A network of biological traits: Profiling consumer-resource interactions

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Full length article

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A R T I C L E   I N F O

A B S T R A C T

Trophic interactions can be both ephemeral and difficult to document, rendering their sampling often incomplete and context-dependent, which makes construction, analysis, and comparison of food webs challenging. Biological traits are central in determining co-occurrence of species (through dispersal, environmental, and interaction filters), as well as the potential for species interactions (through trait matching). Thereby, supplementing empirical, taxonomy-based information on trophic links with trait-based inference may help us build more realistic and adaptable food webs. Here, we go beyond taxonomy to document (i) how traits (e.g., body size, metabolic category and feeding strategy) contribute to local food web structure, and (ii) how associations of consumer-resource traits are structured. We built a trophic-link based trait-interaction network—or trait web—by combining multivariate approaches and network analysis. We found that consumer-resource associations organize into trait profiles that reflect the general vertical structure of the food web, as well as identify groups of limited sets of highly interacting traits. Finally, we discuss the implications of the findings for generating comprehensive and adaptive food webs.

1. Introduction

The study of food webs has been a central part of ecology for almost a century (popularized by Summerhayes and Elton, 1923, Elton, 1927). Though the field has advanced from simply mapping static trophic interactions to encompassing dynamical models, one critical issue has remained unresolved, namely, how to build realistic representations of food web topology both robustly and efficiently (Cohen et al., 1990; Olivier and Planque, 2017; Pringle and Hutchinson, 2020). Sampling empirical topologies requires collection of two main components: 'who' is there and 'who eats whom'. For a comprehensive topology, an extensive and often expensive sampling effort is necessary. This sampling is challenging because of the large diversity of life forms in nature that increases towards the bottom of the food web, and from larger to microscopic organisms. Moreover, it is challenging to properly record rare or cryptic species, let alone observe with which species they interact (Pringle and Hutchinson, 2020). Finally, the dynamic and variable nature of interactions makes them hard to evaluate (Poisot et al., 2015; Lopez et al., 2017).

Trophic interactions vary in how they are realized, and several

conditions need to be met for an interaction to occur. The first condition is for both interactors to co-occur in space and time (Cadotte and Tucker, 2017; Olivier et al., 2019). Organisms need to disperse and arrive at the same destination, through and to an environment favorable for their transit or settlement (i.e., dispersal and environmental filtering, Fraaije et al., 2015). Once at a suitable site, individuals of a species will ultimately interact with local competitors or predators that may prevent establishment of viable local populations (i.e., interaction filtering). Timing is critical and meeting between a resource and a consumer could fail due to mismatch in phenology (Edwards and Richardson, 2004; Durant et al., 2007) or seasonal asynchrony between consumer and resource populations due to high species turnover (Lopez et al., 2017). The final condition is for both potential interactors to have the adaptations to interact with one another (Brodie III and Brodie Jr, 1999; Tien and Ellner, 2012).

The spatiotemporal, environmental, and biological pre-requirements for interactions to occur are largely governed through species' biological traits. Some traits will determine if and when a regional environment or local habitat is suitable for an organism (response traits, Suding et al., 2008, Díaz et al., 2013), thus whether species are likely to meet in space

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and time (e.g., by determining species distributions, Pollock et al., 2012). Others will determine if organisms can interact and at which rates (i.e., through 'trait matching' of topological, consumption and life-history traits, Bartomeus et al., 2016, Gravel et al., 2016). Topological traits enable trophic interactions through a 'lock and key' rule—also known as 'trait matching'—where the traits of one organism need to match with the traits of the other (Bartomeus et al., 2016). Eklöf et al. (2013) identified that only a few specific traits, such as body mass, mobility, and habitat, were needed to reproduce the structure of food webs, whereas additional traits helped refine those food web representations. For instance, we know that body size determines whether a resource can pass through the oral cavity of a consumer, and consequently, a predator generally needs to be larger than its prey, but not too large compared to its resource (Brose et al., 2006). Traits can also identify interactions that are 'forbidden', which happens when the co-occurrence of a specific trait in the consumer with a specific trait in the resource will temporarily or permanently prevent interaction (e.g., the bill length of hummingbirds must match with the corolla depth of the flowers for them to reach the nectar, Vizentin-Bugoni et al., 2014, Morales-Castilla et al., 2015). Shifting the view of trophic interactions to include biological traits can help us understand how interactions may change in response to changes in trait expression, for instance, as a response to changes in the environment (Albouy et al., 2014; Beukhof et al., 2019a; Pecuchet et al., 2020a).

Information on trophic interactions is often scarce, incomplete, and context dependent (Pringle and Hutchinson, 2020). When diet data is lacking, one common solution has been to aggregate similar species and their links together, a procedure known to alter food web structure (Dunne, 2006; Olivier and Planque, 2017). However, traits have the potential to bypass insufficient and ephemeral diet data because trait matching rules contain, not only trophic information, but also taxonomic and environmental information that can help profile and classify where, when, and why a resource and a consumer interact. Trait-based approaches have already shown potential to reproduce food web structure (Eklöf et al., 2013; Laigle et al., 2018). However, traits are often used as supporting information to fulfill a higher goal, for instance, to evaluate prey suitability (Weigel and Bonsdorff, 2018); to estimate likelihood of trophic interactions (Maureaud et al., 2020); to investigate trait-mediated network assembly rules (Blüthgen et al., 2008; Eklöf et al., 2013; Desjardins-Proulx et al., 2017; Brose et al., 2019); to evaluate robustness to secondary extinctions in food webs (Jacob et al., 2011); to identify clusters of species sharing similar functional roles (Siwicka et al., 2019); or to predict shifts in species distributions, and evaluate species invasion and food web rewiring (Albouy et al., 2014). It is even likely that trait-based aggregation would outperform aggregation procedures that solely rely on taxonomic or trophic similarity (Olivier and Planque, 2017; Giacomuzzo and Jordán, 2021). Hence, by harnessing the potential of biological trait information and consumer-resource profiling, we should be able to build more realistic, and even adaptive, food webs.

To the extent of our knowledge, there are few studies where traits are directly used to construct and analyze networks (but see e.g., the plant trait correlation networks by Kleyer et al., 2019). Here, we built a trait-interaction network by combining multivariate approaches and network analysis. Our approach translates species-based food web data into a network of traits, or "trait web", which we used to assess how traits of consumers and resources associate based on documented trophic interactions. We applied the trait-web approach across a selection of local marine habitats to characterize and compare the structure of food webs among coastal benthic communities. More specifically, we evaluate which traits contribute the most to trophic interactions, and whether and how the consumer-trait associations change across habitats, as given by the following research questions: 1) How are communities and food webs structured at a local scale? 2) Which traits contribute to the observed food web structures? and 3) How are trait interactions structured—are there groups, or modules, of traits that interact more strongly

with each other? Despite a general level of similarity in the species compositions and trophic interactions of the local food webs, we were able to discern trait profiles of interacting consumers and resources: some biological trait associations occur across habitats, whereas other associations seemed specific to certain habitats, possibly reflecting unique interactors in those habitats. Groupings of interacting traits mainly captured the vertical structure of the food web, such as predatory fish feeding on invertebrates grazing on benthic primary producers. Finally, we discussed the implications of the findings and the potential use of traits for inference of trophic interactions or aggregation criteria in the compilation of food webs.

