Coastal habitats and their importance for the diversity of benthic communities: A species- and trait-based approach

Christina Henseler[a],[*], Marie C. Nordström[a], Anna Törnroos[a], Martin Snickars[a], Laurene Pecuchet[a],[b], Martin Lindegren[c], Erik Bonsdorff[a]

[a] Environmental and Marine Biology, Åbo Akademi University, Artillerigatan 6, Biocity, 20520, Åbo, Finland
[b] Norwegian College of Fishery Science, UiT the Arctic University of Norway, 9037, Tromsø, Norway
[c] Centre for Ocean Life, National Institute of Aquatic Resources (DTU-Aqua), Technical University of Denmark, Kemitorvet, 2800, Kongens Lyngby, Denmark

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ABSTRACT

Coastal habitats are used by a great variety of organisms during some or all stages of their life cycle. When assessing the link between biological communities and their environment, most studies focus on environmental gradients, whereas the comparison between multiple habitats is rarely considered. Consequently, trait-based aspects of biodiversity in and between habitats have received little attention. Here, we use the biological trait approach in addition to the more common species-based approach to examine trait and taxonomic diversity and composition of invertebrate and fish communities in different coastal habitats, common in the northern Baltic Sea. The habitats include bladderwrack (*Fucus*), seagrass (*Zostera*), rock with associated algal species (*Rock*), and bare sand (*Sand*). We found distinct differences in community diversity and composition between the habitats. For invertebrates, the sediment of the seagrass meadow had the highest taxonomic and trait richness and diversity, whereas *Sand* had the highest for fish. The highest dissimilarity in invertebrate community composition was between epifaunal (*Rock*, *Fucus*, *Zostera Epifauna*) and infaunal habitats (*Sand*, *Zostera Infauna*) on the one hand, and between vegetated (*Zostera Infauna*) and unvegetated sediments (*Sand*) on the other hand, emphasizing the major role vegetation plays in structuring communities. We demonstrate that fish community composition is distinct based on species, and to a lesser degree also distinct based on traits, in the different studied habitats. Both invertebrate and fish communities were more similar on a trait level than taxonomically among the habitats highlighting the presence of similar trait identities in the different habitats. Among the traits examined, *Body size* contributed most to dissimilarities among habitats for both invertebrates and fish, pointing out the ecological importance of body size for differentiating trait composition of communities. Based on our assessment of biodiversity, using the biological trait approach parallel to the taxonomic approach, we show that trait-based measures clearly provide additional information, such as key functions present in a habitat. This aspect cannot be captured by solely using taxonomic indices, which only shed light on diversity from a species identity point of view. Consequently, to include the ecological role of species, we recommend using biological traits in addition to species-based measures in the assessment of biodiversity, and especially in the management and conservation of coastal habitats, given the important ecosystem goods and services these areas provide.

1. Introduction

Coastal habitats, such as seagrass meadows, kelp and mussel beds, and open sand habitats, provide important ecosystem functions, as many species use them during some or all stages of their life cycle (Rönnbäck et al., 2007; ICES, 2008; Seitz et al., 2014). They are highly productive areas, inhabited by various invertebrates and serving as essential areas for feeding, nursery, spawning and migration for commercially and ecologically important fish species (Davidson et al., 1991;

ICES, 2008; Seitz et al., 2014; Jokinen et al., 2015). Coastal habitats differ in terms of their hydrodynamics, structural complexity and substrate composition (Fonseca and Fisher, 1986; Davidson et al., 1991; Koch, 2001), which structures the associated species communities (Boström and Bonsdorff, 1997; Hewitt et al., 2008; Christie et al., 2009; Törnroos et al., 2013). Fish often rely on multiple habitats during their life cycle and frequent coastal habitats seasonally (Bonsdorff and Blomqvist, 1993; Seitz et al., 2014). Habitats are thus not isolated entities, but linked through the migration of mobile organisms and also

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through their hydrology, sediment transport and the transfer of nutrients (Davidson et al., 1991).

To assess and compare the diversity of communities in different areas or habitats, two different approaches have been applied. The more traditional taxonomic way of analysing biodiversity is based on species identities, whereas the other approach is focusing on the biological traits of organisms, often defined as any morphological, physiological, phenological or behavioural characteristic of an organism affecting its individual performance (Violle et al., 2007). It has been suggested that the biological trait approach is better suited to explain ecosystem functioning, since it is not species identity *per se* but species characteristics that dictate their interactions, responses and ecological role within food webs and ecosystems (Díaz and Cabido, 2001; Bremner et al., 2003; Gagic et al., 2015). Thus, a combination of taxonomic and trait-based measures is increasingly applied in the marine environment, in order to study the diversity, structure and functioning of communities (Pecuchet et al., 2016; Dencker et al., 2017; Lindegren et al., 2018).

The abundance and richness of invertebrate species is generally higher in structurally complex habitats compared to more homogeneous ones (Christie et al., 2009; Koivisto and Westerbom, 2010; Törnroos et al., 2013). A distinct community composition, both taxonomically and based on traits, has been found for invertebrates in different coastal habitats (Stål et al., 2007; Weigel et al., 2016; Bolam et al., 2017), but also for infaunal and epifaunal communities within and between these habitats (Törnroos et al., 2013). Likewise, coastal fish community abundance, biomass and species richness have been shown to be higher in vegetated habitats, such as seagrass meadows, shallow muddy habitats and rocky reefs, than in sandy areas (La Mesa et al., 2011; Verdiell-Cubedo et al., 2013). Correlations between biological fish traits and environmental parameters, e.g. salinity and human disturbances, have been identified (Keck et al., 2014; Pecuchet et al., 2016; Teichert et al., 2017; Beukhof et al., 2019) and morphological fish traits have been linked to the structural complexity of stream habitats in Brazil (Ribeiro et al., 2016).

Invertebrates are among the most studied organisms in biological trait analysis in the marine environment (Beauchard et al., 2017), and taxonomic and trait-based aspects of fish communities have been studied quite intensively in relation to environmental variables and gradients (e.g. Keck et al., 2014; Pecuchet et al., 2016; Törnroos et al., 2019). However, only few studies address taxonomic and trait biodiversity of fish in coastal habitats (e.g. Pihl et al., 1994; Pihl and Wennhage, 2002). Instead, there has been a focus on fish diversity in estuaries, without going into detail about habitat classifications within these estuarine areas or directly comparing communities among multiple habitats (e.g. Prista et al., 2003; Cardoso et al., 2011; Vasconcelos et al., 2011; Henriques et al., 2017). Furthermore, trait-based aspects of fish communities have been studied particularly well in tropical coral reefs (e.g. D'agata et al., 2014; Mouillot et al., 2014; Jacquet et al., 2017; Mihalitsis and Bellwood, 2019). Yet, to our knowledge, trait-based diversity and composition of fish communities have not been compared between specifically defined coastal habitat types until now, which could advance knowledge on the link between fish communities and their environment. Moreover, studies investigating communities appear to focus on one or only a few different habitats, as well as only one organism group at the same time (Pihl et al., 1994; Boström and Bonsdorff, 1997; Pihl and Wennhage, 2002; Fredriksen et al., 2010; Kalogirou et al., 2010; Koivisto and Westerbom, 2010; Weigel et al., 2016). Consequently, the comparison of invertebrate and fish communities between multiple habitats has been neglected, although this might provide more in-depth information on how biodiversity is distributed in coastal regions and its implications for ecosystem functioning.

Hence, the overall aim of this study is to compare the taxonomic and trait-based diversity and composition of benthic invertebrate and fish communities among multiple shallow coastal habitats. We include the following habitats in our analysis: a rocky reef, brown algal belt, bare sand and a seagrass meadow, which represent typical coastal habitats in the study area within the northern Baltic Sea (Rönnbäck et al., 2007). More specifically, we assess (1) if and how the habitats differ in terms of taxonomic and trait biodiversity (richness, evenness, diversity) and community structure (composition) of both invertebrates and fish, (2) which habitats display the highest taxonomic and trait-based biodiversity of invertebrates and fish and (3) which species and traits are responsible for between-habitat differences. Based on our results, we discuss whether the diversity pattern among the habitats is similar for invertebrates and fish, and whether the taxonomic and trait approach display diversity in the same way in the different habitats.

