editing, Writing – original draft, Data curation. **Jean-François Blanc:** Writing – review & editing, Writing – original draft, Data curation. **Sonja Salovius-Laurén:** Writing – original draft, Funding acquisition, Conceptualization. **Marie C. Nordström:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

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 abundance data is available at the Finnish national database for benthic fauna, POHJE. The trait data will be made available on request.

Acknowledgments

We thank Niilo Salmela, Niklas Niemi, Anniina Nieminen, Linn Engström, Johan Malmberg, Charlotta Björklund, Erika von Essen and Jaakko Rinne for assistance in fieldwork and/or laboratory analyses. Husö Biological Station and Korposström Archipelago Centre provided working facilities and equipment. Sampling was carried out within the VELMU programme and the ÅlandSeaMap project (HR, ER, J-FB), the former funded by the Finnish Ministry of the Environment, and the latter funded by the Baltic Sea Conservation Foundation and the European Maritime and Fisheries Fund. This manuscript contributes to the MARBEFES (MARine Biodiversity and Ecosystem Functioning leading to Ecosystem Services) project, funded by the European Union under the Horizon Europe Programme, "HORIZON-CL6-2021-BIODIV-01" Theme, Grant Agreement no. 101060937 (TS, MCN) (marbefes.eu) and BIODIVERSEA LIFE IP project (SSL), SSL and MCN acknowledge the support by the Åbo Akademi University Foundation.

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