## 2. Material and methods

2.1. Study communities

To assess trophic organization in coastal benthic communities, we determined community composition, biological traits and trophic interactions for different habitats. Following the definition by Airoldi and Beck (2007), we selected four marine coastal habitat types at locations around the southwestern coast of the Åland Islands in the northern Baltic Sea: hard substrate with bladderwrack belt (*Fucus vesiculosus*, hereafter referred to as "*Fucus*"), unvegetated hard substrate ("rock"), soft sediment with eelgrass (*Zostera marina*, hereafter referred to as "*Zostera*"), and unvegetated soft sediment ("sand") (Fig. 1). Habitats defined by vegetated areas occur as ribbons of vegetation along the coast where availability of light, depth, and exposure determine their width and composition. For a more detailed description of the habitat complexity at the sampling locations, see Henseler et al. (2019).

2.2. Species composition

To determine species composition in the benthic food webs, we sampled the macroinvertebrate and fish communities. The sampling method for invertebrates was adapted from Törnroos et al. (2013). We quantified the invertebrate community through scuba diving using quadrats of 25 cm × 25 cm (with net bags to keep the samples) to collect epifaunal invertebrates (living on the substrate or among the vegetation). For infaunal invertebrates, we used four individual sediment cores at each site across each habitat to sample the invertebrates living in the upper layers (first 15 cm) of the sediment (i.e., the sand and *Zostera* habitats). Each set of sediment cores equaled a total sample volume of 589 cm^3. We sampled quadrats to a total of 15 replicates per habitat. To ensure we collected well-defined communities, we sampled in the center of the habitats to avoid any edge effect that could occur between contrasted habitats (Peyras et al., 2013). Samples were sieved (0.5 mm mesh size) and preserved in 70% ethanol for further taxonomic determination and measurements of biological traits in the lab. The fish community was sampled using four multi-mesh Nordic survey gillnets (30 m length, 1.5 m depth, 5–55 mm mesh sizes; Appelberg et al., 1995) per habitat. Gillnet fishing was complemented with qualitative sampling using four minnow traps and three katsa traps per habitat. Fishing gears were deployed overnight for a soaking time of ca. 12 h. Organisms were identified to species level when possible, following the World Register for Marine Species (WoRMS, 2019).

2.3. Trophic interactions

To describe the structure and topology of food webs, we assembled a metaweb —a food web that encompasses all possible trophic interactions across the four communities (Fig. 2). The metaweb contains 61 trophospecies (i.e., taxon or groups of taxa sharing similar interactions or playing similar roles in the community) with a total of 452 possible trophic interactions. Out of these 61 nodes, two are primary producers, 28 benthic invertebrates (infauna and epifauna), 6 planktonic invertebrates, 19 benthic or pelagic fish. The remaining six
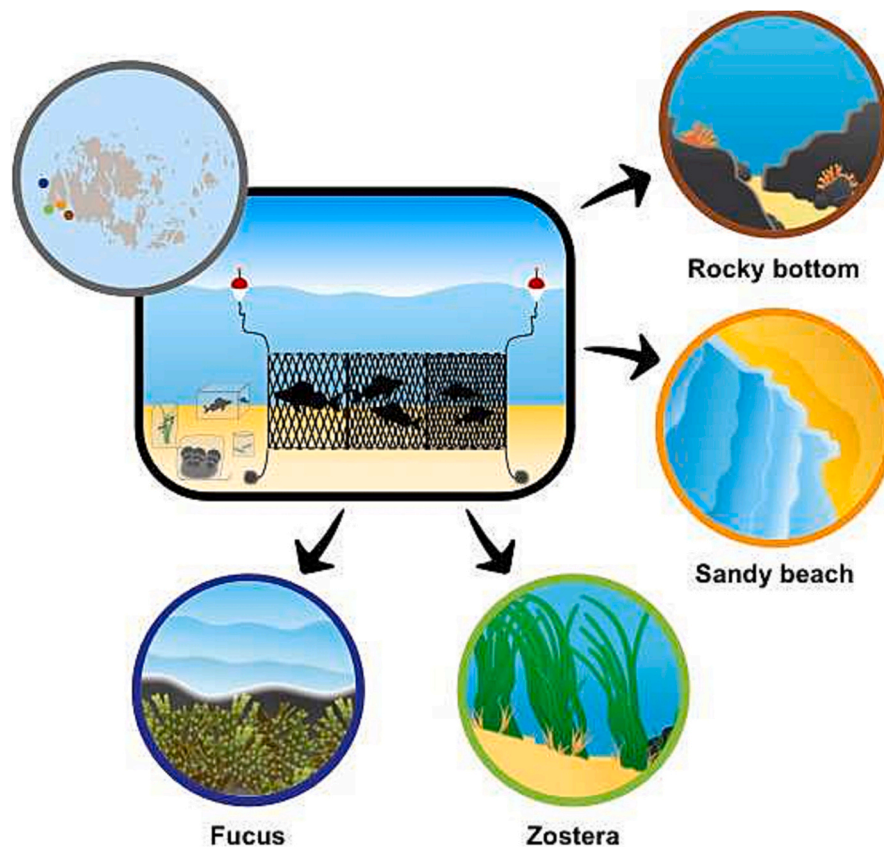
Fig. 1. Illustration of the sampling approach and studied areas around the Åland islands, Baltic Sea. Each colour corresponds to one of the four habitats. In blue = *Fucus* [N 60° 14.275200′; E 19° 28.292400′], brown = rock [N 60° 8.698200′; E 19° 41.224800′], green = *Zostera* [N 60° 9.604200′; E 19° 31.843200′], orange = sand [N 60° 9.057600′; E 19° 35.764800′]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

trophospecies are broader functional groups representing observed and essential components of benthic coastal food webs also serving as food sources for consumers in our food webs: detritus, benthic microalgae, phytoplankton, zooplankton, macroalgae and vascular plants. For the fish, the trophic interactions were determined through stomach content analysis from the fish caught, using the prey encountered to compile fish diets. Invertebrate diets were determined from data collected in previous food web studies conducted around the Åland Islands (Nordström et al., 2015; Nordström and Bonsdorff, 2017). Diet completeness was evaluated using species accumulation curves on the diet of predators with the 'Chao' estimator as described in Olivier et al. (2019). Species diets that were evaluated to be insufficient were further completed with information from the literature or trophic link databases (i.e., Global Biotic Interactions, or GloBI, Poelen et al., 2014). The trophic links collected from the literature were subsequently evaluated prior to inclusion in the metaweb following the procedure described in Olivier et al. (2019). We mainly included trophic links with evidence of consumption in the area, keeping in mind that co-occurrence of species is not evidence for realized trophic interactions (Cazelles et al., 2016; Freilich et al., 2018; Blanchet et al., 2020). Finally, a few taxa that remained insufficiently described, or were completely disconnected in the metaweb even after the literature review (e.g., Hydrachnidia), were removed from the analysis.