2. Methods

2.1. The habitats

We applied the habitat definition of Airoldi and Beck (2007), where a habitat refers to the most dominant characteristic responsible for the structural complexity in an environment. Such structural complexity can arise both from vegetation (e.g. seagrass meadow) or geological structures (e.g. rocky bottoms). We sampled benthic invertebrates (macrofauna) and fish in four coastal habitat types during July and August 2016 including a rocky reef (hereafter "*Rock*"), algal belt (hereafter "*Fucus*"), bare sand (hereafter "*Sand*") and seagrass meadow (hereafter "*Zostera*"). These habitats were located in semi-exposed areas in the south-western part of the Åland Islands, which are situated in the northern Baltic Sea at the entrance of the Gulf of Bothnia (Fig. 1). Salinity in the study area ranges between 5 and 6.

The *Rock* habitat was characterized by large boulders and rocks covered with branching and filamentous red (*Furcellaria lumbricalis*, *Vertebrata fucoides*, *Coccotylus truncates*, *Phyllophora pseudoceranoides*, *Ceramium tenuicorne*), green (*Cladophora glomerata*) and brown algae (*Chorda filum*, *Pylaiella littoralis*, *Ectocarpus siliculosus*). The *Fucus* habitat was dominated by bladderwrack (*Fucus vesiculosus*) and associated epiphytic algae (*Pylaiella littoralis*, *Ectocarpus siliculosus*, *Elachista fucicola*) and some filamentous red and green algae (e.g. *Ceramium tenuicorne*, *Cladophora glomerata*) (Törnroos et al., 2013). The *Sand* habitat consisted of bare sand sediment, whereas the *Zostera* habitat consisted mainly of seagrass (*Zostera marina*) and to a smaller extent of macrophytes (e.g. *Stuckenia* spp.), *Chorda filum* and filamentous algae. For the analysis of the invertebrate community, the *Zostera* habitat was additionally divided into two sub-communities: "*Zostera Epifauna*" and "*Zostera Infauna*". This was done because the seagrass aboveground and belowground areas constitute two sub-habitats within *Zostera*, characterized by differing, yet linked, structures determining their complexity (seagrass blades above the sediment surface versus sediment and seagrass roots below the sediment surface).

2.2. Invertebrate and fish community sampling

Invertebrates and fish were collected in the centre of the habitats in order to avoid edge effects potentially biasing community composition. The sampling procedure for invertebrates was adopted from Törnroos et al. (2013). Benthic invertebrates were sampled through SCUBA diving at a depth of two to five meters. In each habitat, 15 replicate samples were taken. Invertebrate epifauna in *Rock*, *Fucus* and *Zostera* were sampled with net bags in a 25 cm × 25 cm area by collecting plant and algal material including the associated organisms within a frame. Infauna in the *Zostera* and *Sand* habitat was sampled with sediment cores, so that one replicate sample consisted of four sediment cores deployed in a 25 cm × 25 cm area (volume = 0.589 dm^3). Invertebrate samples were sieved (0.5 mm mesh size) and preserved in 70% ethanol until further processing. Organisms were identified to the lowest possible taxonomic level and the corresponding number of individuals counted. Epifaunal invertebrate densities were standardized to sample
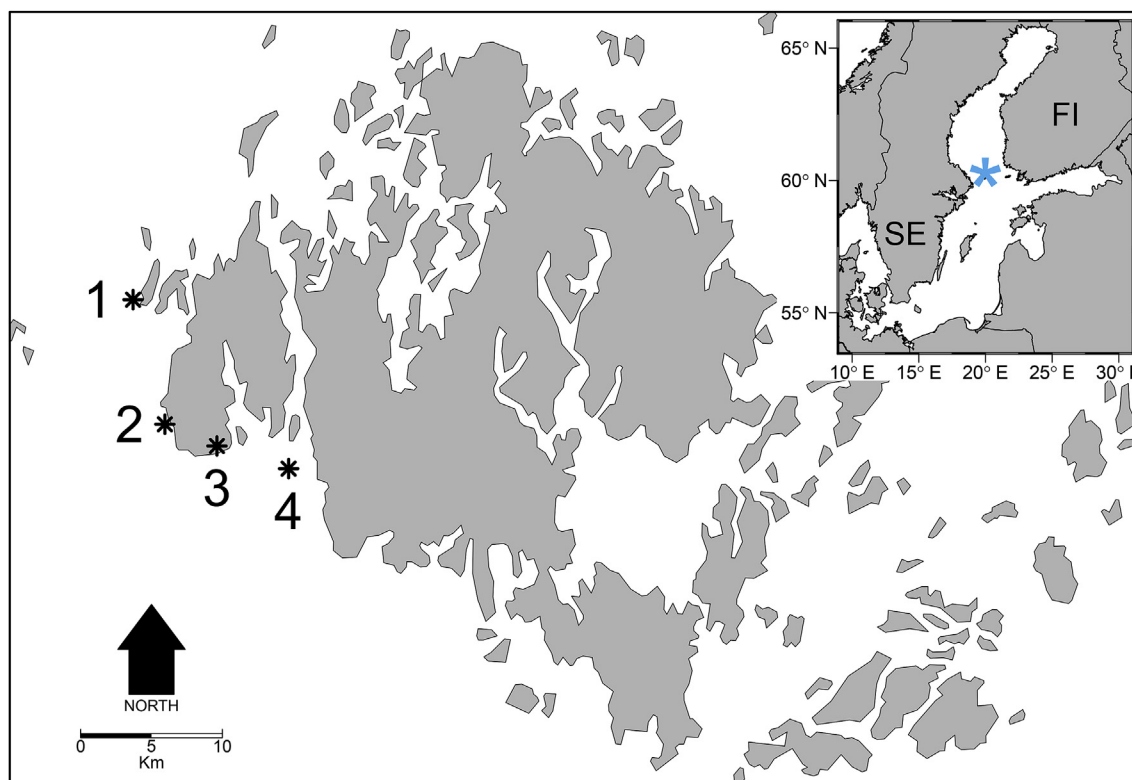
Fig. 1. Location of study sites on the Åland Islands where invertebrate and fish communities were sampled, including a *Fucus* (1), *Zostera* (2), *Sand* (3) and *Rock* (4) habitat. The blue star in the inset map marks the location of the Åland Islands and its position within the Baltic Sea between Sweden (SE) and Finland (FI). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

volume. This was measured as the volume of algae, bladderwrack, seagrass and macrophytes with the water replacement method (mean sample volume ± SD for *Rock*: 0.042 ± 0.014 dm^3, *Fucus*: 0.333 ± 0.109 dm^3, *Zostera Epifauna*: 0.099 ± 0.039 dm^3) for each replicate making it possible to quantitatively compare samples from different habitats with each other. For the biological trait analysis, the body size of individuals was measured under a light microscope to the nearest μm. When there were more than 100 individuals of a species in a sample, body size was recorded for a representative subsample of at least 50 individuals.

Fish were sampled using four gillnets (multi-mesh Nordic survey nets, 30 m length, 1.5 m depth, 5–55 mm mesh sizes; see Appelberg et al., 1995) per habitat at three to seven meters depth. Four gillnets were assumed to present a sufficient number of replicates in order to representatively sample the fish community considering the size of the habitats. The nets were deployed in the evening and retrieved the following morning, resulting in a fishing effort of approximately 12 h. In conjunction with the gillnets, qualitative fishing was carried out at the same sites using minnow traps for comparison with the gillnet communities in order to assess whether gillnets were selective in catching fish species. Individual fish were identified to species level and counted. The body size was measured to the nearest mm for each individual.

2.3. Invertebrate and fish traits

Although the approach falls under a general functionality framework, the traits examined in this study were not directly linked to specific ecosystem processes. More specifically, traits were chosen to characterize the basic ecology of the organisms, covering fundamental life-history aspects related to size, reproduction, movement, feeding, morphology and living environment (Beauchard et al., 2017). For the analysis, six traits were used for fish, (adapted from Stuart-Smith et al., 2013; Pecuchet et al., 2016; Törnroos et al., 2019), and nine traits for

invertebrates (Törnroos and Bonsdorff, 2012, Table 1, for trait sources see supplement). All traits included in the analysis where categorical, except for *Body size*. For instance, the trait *Habitat* for fish was separated into the categories *benthopelagic*, *demersal* and *pelagic*. Each recorded species was assigned to one or, if applicable, several trait categories by scoring them as either 1 (trait category present) or 0 (trait category absent). To standardize between traits with a differing number of categories, all categories were divided by the total number of categories expressed to sum up to one per trait. The mean body size per replicate was included as a continuous trait for both invertebrates and fish. When length was missing for a replicate due to e.g. non-intact individuals, the mean length of the species from all other replicates within the respective habitat was used. In the cases where trait data of a certain species were not available, trait information was derived from the closest taxon. The trait information for each species was combined in a species-trait matrix.