2.4. Biological traits

To describe the characteristics of interacting species, we collated information on biological traits that have previously been identified as important for the occurrence of trophic interactions (Eklöf et al., 2013; Gravel et al., 2016; Cirtwill and Eklöf, 2018; Brose et al., 2019; Pecuchet et al., 2020b). In our study, we focus solely on topological traits, e.g.,

traits that influence the occurrence of trophic interactions through the characteristics a consumer has to detect, capture and consume resources, and the characteristics a resource has to avoid or defend itself against consumer attacks (Gravel et al., 2016). Eklöf et al. (2013) identified that already a limited number of well-selected traits could constrain and reproduce the structure of food webs, namely the traits body mass, metabolic category, feeding strategy, consumer type, and habitat. We expanded this set to, in total, nine traits, also including descriptions of body shape, protection, gut morphology, and mobility (Table 1). The trait protection was only included for resources, whereas the trait 'gut morphology' was only included for consumers. We included both quantitative and qualitative traits. Quantitative traits of resources were measured on sampled organisms and not on partly digested items in the stomachs of predators, which could bias measurements. We computed average values for each species subsequently converting the quantitative traits to categorical traits to meet the requirements of the trait association analysis (i.e., fourth-corner, see below). For body size, categories 'XS' and 'S' represent organisms for which body mass was not measured in the lab. XS includes organisms such as phytoplankton, whereas category S represents their consumers, copepods and alike. Subsequent size classes were based on the total size range in the dataset and species were added to respective size classes based on their average body mass (wet weight in g). Qualitative traits were either determined from pictures taken of the collected individuals (e.g., gut morphology), collated from the literature, or based on expert opinion.

2.5. Statistical analysis

In this study, we determined community structure (taxonomy, traits and trophic interactions) across four coastal habitats. For each food web,
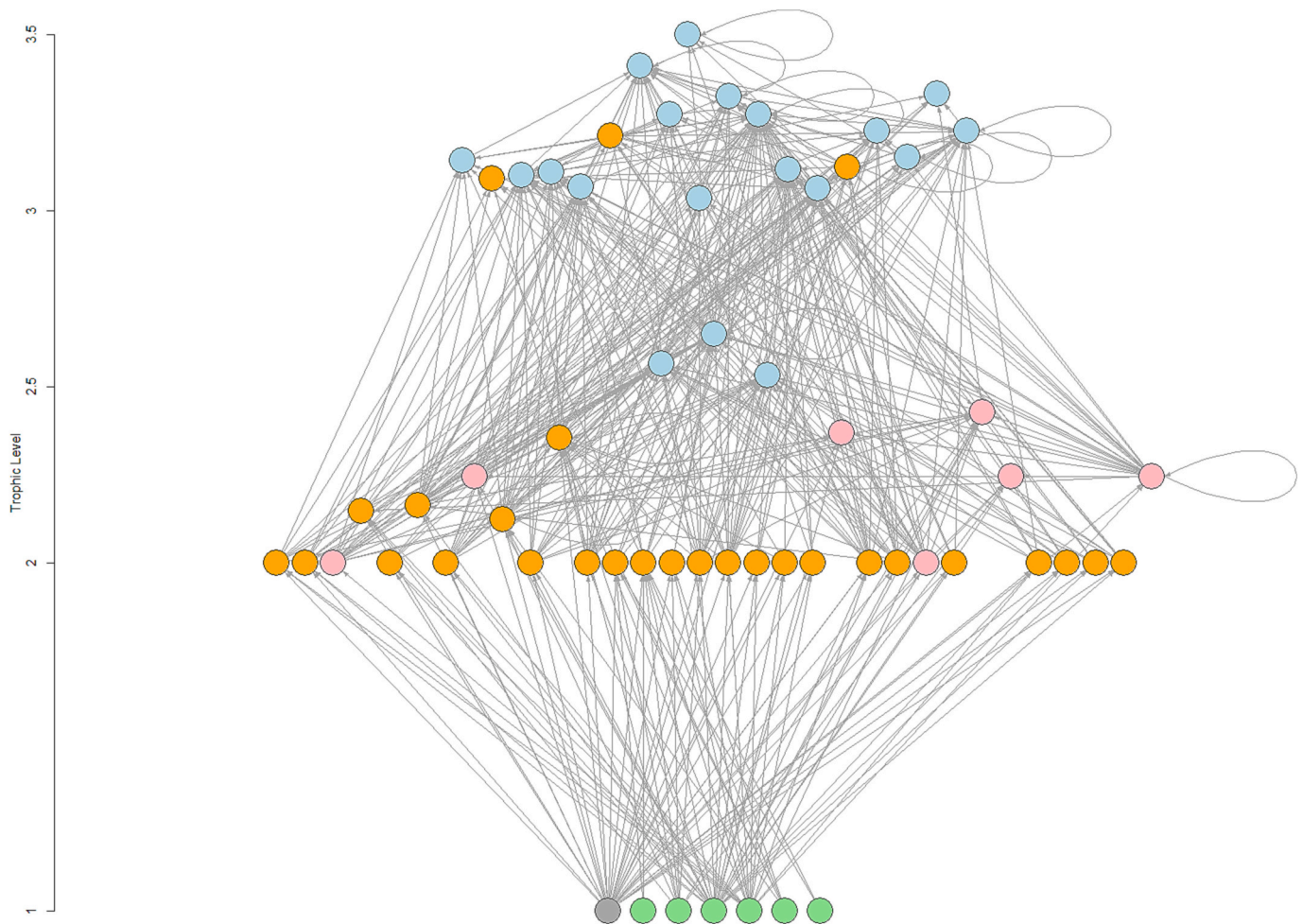
Fig. 2. Metaweb of the Åland Islands. The metaweb combines data of four coastal benthic habitat food webs (*Fucus*, rock, sand, *Zostera*). The y-axis represents the short-weighted trophic level of the nodes. Basal species are represented at the bottom and connect to higher trophic levels through directed trophic links. Black, green, orange, pink and blue nodes represent detritus, primary producers, zoobenthos, zooplankton and fish, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

we also assessed the contributions of traits to food web structure, as well as the potential presence of modules in the structure of interacting traits, i.e., subsets of traits that interact more frequently. All data analyses were performed with the statistical software environment R version 4.1.1 (R Core Team, 2021). The approaches were performed using data from each habitat separately, and results were compared to derive patterns.