2.4. Statistical analysis

To compare taxonomic and trait diversity of the communities between the habitats, univariate analyses were performed on both taxonomic (species richness, Pielou's evenness and Shannon index) and corresponding trait-based indices (trait richness, trait evenness and trait dispersion). The structure of the communities expressed as the taxonomic (species) and trait composition within the habitats was analysed using multivariate analysis.

The taxonomic indices were calculated for each habitat and organism group, with the vegan package (Oksanen et al., 2018) in the open source software R, version 3.4.2 (R Core Team, 2017). The analysis of trait diversity and composition within the habitats was conducted with the FD package (Laliberté and Legendre, 2010; Laliberté et al., 2014). In this analysis, the species-trait matrix was weighted by mean log-transformed abundances (dm^{-3} for invertebrates and catch-

Table 1
List of invertebrate traits (8 categorical, 1 continuous) and fish traits (5 categorical, 1 continuous) and their categories used in the biological trait analysis. Labels correspond to the trait categories displayed in Figs. 5 and 6.

Trait	Categories	Labels	Relevance
Invertebrates			
Body size	continuous[a]	–	Growth rate, productivity, metabolism, feeding interactions
Longevity	very short (< 1 yr)	vsho	Life cycle/lifespan, productivity
	short (1–2 yrs)	sho	
	long (2–5 yrs)	lon	
	very long (5–10 yrs)	vlon	
Reproductive frequency	annual episodic	anep	Reproduction, productivity
	annual protracted	anpr	
	semelparous	sem	
Living habit	attached	att	Living environment, dispersal, foraging mode
	burrow dweller	budw	
	free	free	
	tube dweller	tub	
Feeding position	suspension feeder	sus	Food acquisition, feeding mode
	surface feeder	surf	
	sub-surface feeder	susurf	
	selection feeder	sel	
	miner	min	
	parasite	para	
Resource capture method	cirri	cirr	Food acquisition, complementary to *Feeding position*: summarize diet
	jawed	jaw	
	net	net	
	pharynx	phar	
	radula	rad	
	siphon	siph	
	tentaculate	tent	
Movement type	no movement	nom	Mobility, dispersal, ability to escape predation
	swimmer	swim	
	rafter-drifter	raft	
	crawler	crawl	
	byssus threads	byss	
	tube	tube	
	burrower	burr	
Body design	articulate	art	Body structure, protection against predation
	bivalved	biv	
	conical	con	
	turbinate	tur	
	vermiform segmented	ves	
	vermiform unsegmented	veun	
Sociability	solitary	sol	Social behaviour
	gregarious	greg	
	aggregated	agg	
Fish			
Body size	continuous[a]	–	Growth rate, productivity, metabolism, feeding interactions
Diet	piscivorous	pisc	Feeding type, food acquisition, ecological niche occupation
	benthivorous	benth	
	planktivorous	plank	
	generalist	gen	
Habitat	benthopelagic	benpel	Living environment/habit
	demersal	dem	
	pelagic	pel	
Caudal fin shape	continuous	con	Movement and activity
	emarginated	emar	
	forked	fork	
	rounded	roun	
	truncated	trun	
Body shape	deep	deep	Habitat, activity, position in the water column
	eel-like	eel	
	elongated	elon	
	flat	flat	
	normal	nor	

Table 1 (*continued*)

Trait	Categories	Labels	Relevance
Schooling behaviour	singleton	singl	Social behaviour, foraging strategy
	paired, sometimes small schools	pair	
	always schools	scho	

[a] Derived from measurements of individuals of each species in the samples.

per-unit-effort for fish) per replicate which corresponds to one gillnet for fish (in total four replicates per habitat) and to the sum of four sediment cores or one net-bag for invertebrates (in total 15 replicates per habitat). In this FD calculation, we weighted each trait category by the total number of categories expressed in the given trait, giving an equal importance to the trait categories during the computation. To compare the trait diversity between habitats, the following indices were calculated. Trait richness, describes the amount of trait space that is occupied by the species within a community (referred to as functional richness in Mason et al., 2005) and therefore represents the number of trait categories that are expressed within a habitat. Trait evenness refers to how evenly species abundances are distributed between the expressed trait categories (referred to as functional evenness in Mason et al., 2005). Trait dispersion describes the abundance weighted mean distance of individual species to their weighted group centroid in the multidimensional trait space, hence reflecting the spread of the community in the trait space. Thus, it can be considered as a measure for trait diversity, with higher values pointing to a higher trait diversity, since the community is then more spread around their group centroid in the trait space (referred to as functional dispersion in Laliberté and Legendre, 2010). Additionally, community-level weighted means of trait values (CWM), representing the expressed trait categories weighted by abundances, were computed for each replicate and are used to compare the trait composition between the habitats. To display the high variability between the two dimensions of the *Zostera* habitat for invertebrates, the indices were calculated both for the entire *Zostera* habitat, and separately for *Zostera Epifauna* and *Zostera Infauna*. In the entire univariate and multivariate analysis of the invertebrate data, three replicates from the *Sand* habitat were excluded due to a sampling error. Differences in the indices between the habitats were analysed with generalized linear models (glm) using the *glm*-function in R. We used a normal distribution to model all taxonomic and trait-based indices for the fish community, as well as for Pielou's evenness, the Shannon index, and the trait evenness and dispersion of invertebrates. For invertebrate species richness, we used a quasipoisson distribution with a log-link function to account for underdispersion. Due to unequal variances, generalized least squares (gls) from the nlme package (Pinheiro et al., 2017) were conducted for the trait richness of invertebrates, since gls allow heteroscedasticity (the variances are weighted). An ANOVA of Type II Sum of Squares from the car package (Fox and Weisberg, 2011) was applied to conduct the F-test on the glm outputs and the Wald Chi-Squared test on gls outputs. For both glm and gls, residuals were plotted against fitted values to check that the models met their assumptions regarding data normality and homoscedasticity. To test how specific habitats differed from each other, post-hoc tests were conducted after F/Chi-Squared tests using the Bonferroni correction.

To assess structural community differences between habitats, we performed non-metric multidimensional scaling (nMDS) on the taxonomic (based on abundance values) and trait (based on CWM values) composition of invertebrates and fish separately. We applied the Bray-Curtis dissimilarity for species abundances and the Gower distance for CWM trait values. To test for differences in taxonomic and trait composition among habitats, we used permutational multivariate ANOVAs (PERMANOVA) with 9999 permutations. For each PERMANOVA, a permutational test of multivariate dispersion (PERMDISP) was

conducted to check if the within-group spread from the observations to their group centroid (multivariate dispersions) was equal between the habitats. The data on invertebrate taxonomic and trait composition displayed heterogeneous dispersions and an unbalanced design due to the removed replicates from the *Sand* habitat (only 12 instead of 15 replicates). Since PERMANOVA is very robust to heterogeneity, but only if the design is balanced (Anderson and Walsh, 2013), a balanced design was achieved by randomly selecting 12 replicates from each of the other four habitats (*Fucus, Rock, Zostera Epifauna, Zostera Infauna*). This randomization was repeated several times. Results from these PERMANOVAs with a reduced replicate number were compared to those that were obtained when using the complete dataset with the unbalanced design, showing a great concordance between the results (not shown). We therefore used the results from the PERMANOVA with the reduced/balanced replicate number. A SIMPER (similarity percentage) analysis was applied to examine the dissimilarity between the habitats concerning taxonomic and trait composition, and additionally to identify the contribution of species and traits to these habitat differences. All multivariate analyses were performed with the vegan package (Oksanen et al., 2018). For the invertebrates, the epifaunal and infaunal data from the *Zostera* habitat were kept separate for both univariate and multivariate analyses. All invertebrate and fish abundances were log-transformed prior to analysis. Maps were generated in R using the packages: GISTools, rgdal, raster, oceanmap (Brunsdon and Chen, 2014; Bivand et al., 2017; Hijmans, 2017; Bauer, 2018).

3. Results

3.1. Taxonomic and trait diversity in coastal habitats

In total, 34 invertebrate taxa and 18 fish species were found in the studied habitats. For both invertebrates and fish, the species- and the trait-based indices differed significantly among the habitat types (Table 2).