2.5.1. Differences in community composition and food web structure among habitats

We evaluated differences among habitats, first, by calculating the dissimilarities in species composition, trait composition and trophic interactions. Dissimilarities in species composition and trophic interactions were estimated by calculating β-diversity between food webs for the different habitats using the 'betalink' R package (Poisot et al., 2012). To make calculations of dissimilarities comparable, dissimilarity in trait composition was calculated as the Jaccard distance on the presence-absence of categories in respective communities—using the 'ecodist' R package (Goslee and Urban, 2007; Goslee and Urban, 2020). Second, we applied network topology analysis to describe the structure of the food webs, including both the overall metaweb and the four local sub-webs in each habitat. The metaweb was subsampled for each habitat based on species composition. We calculated the following ten topological metrics: species richness of the food web (S), number of links (L), link density (Z), connectance (C), generality (G), normalized standard deviation in generality (GenSD), vulnerability (V), normalized standard

deviation in vulnerability (VulSD), maximum trophic similarity (MxSim) and maximum short-weighted trophic level (MaxTL). For a more detailed description of the metrics, please see Table 1 in Olivier et al. (2019). Food webs were analyzed and visualized using the 'igraph' R package (Csárdi and Nepusz, 2006).

2.5.2. Trait interactions between consumers and resources in the food web

We adapted the fourth-corner method (Legendre et al., 1997; Dray and Legendre, 2008; Ter Braak et al., 2012; Dray et al., 2014) to test pairwise relationships between consumer traits and resource traits based on trophic interactions between species. The fourth-corner method was originally developed to assess whether the characteristics of the environment govern variations in trait expressions, which would explain observed species distributions (Legendre et al., 1997), and has been used, e.g., in the marine environment (Beukhof et al., 2019b) and in lakes (Brind'Amour et al., 2011). Here, the fourth-corner tests for associations between consumer and resource traits (a consumer trait category with a resource trait category) in a matrix D ($n \times k$), linking together three matrices: R ($m \times k$) that lists resource taxa and their trait categories, Q' ($n \times p$) that lists the consumer taxa and their trait categories, and L ($m \times p$) that is the binary matrix of trophic interactions between resources and consumers (Fig. 3). More specifically, the fourth-corner tests the null hypothesis H_0 that trophic interactions occur at random such that consumer traits are unrelated to resource traits. Though versatile, the fourth-corner was not originally developed to

Table 1
Description of the traits and categories included in the analysis.

Traits	Categories	Labels	Description and relevance	References
Mean Body size	XS	MS1	Local average body mass for a species represented as size classes. Smaller size of a resource compared to a consumer increases resource vulnerability.	[1, 2, 3, 8, 9] (2, 3, 4, 5 7)
	S	MS2		
	SM	MS3		
	M	MS4	*Both a consumer and resource trait.*	
	ML	MS5		
	L	MS6		
	XL	MS7		
Metabolic category	Primary producer	MC1	Relates to the metabolic hierarchy in food webs where consumers feed on the same or lower metabolic category	[1, 2, 3, 4] (7)
	Invertebrate	MC2		
	Ectotherm vertebrate	MC3	*Both a consumer and resource trait.*	
Foraging strategy	None	FS0	Strategy used by organisms to capture their food. Foraging strategies may influence predation risk (e. g., organisms roaming for food are more easily detected by consumers vs. organisms that stay still and filter water).	[1, 2, 3, 8, 9] (2, 3, 4, 5 7)
	Predator	FS1		
	Scavenger	FS2		
	Parasite	FS3		
	Grazer	FS4		
	Deposit feeder	FS5	*Both a consumer and resource trait.*	
	Filter feeder	FS6		
Consumer type	Primary producer	CT1	Indicates role in trophic pathway. Match and mismatch between consumer-resource consumer types can be responsible for some forbidden interactions.	[1, 2, 8, 9, 10, 12] (7)
	Detritivore	CT2		
	Herbivore	CT3		
	Carnivore	CT4	*Both a consumer and resource trait.*	
	Omnivore	CT5		
Mobility	Sessile	MB1	Escape and attack abilities of a resource or a consumer, respectively, increases resource availability and vulnerability.	[2, 3, 8, 9, 10] (4, 5, 7)
	Passive floater	MB2		
	Crawler-Burrower	MB3		
	Facultative swimmer	MB4	*Both a consumer and resource trait.*	
	Obligate swimmer	MB5		
Environmental positioning	Infauna	EP1	Spatial overlap of predator and prey niche increases resource availability and vulnerability.	[1, 2, 3, 8, 9, 10] (4, 5, 7)
	Epibenthic	EP2		
	Benthopelagic	EP3		
	Pelagic	EP4	*Both a consumer and resource trait.*	
Body shape	Plant-like	BS1	Body design of a consumer relates to its mobility in its environment to	[1, 2, 3, 8] (6)
	Fusiform	BS2		
	Deep	BS3		
	Flat	BS4		

Table 1 (*continued*)

Traits	Categories	Labels	Description and relevance	References
	Elongated	BS5	forage for resources. Body design of a resource influences ingestion success. A more streamlined body is more easily ingested.	
	Eel-like	BS6	*Both a consumer and resource trait.*	
	Unsegmented verminiform	BS7		
	Segmented verminiform	BS8		
	Bivalved	BS9		
	Turbinate	BS10		
	Articulate	BS11		
Gut morphology	No gut	GM0	Length and morphology of the digestive tract relates to the consumers' diet and their ability to digest and absorb varied resources.	[1] (13, 14)
	Simple gut	GM1		
	Stomach	GM2		
	Pyloric caecum	GM3	*Consumer trait.*	
	Intestine	GM4		
Protection	No protection	PR0	Indicates level of palatability from a consumer's perspective. Provide a defense against consumers, from the perspective of a resource.	[1, 2, 3, 8, 9, 10, 12] (4, 5)
	Shoaling-Schooling	PR1		
	Tube	PR2		
	Burrow	PR3	*Resource trait.*	
	Case	PR4		
	Soft shell	PR5		
	Hard shell	PR6		
	Few spines	PR7		
	Armoured	PR8		

Traits are regarded, either from the perspective of the consumers if it helps capturing and consuming resources (e.g., 'Does the gut morphology influence resource consumption?'), or from the perspective of the resource if it determines vulnerability against consumers. Most traits can be both consumer and resource traits.