Invertebrate species richness (Fig. 2a) was higher in the vegetated habitats, *Rock, Fucus, Zostera Epifauna* and *Zostera Infauna*, than in the *Sand* habitat (p < 0.001), which displayed the lowest number of species (7.7 ± 3.0 species). The highest species richness was found in *Zostera Infauna* (19.5 ± 1.8 species). Similar to species richness, trait richness differed between habitats (p < 0.001), and was lowest, but highly variable, in the *Sand* habitat (0.8 ± 0.4) and greatest in *Zostera Infauna* (1.3 ± 0.03, Fig. 2b). Both Pielou's evenness (Fig. 2c) and the

Table 2
Results from the statistical analysis on habitat differences concerning taxonomic and trait-based indices using glms (exception: gls for trait richness of invertebrates) and taxonomic and trait composition using PERMDISP and PERMANOVA, for both invertebrates and fish. * indicate significant differences among habitats. The significance level was set to 0.05.

Variables (method used)	Invertebrates			Fish		
	df	F	p	df	F	p
Species richness (glm)	4	38.42	< 0.001*	3	2.62	0.099
Pielou's evenness (glm)	4	5.13	0.001*	3	3.73	0.042*
Shannon index (glm)	4	26.92	< 0.001*	3	2.81	0.085
Trait richness (gls, glm)	4	93.30 (Chisq)	< 0.001*	3	4.31	0.028*
Trait evenness (glm)	4	40.72	< 0.001*	3	1.93	0.179
Trait dispersion (glm)	4	47.68	< 0.001*	3	3.14	0.065
Taxonomic composition (PERMDISP)	4	16.15	< 0.001*	3	2.13	0.149
Taxonomic composition (PERMANOVA)	4	50.34	< 0.001*	3	8.99	< 0.001*
Trait composition (PERMDISP)	4	8.59	< 0.001*	3	0.65	0.599
Trait composition (PERMANOVA)	4	31.63	< 0.001*	3	4.47	0.013*

trait evenness (Fig. 2d) of invertebrates displayed differences between habitats (Pielou's evenness, p = 0.001; trait evenness, p < 0.001). Whereas the epifauna in the *Zostera* habitat had the highest Pielou's evenness (0.7 ± 0.1, significant difference from *Rock* and *Fucus*), which points to rather evenly distributed species abundances in this habitat, the highest trait evenness was found in *Rock* (0.9 ± 0.02, significant difference from *Fucus, Sand* and *Zostera Infauna*), representing an even distribution of abundances between the expressed trait categories. Species abundances were least evenly distributed in the *Fucus* habitat (0.6 ± 0.07, significant difference from *Zostera Epifauna* and *Infauna*), suggesting the presence of certain dominant species. The dominating taxa in this habitat were gammarids and chironomids, contributing with 50% and 23%, respectively, to the overall abundance (Supplement, Fig. S1). *Zostera Infauna* displayed the most uneven distribution of abundances between the trait categories (0.7 ± 0.1) with the traits *Body size, solitary* and *annual protracted* exhibiting the highest CWM values (CWM > 0.5, Fig. 5d) in this habitat. These results show that evenness of abundances distributed between species does not necessarily reflect abundances distributed between the trait categories in the same habitat. For invertebrates, the Shannon index (Fig. 2e) resembled the species richness with the highest values in the *Zostera Infauna* habitat (2.0 ± 0.2, significant difference from *Rock, Fucus* and *Sand*) and the lowest values in *Sand* (1.2 ± 0.3, significant difference from *Rock, Zostera Epifauna* and *Infauna*), pointing to differences regarding the biodiversity of species between the habitats (p < 0.001). Differences between the habitats were likewise found for trait dispersion (Fig. 2f), which represents the trait diversity of the communities (p < 0.001). Invertebrates in the *Zostera Infauna* habitat expressed the highest trait diversity (0.4 ± 0.004), whereas *Fucus* and *Zostera Epifauna* had the lowest values (*Fucus*: 0.3 ± 0.02, *Zostera Epifauna*: 0.3 ± 0.01).
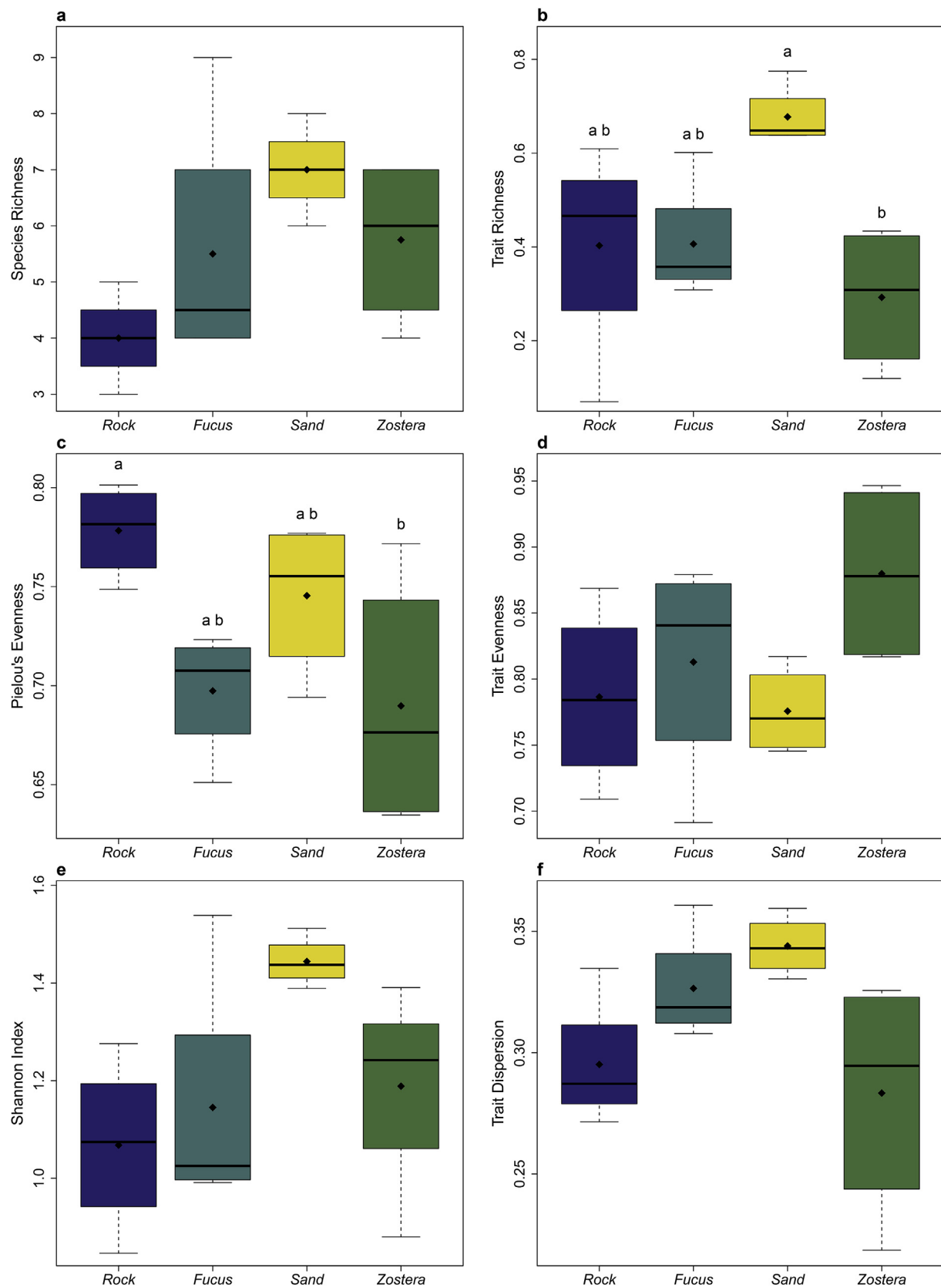
For the fish community, both species and trait richness (Fig. 3a and b) were highest in the *Sand* habitat (7.0 ± 0.8 and 0.7 ± 0.07, respectively). Trait richness differed among habitats (p = 0.028), however, the difference in species richness was statistically non-significant (p = 0.099), most likely due to the small number of replicates. Trait richness in the *Sand* habitat was significantly higher than in *Zostera* and higher, though not significantly, compared to *Rock* and *Fucus*. Pielou's evenness (Fig. 3c) differed among habitats (p = 0.042) with the most evenly distributed abundances between the fish species in *Rock* (0.8 ± 0.02), which were significantly more even than abundances in *Zostera*. Trait evenness (Fig. 3d) did not differ statistically among habitats (p = 0.179), nor did the Shannon index (p = 0.085, Fig. 3e) or trait dispersion (p = 0.065, Fig. 3f). Keeping in mind the non-significant differences among habitats, the highest taxonomic and trait diversity were found for the *Sand* habitat (Shannon index: 1.4 ± 0.05; trait dispersion: 0.3 ± 0.01). Fishing with minnow traps revealed that gillnets were selective, with smaller individuals not caught in them and thus some species not recorded at all (e.g. pipefish and sticklebacks). This sampling bias should be kept in mind when interpreting the results.

3.2. Taxonomic and trait composition in coastal habitats

We found distinct differences in the taxonomic composition of invertebrates among habitats (p < 0.001; Fig. 4a), although one has to consider that the data displayed heterogeneous dispersions due to the high variability in the *Sand* habitat (Table 2). However, this should not impair the PERMANOVA results, since the design was balanced (see Method section "Statistical Analysis"). The SIMPER analysis revealed a distinct separation in the taxonomic composition between the epifauna habitats, *Fucus, Rock* and *Zostera Epifauna*, and the two infauna habitats, *Sand* and *Zostera Infauna*, with between-group dissimilarities > 60% between epifauna and infauna habitats, respectively (Table 3). Moreover, the two infauna habitats differed clearly from each other with a dissimilarity of 67% between *Sand* and *Zostera Infauna*. The habitats'
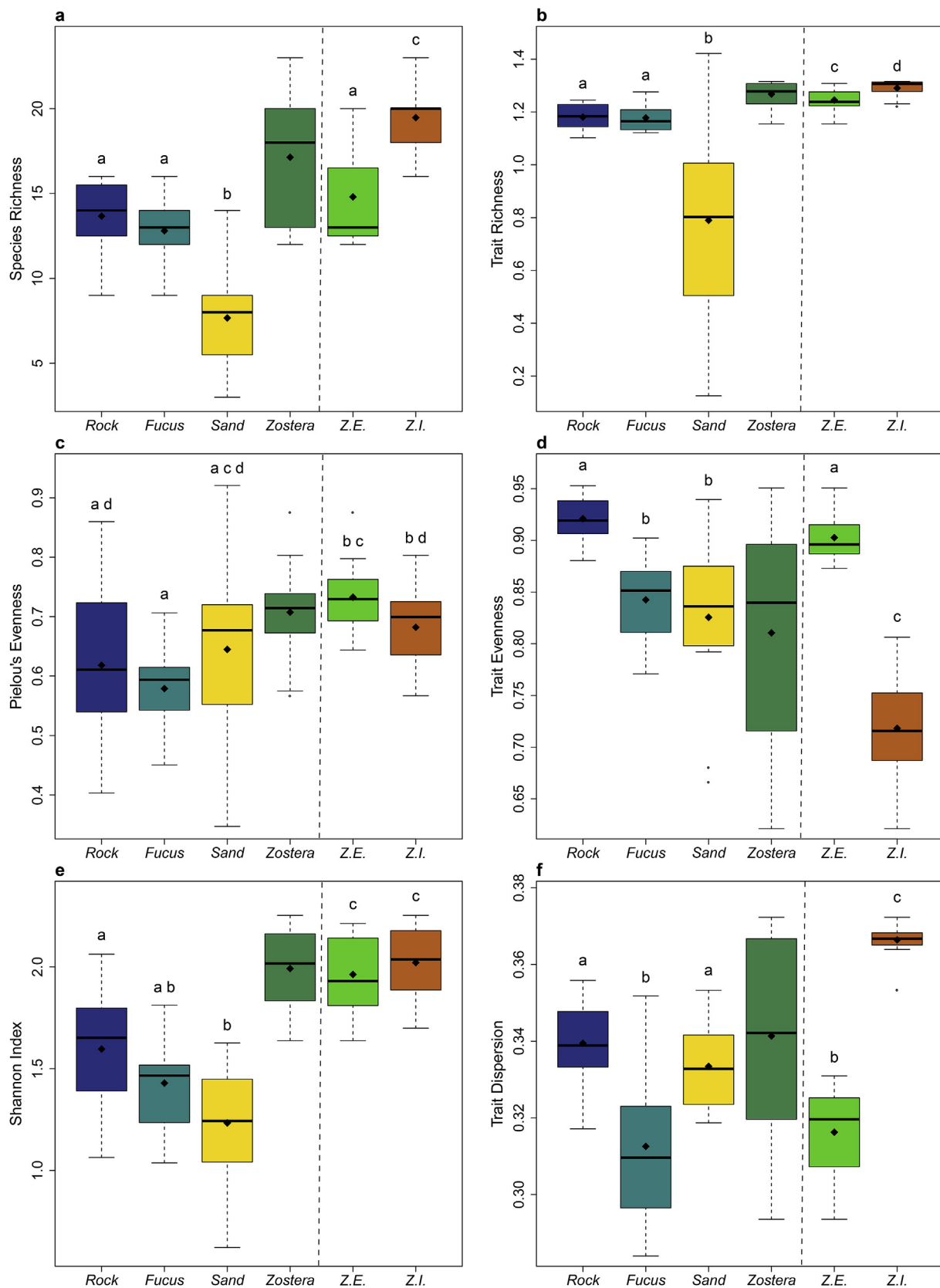
Fig. 2. Taxonomic and trait-based indices of the invertebrate communities in the different habitat types: species richness (a) and trait richness (b), Pielou's evenness (c) and trait evenness (d), Shannon index (e) and trait dispersion (f). Note that the *Zostera* habitat is additionally divided into *Zostera Epifauna* (*Z.E.*) and *Zostera Infauna* (*Z.I.*). Whiskers of the boxes represent the lowest/highest values that still lie within 1.5 x the interquartile range from the box and thus represent minima and maxima when no outliers exist. Outliers are displayed as dots in the plots. Diamonds represent the mean value for each habitat and letters indicate significant differences between habitats. Habitats with the same letter are not significantly different. The significance level was set to 0.05.