Notes: References: [1] This study; [2] Nordström et al. (2015); [3] Törnroos and Bonsdorff (2012); [4] Törnroos et al. (2013); [5] Spitz et al. (2014); [6] Pecuchet et al. (2016); [7] Eklöf et al. (2013); [8] Froese and Pauly (2019, FishBase); [9] Palomares and Pauly (2019, SeaLifeBase); [10] MarLIN (2006, BIOTIC); [11] Poelen et al. (2014, GLOBI); [12] Encyclopedia of Life from Parr et al. (2014); [13] German et al. (2009); [14] Smith (1980). In the table, literature in brackets lists the sources for collecting and completing data. Literature in parenthesis lists descriptive literature on the trait.

accommodate combinatory traits in which a species can express one or more categories of the same trait. We included each category separately as part of the analysis (see Supplementary Appendix A), which influences how the function outputs the significances of associations in matrix **D**. To test the null hypothesis on categorical combinatory traits, we used the X^2 statistics with 100,000 permutations and chose outputs of Monte Carlo simulations from permutation model type 6 (Dray and Legendre, 2008; Legendre and Legendre, 2012; Dray et al., 2014), based on the sequential method by Ter Braak et al. (2012) that controls for type I errors. Permutation model type 6 tests the null hypothesis that at least one trait matrix (**R** or **Q'**) is not linked to the matrix of interaction **L** against the alternative hypothesis that both trait matrices are linked to the distribution of trophic interactions within the **L** matrix. Additionally,
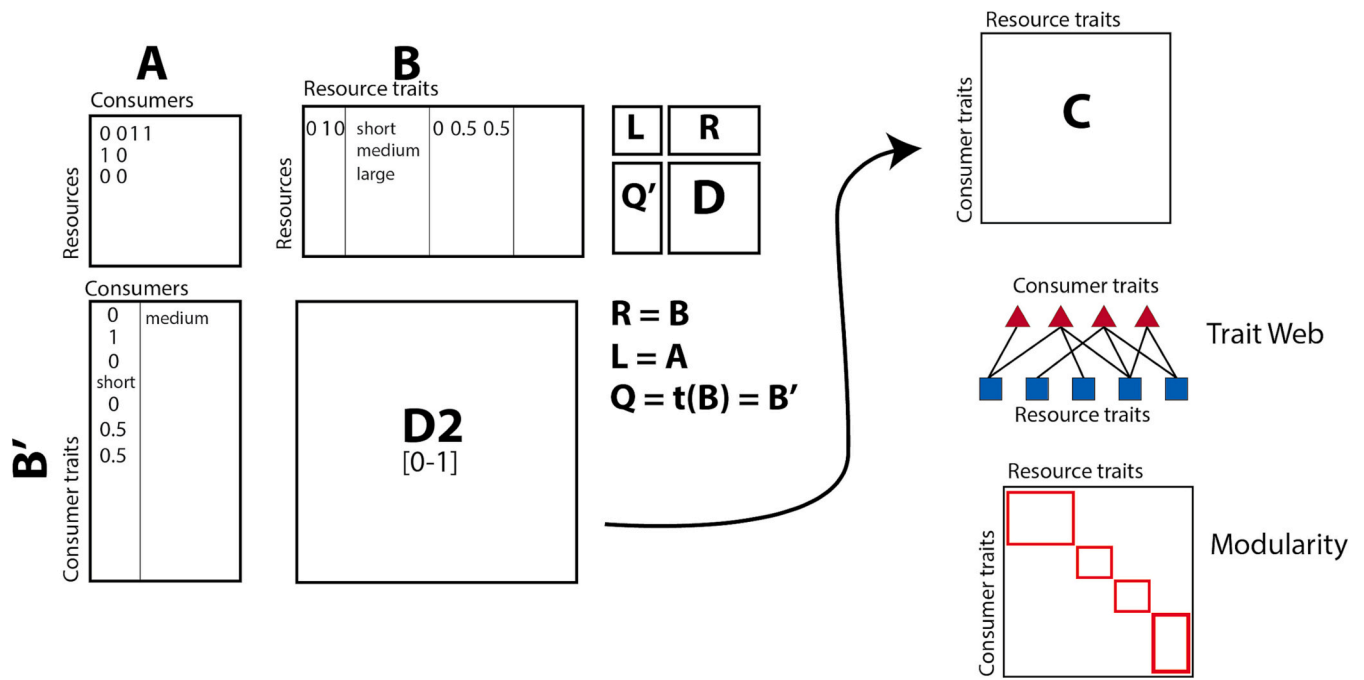
Fig. 3. Flow of the conversion process from a food web to a trait web. Trophic link information is inserted as a reduced binary matrix **A** that binds information between consumer and resource trait matrices **B** and **B**′.

we adjusted *P*-values using the false discovery rate method (FDR, Benjamini and Hochberg, 1995) as recommended by Dray et al. (2014). The fourth-corner analysis was performed using the *fourthcorner* function from the 'ade4' package in R (Dray and Dufour, 2007).

### 2.5.3. Modularity of trait interactions between consumers and resources

We assessed the structure of trait interactions by testing if trait associations organize as modules, i.e., groups of nodes that interact more frequently with members of the same module (Newman, 2006). We used the trait associations identified in the fourth-corner analysis to build a weighted bipartite network of traits—the "trait web"—for each habitat. We used the frequency of observed trait category associations as weights for the interactions. Unlike food web networks where nodes (i.e., species) are found across multiple trophic levels and can interact within and between levels (i.e., unipartite networks), bipartite networks are two-level networks where members of the lower level can only interact with members of the higher level, and vice versa. Bipartite networks are ideal for representing interactions between consumer and resource traits as consumer and resource traits split into two distinct sets. Traits that can be expressed by both consumers and resources (e.g., a certain body size) were regarded separately assuming that they alternatively influence consumer foraging or resource suitability for consumption, respectively. To test for the presence of trait modules, we calculated modularity of weighted bipartite networks using the DIRTLPAwb+ community detection algorithm by Beckett (2016) implemented in the 'bipartite' package in R (Dormann et al., 2008; Dormann et al., 2020). Finally, to assess the presence of common modules across habitats, we calculated module dissimilarity across habitats based on trait category presence/absence in modules. Modules were compared using the Jaccard distance calculated with the 'ecodist' R package (Goslee and Urban, 2007; Goslee and Urban, 2020).

3. Results

3.1. Habitat-specific communities and food web structure

Of the 61 trophospecies recorded in the overall metaweb, 34 and 36 were observed in the unvegetated sand and rock habitats, compared to

42 and 47 in the *Fucus* and *Zostera* habitats. Comparison of species composition among the habitats revealed that *Fucus* and sand had the highest level of dissimilarity (39%), whereas the other habitats ranged between 23 and 28% dissimilarity (Fig. 4). In terms of trophic interactions, communities differed by 34–58% because of differences in community composition. *Fucus* and sand again showed the highest level of dissimilarity, whereas sand and rock were least dissimilar. Compared
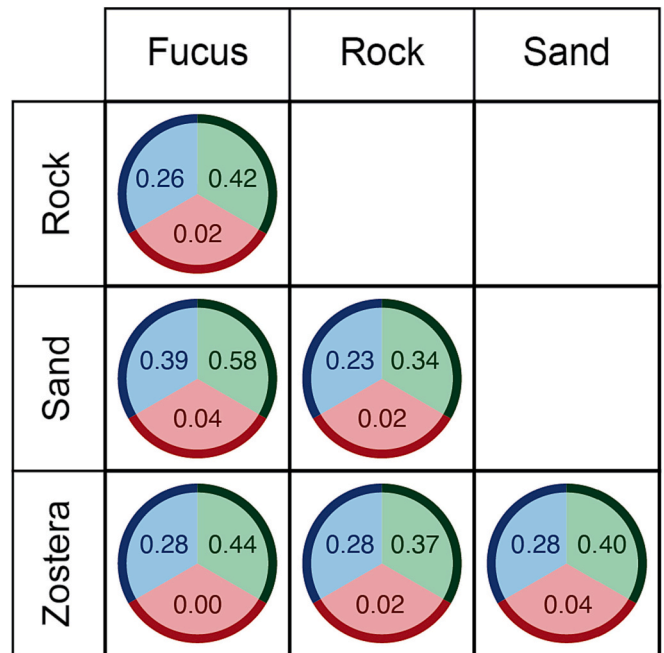
Fig. 4. Dissimilarity in species composition (blue), trophic interactions (green) and trait composition (red) among the different habitats. The two first were calculated using the beta-diversity index. Trait dissimilarity was calculated using the Jaccard distance on the presence-absence scores of categories in respective communities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to dissimilarities in both species composition and trophic interactions, dissimilarity in trait composition was low (0–4%). The two vegetated habitats showed no differences in the presence/absence of traits.