Fig. 3. Taxonomic and trait-based indices of the fish communities in the different habitat types: species richness (a) and trait richness (b), Pielou's evenness (c) and trait evenness (d), Shannon index (e) and trait dispersion (f). Whiskers of the boxes represent the lowest/highest values that still lie within 1.5 x the interquartile range from the box and thus represent minima and maxima when no outliers exist. Diamonds represent the mean value for each habitat and letters indicate significant differences between habitats. Habitats with the same letter are not significantly different. The significance level was set to 0.05.
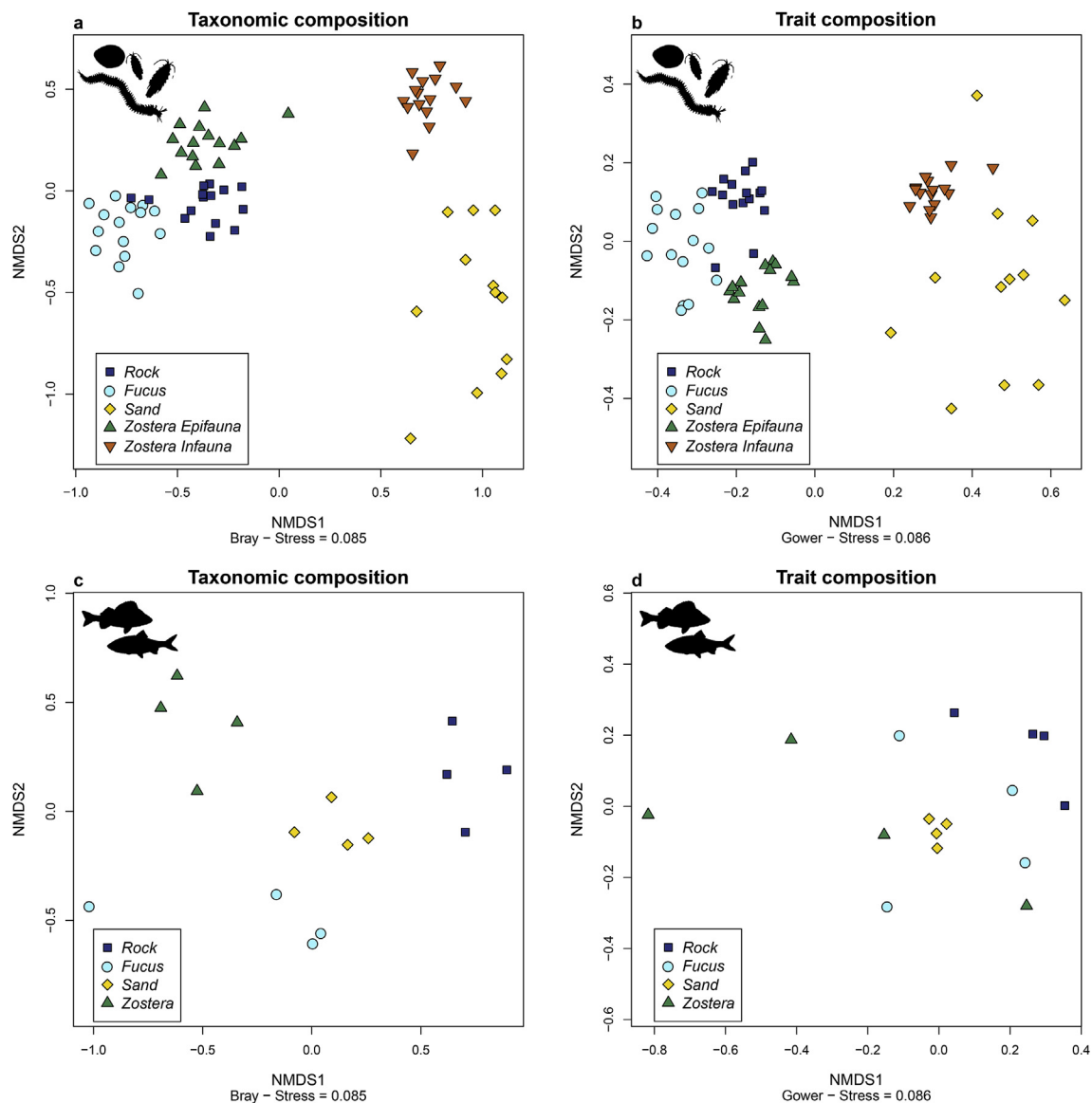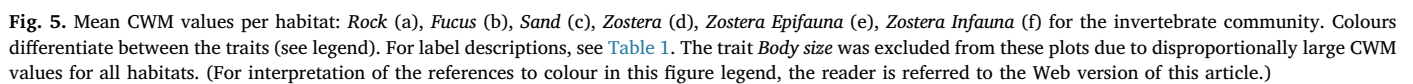
Fig. 4. nMDS on taxonomic composition based on abundances (a, c) and trait composition based on CWM values (b, d) for invertebrates (a, b) and fish (c, d).
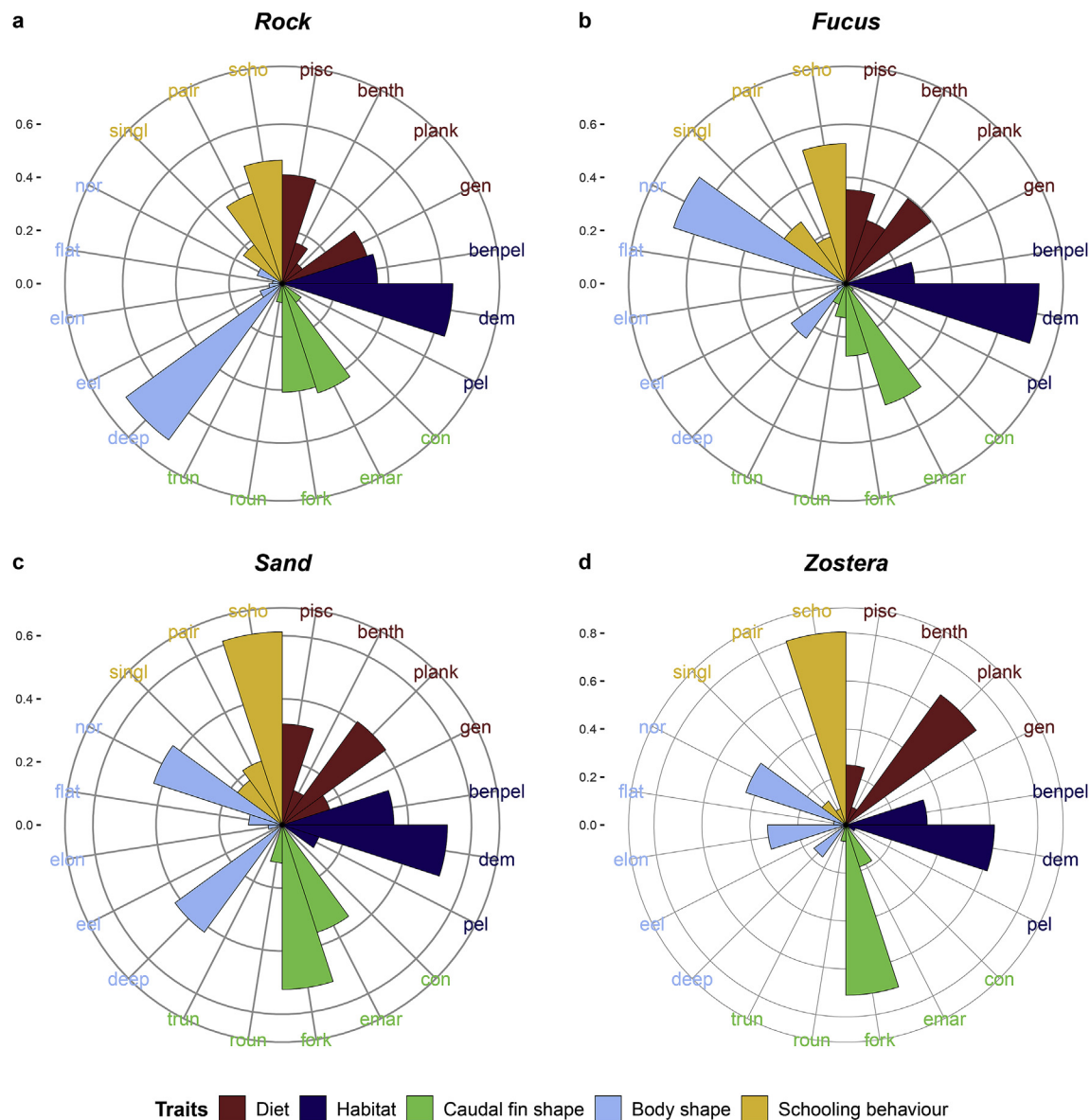
dissimilarity based on the trait composition of invertebrates (Fig. 4b) resembled the one on taxonomic composition, displaying clear differences between the habitats (p < 0.001). There was a dissimilarity of > 20% between the respective epifauna (*Fucus, Rock, Zostera Epifauna*) and the infauna (*Sand, Zostera Infauna*) habitats, and additionally a 23% dissimilarity between *Sand* and *Zostera Infauna* (Table 3). The traits contributing most to the between-habitat differences of *Sand* and *Zostera Infauna* were *Body size, Longevity, Resource capture method, Sociability* and *Body design*, explaining together 56% of the between-habitat dissimilarities (Supplement, Table S2). In *Sand,* the trait categories *very short* longevity, *pharynx* and *gregarious* dominated (Fig. 5e), whereas a *short* longevity, *radula* and a *turbinate* body design were more expressed in *Zostera Infauna* (Fig. 5d). Of all traits, *Body size* contributed most to all between-habitat dissimilarities regarding the trait composition (Supplement, Table S2, Fig. S3a). Generally, the habitats were more similar from a trait-based point of view with dissimilarities between 11 and 34%, than taxonomically (36–95% dissimilarities) (Table 3).