With regards to overall food-web topology, the *Fucus* and *Zostera* habitats were similar in terms of connectance, whereas rock was more similar to sand (Table 2). On average, consumers were feeding on 6–7 resources in all food webs (i.e., G), whereas resources had ca. 6 consumers (i.e., V). Generality varied more from consumer to consumer, as shown by GenSD being higher than one. In contrast, vulnerability showed little variation from resource to resource, as shown by VulSD being lower than one. All habitats shared similar values in MxSim (ca. 0.6) indicating that species in each food web share on average at most 60% of their consumers or resources with other species. Finally, the MaxTL was overall similar across food webs (3.21–3.52).

3.2. Trait contributions to food web structure

Out of 1529 unique observed consumer-resource trait associations, 101 associations were significant ($P < 0.05$) in at least one habitat (Fig. 5; Table S1). We found 51 significant associations in sand, 44 in *Fucus*, 36 in *Zostera*, and 31 in rock, respectively. Among the 101 significant trait associations, 13 associations were found occurring in all four habitats (Table 3). These significant associations involve consumer metabolic category, gut morphology, and mobility, on one hand, and resource traits like mean body size, metabolic category, foraging strategy, consumer type, and body shape, on the other hand. Some fundamental examples are 'ectotherm vertebrates' feeding on 'invertebrates', and 'invertebrates' feeding on 'primary producers'. In addition, 17 significant associations were shared across multiple habitats (i.e., found in two to three habitats out of four). When trait associations were shared between two habitats, most often they were found either in the two vegetated or the two unvegetated habitats. For example, in vegetated habitats, 'primary producers' were associated with 'crawler-burrower' consumers, in unvegetated habitats, 'articulate' resources were associated with 'fusiform' consumers).

Most trait associations were only found in specific habitats (Table B.1). In total, 71 significant associations were unique to a habitat. The *Fucus* habitat accounted for 20 unique associations: for instance, some 'obligate swimmer' species fed on 'primary producers', and the environmental positioning of consumers as 'benthopelagic' consumers connected to 'small-sized' resources. Rock accounted for six unique significant associations that involved feeding by larger consumers (fish) on small invertebrates: for instance, 'extra large', 'fusiform' fish feeding on 'crawling' 'invertebrate' prey. *Zostera* accounted for 12 unique significant associations that most often involved the foraging strategy of consumers: 'grazers' feeding on traits that are characteristic of 'primary producers', and 'predators' feeding on 'detritivores'. Sand accounted for 33 unique significant associations which was the highest number of unique significant associations. They mainly involved traits of predatory fish (e.g., gut with three segments 'stomach', 'pyloric caecum', and 'intestine') and traits describing the vulnerability of isopod prey to predators (e.g., their protection 'soft shell', or an 'articulate' body shape).

3.3. Modules of trait associations

For each habitat, we built a trait-web and computed modularity. Each community contained two modules, one larger and one smaller, that reflect food web interactions across trophic levels (Fig. 6). The larger modules contained 16–18 consumer categories interacting with 36–38 resource categories and were characterized by traits representative of fish consumers and invertebrate resources. The smaller modules were detected among 22–24 consumer categories and 11–12 resource categories and were representative of invertebrate consumers and basal resources. We analyzed the two modules separately for dissimilarity in module membership across habitats. The dissimilarity analysis revealed that the modules show little dissimilarity across habitats (3–10%) and thus contain similar sets of frequently connected categories—despite a relatively high number of uniquely occurring trait associations, as well as varying species composition and trophic interactions between habitats (see Fig. 4). Modules in vegetated habitats (*Fucus* and *Zostera*) showed the highest levels of similarity (95–97%), whereas sand showed the lowest similarities with other modules (90–92%, Table 4). Members of each module can be found in Appendix Table B.2.
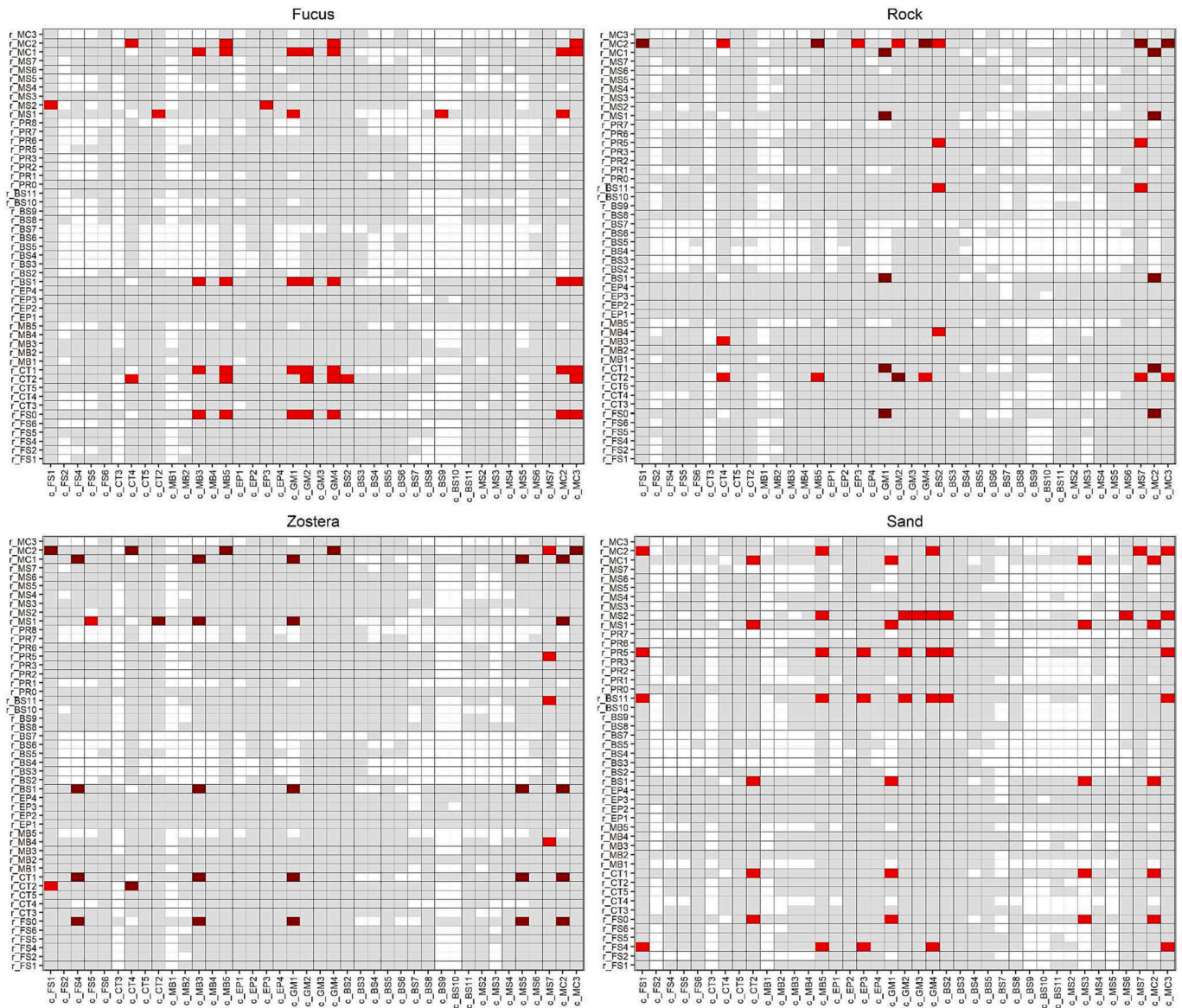
Our results revealed that trait webs can describe the overall structure of food webs, identifying e.g., interactions between trophic levels, as well as modules of trait categories, i.e., groups of limited sets of interacting traits. For instance, across habitats, the smaller modules represented resource categories characteristic of small (e.g., phytoplankton, benthic microalgae), and large primary producers (e.g., *Zostera marina*, *Fucus vesiculosus*): for instance, 'XS', 'plant-like' or 'passive-floater'. The consumer categories interacting in the smaller modules were characteristic of small to medium size invertebrate grazers: for instance, 'grazer', 'facultative swimmer', 'articulate'. The bigger module contained a larger range of resources from invertebrates to fish covering a spectrum of small to extra-large resources: for instance, 'ectotherm vertebrate', 'bivalved', 'shoaling or schooling'. The consumer categories connected to them profiled large benthivorous and planktivorous fish, and ribbon worm: for instance, 'predator', 'bentho-pelagic', and a 'deep' body shape for fish.