For fish, the taxonomic composition (Fig. 4c) differed clearly between habitat types (p < 0.001). The highest between-habitat dissimilarity was found between *Rock* and *Zostera* (73%, Table 3) with

herring (*Clupea harengus*), roach (*Rutilus rutilus*) and lesser sandeel (*Ammodytes tobianus*) contributing most to the differences (61% cumulative contribution; Supplement, Table S3). The *Rock* habitat also differed distinctly from the *Fucus* habitat (69% dissimilarity, Table 3) with roach, herring and ruffe (*Gymnocephalus cernua*) making up 56% of the habitat dissimilarities (Supplement, Table S3). Thus, *Rock* differed from the other habitats due to its high abundances of roach and low abundances of herring, respectively (compare Supplement, Fig. S2). The PERMANOVA also showed differences in the trait composition of fish (Fig. 4d) between the habitats (p = 0.013). Dissimilarities concerning the trait composition ranged between 3 and 7%, whereas dissimilarities based on taxonomic composition were between 48 and 73% (Table 3) suggesting that the habitats were more similar based on traits than taxonomically. The highest between-habitat difference based on traits was found between *Rock* and *Sand* (7% dissimilarity). The responsible traits for this difference were *Body size*, a *normal* body shape and a *planktivorous* diet of the fish in *Sand* and *Body size*, a *deep* body shape and a *generalist* diet in the *Rock* habitat (Supplement, Table S4; Fig. 6b and d). Therefore, the fish community in *Rock* is most dissimilar from the other habitats based on taxonomic as well as trait composition. As for invertebrates, *Body size* was the trait contributing most to all

Fig. 5. Mean CWM values per habitat: *Rock* (a), *Fucus* (b), *Sand* (c), *Zostera* (d), *Zostera Epifauna* (e), *Zostera Infauna* (f) for the invertebrate community. Colours differentiate between the traits (see legend). For label descriptions, see Table 1. The trait *Body size* was excluded from these plots due to disproportionally large CWM values for all habitats. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 6. Mean CWM values per habitat: *Rock* (a), *Fucus* (b), *Sand* (c), *Zostera* (d) for the fish community. Colours differentiate between the traits (see legend). For label descriptions, see Table 1. The trait *Body size* was excluded from these plots due to disproportionally large CWM values for all habitats. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

between-habitat dissimilarities concerning the trait composition of the fish community (Supplement, Tables S2 and S4, Fig. S3b).

4. Discussion

To improve the knowledge on the link between organisms and their environment, we examined the taxonomic and trait diversity and community composition of invertebrates and fish in different coastal habitat types in the northern Baltic Sea. Our study revealed that communities in rocky reef, algal belt, bare sand and seagrass habitats possess a distinct diversity and composition from both a taxonomic and trait-based point of view, which suggests potential implications for the ecosystem functioning in these different areas.

4.1. Invertebrate and fish biodiversity in coastal habitats

The invertebrate community in the *Zostera Infauna* habitat displayed the highest number of species and expressed trait categories, as well as the highest taxonomic and trait diversity, making it the most diverse

habitat for invertebrates in this study. Thus, *Zostera* sediments provide an important habitat for this organism group, which emphasizes the significance of seagrass meadows for biodiversity. It is commonly recognized that seagrass habitats belong to the most species-rich areas in the marine environment (Boström and Bonsdorff, 1997; Duarte, 2002), providing numerous important ecosystem services. Besides the fact that seagrass meadows on a global scale offer habitats for several endangered and commercially important organisms, including invertebrates, they also contribute with high primary production, improved water clarity, stabilization of sediments and play an important role in nutrient cycling (Duarte, 2002; Nordlund et al., 2016).

Coastal habitats associated with vegetation typically demonstrate a higher invertebrate biodiversity than non-vegetated habitats (Boström and Bonsdorff, 1997; Törnroos et al., 2013). This was also the case in our study, illustrated by the higher species and trait richness, as well as Shannon diversity, in the vegetated habitats (i.e. algal growth in the *Rock* habitat, bladderwrack and seagrass) compared to *Sand*. Additionally, the invertebrate community in *Zostera Infauna* was more diverse compared to the *Sand* infauna community emphasizing that

Table 3
Average between-group dissimilarities (%) between the habitats for the taxonomic and trait composition of invertebrates and fish, as result of the SIMPER analysis.

Average between-group dissimilarity (%)		
Habitats	Taxonomic Composition	Trait Composition
Invertebrates		
Fucus - Rock	39.63	14.45
Fucus - Zostera Epifauna	41.23	11.35
Fucus - Zostera Infauna	81.29	25.71
Fucus - Sand	94.52	34.30
Rock - Zostera Epifauna	35.94	14.42
Rock - Zostera Infauna	68.42	22.08
Rock - Sand	87.68	32.15
Zostera Epifauna - Zostera Infauna	62.84	23.63
Zostera Epifauna - Sand	87.09	29.94
Zostera Infauna - Sand	66.74	22.84
Fish		
Fucus - Rock	69.36	3.75
Fucus - Sand	47.84	4.99
Fucus - Zostera	59.42	3.03
Rock - Sand	48.77	6.69
Rock - Zostera	73.38	3.48
Sand - Zostera	54.20	5.80

invertebrate biodiversity is higher in vegetated sediments than in unvegetated sediments (Boström and Bonsdorff, 1997; Fredriksen et al., 2010; Törnroos et al., 2013). Aquatic vegetation change hydrodynamic conditions by reducing current velocities and wave energy, which increases the deposition of organic material as a food resource and the settlement of larvae leading to increased species diversity in these areas compared to non-vegetated sediments. Furthermore, vegetation alters sediment properties by reducing subtidal sediment erosion causing a higher sediment stability in vegetated areas (Fonseca and Fisher, 1986; Koch, 2001; Boström et al., 2010). The root-rhizome system of *Zostera* meadows provides additional structure in the sediment, thus offering more potential niches for organisms (Boström and Bonsdorff, 1997). Hard substrates, such as rocks, represent another structure increasing species richness and diversity in coastal environments by enhancing the settlement of sessile organisms and providing shelter for mobile invertebrates by offering increased structural complexity (McGuinness and Underwood, 1986; Walters and Wethey, 1996; Downes et al., 1998). Our study therefore highlights the importance of vegetation and hard substrates for invertebrate diversity in coastal habitats.

For most indices, as well as the taxonomic and trait composition, the invertebrate data in *Sand* was spread rather broadly, suggesting a high species and trait heterogeneity within this habitat compared to the others. Sand habitats thus represent highly variable and dynamic habitats regarding their invertebrate communities (Quillien et al., 2015). This might be due to the lack of stabilizing forces provided by additional structure, such as rocks and vegetation, and therefore a higher exposure to physical forces (e.g. waves) disturbing the environment and making it more heterogeneous.

Contrary to invertebrates, the fish community was taxonomically and from a trait-based point of view most diverse in the *Sand* habitat. This might seem rather unexpected, since higher fish abundances and diversity have been related to habitats that possess a higher structural complexity in more marine waters, for example at the Swedish west coast and in the Mediterranean Sea, such as vegetated areas and mussel beds (Pihl and Wennhage, 2002; La Mesa et al., 2011; Verdiell-Cubedo et al., 2013; Kristensen et al., 2015; Bergström et al., 2016). However, many fish species use shallow soft-bottom habitats as feeding, nursery and spawning grounds. For instance, juvenile flatfish utilize these regions in the northern Baltic Sea (Jokinen et al., 2015). Additionally, fish

migrate through shallow open water areas (Seitz et al., 2014), which could be another explanation for the higher richness and diversity in the *Sand* habitat. Yet, it is important to consider the sampling method and fish behaviour when interpreting the results. Due to the size-selectivity of gillnets that generally underestimate the amount of small fish (Olin et al., 2009) and the high mobility of fish that move regularly between different habitat areas (Seitz et al., 2014), one can only obtain a specific snapshot of the fish community composition in the habitats at a certain time (Mustamäki et al., 2015). This is complicated by the fact that the composition and number of fish species vary strongly with the time of day, with higher observed fish abundances during night (Pihl and Wennhage, 2002; Taal et al., 2017) when most species are active and therefore susceptible to passive fishing gears due to low visibility and probability of gear avoidance (He, 2006). These aspects make the assessment of fish communities and their association to any specific habitat difficult.

4.2. Invertebrate and fish community composition in coastal habitats

The taxonomic and trait composition of invertebrates showed a very similar arrangement of the habitats pointing out concordance between the species- and trait-based measures concerning community structure. The habitats display a characteristic community composition with a clear separation between the epifauna (*Rock*, *Fucus*, *Zostera Epifauna*) and infauna (*Zostera Infauna*, *Sand*) habitats, but also between the two infauna habitats emphasizing a distinct taxonomic and trait invertebrate community composition for vegetated and for non-vegetated habitats and sediments. A unique taxonomic invertebrate composition has been recorded in seagrass epifauna and infauna, *Fucus* and bare sand habitats in marine waters in Norway (Christie et al., 2009; Fredriksen et al., 2010). Furthermore, the same separation between epifaunal and infaunal invertebrate assemblages regarding species and traits has been noted in the northern Baltic Sea (Törnroos et al., 2013). Thus, taxonomic and trait composition of invertebrate assemblages seem to depend on the structural complexity of the respective habitat.