4. Discussion

Our comparison of food webs across habitats emphasizes the need to go beyond the concept of species taxonomy when looking at diversity and trophic interactions. At the local scale, we observed that community composition and food web structure differ along a continuum determined by habitat characteristics (i.e., vegetated vs. unvegetated) and the adaptations (i.e., traits) species share to feed and survive in those habitats. This would imply that communities in habitats with similar characteristics share ecological roles through species traits and interaction architecture (e.g., levels of structural complexity and connectedness). Going beyond species taxonomy, traits revealed the basic organization of food webs and trophic levels, providing additional information that may help infer trophic links, as well as aggregate and simplify complex food webs.

At the local scale, we observed that vegetated habitats (i.e., *Fucus* and *Zostera*) shared similar species composition and food web structural

Table 2

Ecological Network Analysis (ENA) of the metaweb (Åland) and the four habitat food webs.

Habitat	S	L	Z	C	G	GenSD	V	VulSD	MxSim	MaxTL
Åland	61	452	7.41	0.12	8.37	1.11	7.66	0.96	0.56	3.51
Fucus	42	240	5.71	0.13	6.67	1.11	6.00	0.88	0.57	3.41
Rock	36	224	6.22	0.17	7.00	1.15	6.40	0.75	0.65	3.21
Zostera	47	292	6.21	0.13	7.12	1.10	6.35	0.88	0.57	3.50
Sand	34	189	5.55	0.16	6.10	1.03	5.73	0.84	0.62	3.52

The metrics are as follows, from left to right: species richness of the food web (S), number of links (L), link density (Z), directed connectance (C), generality (G), standard deviation of generality (GenSD), vulnerability (V), standard deviation of vulnerability (VulSD), maximum trophic similarity (MxSim), maximum short-weighted trophic level (MaxTL).

Fig. 5. Matrix **D** extract from the fourth-corner representing the results of the X^2 tests of associations between predator and prey traits. White boxes indicate absence of an interaction; grey boxes indicate no significant correlations; red boxes indicate significant adjusted *P* values between 0.01 and 0.05; dark red boxes indicate *P* values strictly inferior to 0.01. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Summary of commonness of significant consumer/resource trait interactions in each habitat.

Habitat	Total	Unique	Shared	Common
Fucus	44	20	11	13
Rock	32	6	13	13
Zostera	36	12	11	13
Sand	55	33	9	13

'Unique' interactions are found in a single habitat only. 'Shared' interactions are found in two to three habitats. 'Common' interactions are found in all four habitats. A total of 101 significant consumer-resource interactions were found across habitats. The total number of significant interactions found in a habitat is the sum of unique, shared and common interactions.

properties. The same holds true for unvegetated habitats (i.e., sand and rock). However, we did not observe strong differences between vegetated and unvegetated habitats when they shared habitat characteristics (e.g., the hard substrate shared between rock and *Fucus*). For instance,

Fucus vesiculosus grows on rocks making both rock and *Fucus* habitats suitable for species living on rock, with some species fully utilizing the vegetation coverage, and others taking advantage of bare rocky patches. Mobile species able to take advantage of two or more habitats then contribute to the spatial coupling of local food webs (McMeans et al., 2015). Finally, dissimilarity in trait composition was low in all habitats which suggests that trait categories are found across habitats, despite differences in species composition.