As for invertebrates, the taxonomic and trait composition of the fish community differed between habitats. In particular, the samples from the *Rock* habitat clustered together and were most dissimilar from the other habitat types. A distinct taxonomic composition has been documented for marine areas, for instance in shallow rocky and soft bottom habitats along the Swedish west coast (Pihl et al., 1994; Pihl and Wennhage, 2002) and in seagrass, rocky algal reefs, sand and mud habitats in the Mediterranean Sea (La Mesa et al., 2011; Verdiell-Cubedo et al., 2013). However, the trait composition of fish communities in habitats has so far been unexplored. In our study, *Zostera* was dominated by marine species, such as herring and lesser sandeel. On the contrary, the *Rock* habitat hosted a higher proportion of freshwater species, such as roach and perch, and only few marine species, displaying the lowest abundances of herring. This is likely due to its position around the Åland islands, closest to the inner archipelago, where freshwater species predominantly occur. These features of the taxonomic composition are reflected in the trait composition of fish in *Rock*, as the traits *deep* body shape and a *generalist* diet, representing traits of roach and perch, were more expressed in *Rock* compared to the other habitats. Our study therefore shows that fish communities in different coastal habitats have a specific trait composition, though to a lesser degree in comparison to the already documented distinct taxonomic composition. Certain fish species with a certain set of traits appear to be associated with some habitats rather than with others, potentially expressing habitat preferences.

Occurrence and number of functional traits have been linked to the rates and scale of various ecosystem processes (Díaz and Cabido, 2001; Gagic et al., 2015). Traits included in this study were not chosen based on their relevance for ecosystem functioning *per se*, but rather to capture a broad variety of organism characteristics. Thus, not all of them can be referred to as "functional" in the context of being associated with

ecosystem scale processes. Instead, some of the traits are rather important for the organism itself and for it to occupy a certain environment, e.g. *caudal fin shape* of fish. However, the expression of different biological traits in the habitats for both invertebrates and fish, displayed by the characteristic trait composition in the habitats (Figs. 5 and 6), suggests that assemblages in different habitats may contribute differently to ecosystem processes. For example, the *feeding mode* of an organism provides information on the role it plays within trophic processes. In the *Sand* and *Zostera* habitat, *planktivorous* fish species dominated, suggesting that these habitats support the pelagic energy pathway. However, *Rock* and *Fucus* had higher proportions of *benthivorous* and *generalist* (i.e. feeding on plant material and detritus in addition to benthic and planktonic organisms) fish. This suggests that the latter habitats have a stronger benthic trophic pathway compared to the other habitats. Correspondingly, *suspension feeding* represents one of the dominating *feeding modes* for the invertebrate community in *Sand* and *Zostera*, supporting the pelagic pathway in these habitats. This indicates that different habitats have a potentially varying, and complementary, importance for ecosystem functioning. However, this aspect should be examined more thoroughly using targeted functional traits and linking them directly to ecosystem processes.

4.3. Invertebrate versus fish community

We did not find the same biodiversity pattern for invertebrates and fish in the studied habitats, as the highest taxonomic and trait diversity for invertebrates was found in the *Zostera Infauna* habitat, and in the *Sand* habitat for fish. However, there were some commonalities between the two organism groups, as they were both more similar regarding traits than taxonomically between habitats and the trait *Body size* of both invertebrates and fish contributed most to all between-habitat dissimilarities from a trait-based point of view. Since benthic invertebrates and fish are linked by a trophic relationship (Bonsdorff and Blomqvist, 1993), a correlation between their richness and diversity measures in the habitats could be expected. However, previous studies indicate that such correlations are not always supported by evidence from the field (Törnroos et al., 2019). In terms of food web architecture, the basal resources (habitats) with associated invertebrate consumers provide a heterogeneous landscape, whereas higher-level organisms (mobile fish) spatially couple the available resources (Rooney et al., 2008). In addition, since fish do not only utilize these habitats for feeding, but also for other purposes (Seitz et al., 2014), a correlation between the two organism groups might not be possible to find. A higher trait similarity than a taxonomic one has previously been recorded for invertebrate communities between different coastal habitats (Törnroos et al., 2013), and fish assemblages in European rivers express a lower trait-based than taxonomic dissimilarity (Villéger et al., 2014). Likewise, tropical fish in the Gulf of Mexico have a low trait but simultaneously a high taxonomic beta-diversity between assemblages (Villéger et al., 2010, 2012). Correspondingly, we show that although two habitats might differ in their taxonomic composition, the species present possess overlapping traits (i.e. similar trait identities), making the habitats more similar from a trait-based point of view than from a taxonomic one. Our results highlight that this pattern applies to both organism groups, invertebrates and fish, among multiple habitats. Body size generally plays a significant role in ecology and has been described as the master trait for many organisms (Andersen et al., 2016; Brose et al., 2017). It is correlated with many life-history traits, such as growth rate, productivity, mortality and the metabolism of organisms. Additionally, body size plays a pivotal role in the structure and dynamics of food webs (Brown et al., 2004; Woodward et al., 2005; Nordström et al., 2015). Our study emphasizes the importance of body size as a trait in ecosystems, since it plays a major role in differentiating communities between different habitats based on traits.

4.4. Taxonomic versus trait-based approach

Part of the study was to examine whether the taxonomic and biological trait approach agree when describing biodiversity and community composition in the habitats. The indices based on species and traits corresponded quite well with each other (e.g. species and trait richness for invertebrates) and the taxonomic and trait composition of invertebrates displayed a similar picture of the habitats. Yet, some indices diverged regarding species and trait diversity in the habitats. Invertebrates in *Zostera Epifauna* had a high Shannon index, but a comparatively low trait dispersion compared to the other habitats. Hence, habitats can display a high species diversity, but simultaneously be less diverse concerning traits, which points to redundant i.e. similar species regarding their traits in this habitat. Furthermore, abundances might be distributed rather evenly among species, but at the same time, they are distributed more unevenly among traits, as was the case for invertebrates in *Zostera Infauna*. Consequently, this habitat had some dominating traits, such as *Body size*, a *solitary* sociability, and an *annual protracted* reproductive frequency, emphasizing that there can be key functions in a habitat, even if no key/dominating species are present. This suggests that taxonomic measures cannot be solely applied to assess the diversity of communities since biological traits provide additional information on functions present in a community that cannot be captured by species-based indices. Accordingly, we conclude that it is necessary to consider both taxonomic and trait-based measures when assessing the biodiversity of organism assemblages in different habitats (Villéger et al., 2010, 2012; 2014; Aarnio et al., 2011; Taupp and Wetzel, 2018).

5. Conclusion

Our study provides new insights into the link between organism assemblages and their environment by demonstrating taxonomically and trait-based distinct communities of invertebrates and fish in different coastal habitats. Our results highlight the importance of structurally complex seagrass meadows, which support high taxonomic and trait diversity of invertebrates. Since these key habitats are severely threatened by human activities, efficient management measures are needed to protect them and safeguard their unique biota (Duarte, 2002; Airoldi and Beck, 2007). Taxonomic and trait composition of invertebrates depended on structural complexity i.e. the vegetation of the habitat. Bare sand habitats were important for the trait- and species-based diversity of fish, and we could show that different coastal habitats possess a certain trait composition in addition to a distinct taxonomic composition for the fish community. Communities differed more strongly taxonomically than based on their traits between habitats for both organism groups, emphasizing the existence of similar trait identities in the habitats. Moreover, we stress body size as the most important trait in distinguishing the trait composition of both invertebrate and fish communities between coastal habitats. Consequently, incorporating biological traits in the analysis of biodiversity clearly adds information to species-based measures, as these are only able to capture diversity on the level of species identities and cannot be related to the trait-based properties of a community. However, more knowledge on the ecological role of organisms is needed in order to evaluate the contribution of these communities to ecosystem functioning. Correspondingly, management and conservation of coastal habitats should include the biological traits of organisms in order to obtain a more comprehensive picture in the assessment of biodiversity.

Author contributions

- designed the field study: CH, MCN, AT, MS, EB.
- performed the field work and lab analysis: CH.
- conducted the statistical analysis of the data: CH, AT, LP, ML.
- wrote the manuscript: CH, MCN, AT, MS, LP, ML, EB.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106272.

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