Furthermore, we show that some trait associations are also similar across habitats, at least when the habitats share some component of habitat complexity. More specifically, consumer traits that involve metabolic category, consumer type, mobility and gut morphology, as well as resource traits including metabolic category, consumer type and body size were involved more frequently and significantly in trophic interactions in all habitats. Consequently, such fundamental traits and trait associations may be useful for inferring trophic links in marine coastal food webs, well beyond the study area in question. Similar sets of traits have indeed been used to calculate interaction probabilities and infer links e.g., in above-ground food webs in grasslands (Giling et al.,
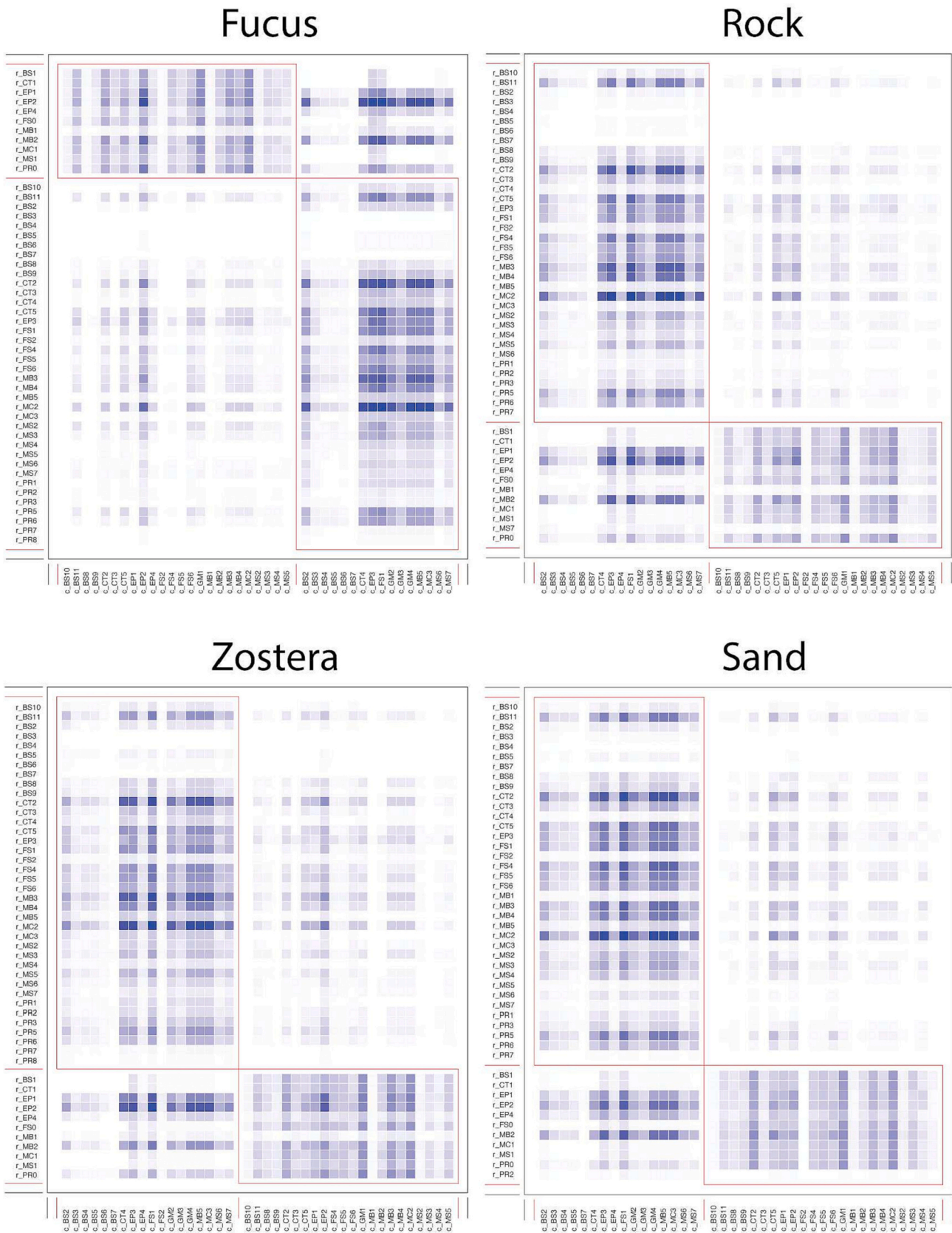
Fig. 6. Modules of the consumer-resource bipartite trait web networks. The colour gradient indicates frequencies of occurrence for the significant consumer-resource trait associations. Cells in white indicate no significant associations, or no association at all.

Table 4
Dissimilarity in module memberships comparing the smaller and bigger modules separately, across the four habitats.

		Fucus	Rock	*Zostera*
Small Module	Rock	0.05		
	Zostera	0.05	0.05	
	Sand	0.08	0.08	0.08
Big Module	Rock	0.05		
	Zostera	0.03	0.05	
	Sand	0.10	0.08	0.10

Module membership dissimilarity was evaluated using the Jaccard distance on presence/absence of predator and prey trait categories in the modules.

2019), or to predict novel trophic links in Arctic marine communities (Pecuchet et al., 2020b) and ground beetle assemblages (Brousseau et al., 2018). More generally, food webs have been shown to be size structured (Brose et al., 2006; Eklöf et al., 2013). However, using body size in combination with both resource traits and consumer traits drastically improved the characterization of food web structure. Laigle et al. (2018) confirmed these conclusions and found correlations between the trait-based structure of communities and food web structure. Consequently, we would expect that important consumer-resource trait associations would emerge as significant or at least occurring at higher frequencies in our study. Regarding body mass, we did observe significant trait associations between body mass of consumers and of resources, but only for a few size classes. Size-structured feeding relationships are thought to be more prevalent for pelagic predators and prey, than in benthic communities (Brose et al., 2019). Our study (which included other feeding relationships than strictly predator-prey interactions) comprised seven size classes, two being inferred. Having too few or too broad categorical classes for quantitative traits without representing ontogenetic diet shift may inaccurately describe size-structure constraints at the scale of a food web.

Our observations are in line with recent literature on the importance of traits such as consumer and resource metabolic category, and mobility, influencing the structure of food webs (e.g., Eklöf et al., 2013; Brose et al., 2019). However, it is difficult to discern whether our trait associations represent traits that are vital for, or only participate in, interactions. For example, secondary traits can facilitate or limit the interactions of fundamental 'lock and key' traits, and what appears as an essential association between two traits may in fact only be possible through secondary traits (e.g., an association between a mesopelagic planktivorous fish and an epipelagic plankton species is facilitated or limited by diel vertical migration of the plankton, Pinti et al., 2019). Assessing the right traits is thus critical to understand and decide whether an association is essential for the structure of food webs.

Because we will probably never be able to empirically sample complete food webs, predicting possible or novel trophic interactions, as well as refining observed trophic interactions according to the spatio-temporal context, is challenging, but necessary. The fourth-corner as set up in our analysis is a step towards identifying species and traits participating in trophic interactions. However, although the fourth-corner method identifies consumer-resource trait associations likely involved in food web assembly rules, the approach lacks the ability to identify trophic interactions based on traits. First, to be able to identify the relative importance of consumer and resource traits would help conclude on the mechanism behind trophic interactions, and whether consumer traits, resource traits, or both, enable or prevent trophic interactions. Eklöf et al. (2013) pointed out that the best combinations of two traits involved both traits of consumers and resources, and in some cases, that the best predictions involved a single trait, a resource trait. For instance, when the resource trait category 'protection' is more significantly associated with consumer traits, is it because the species characteristics generally do not provide good enough protection against consumers with certain traits? Or because some consumers are well equipped in disarming this protection because of other traits they

express? Second, some trophic interactions never occur in nature (e.g., primary producer traits interacting with anything other than primary consumer traits) and are neither represented nor constrained in the fourth-corner analysis. The absence of associations is as valuable when inferring trophic interactions as the presence of significant associations. Moreover, we do not know how well the fourth-corner algorithm maintains a realistic food web structure (e.g., basal species, top consumers, forbidden interactions). By decomposing the square interaction matrix into a rectangular matrix (i.e., basal and intermediate species, intermediate and top species), we should have avoided certain issues that may rise with rows and columns full of zeros (i.e., top species and basal species, respectively). However, we would recommend developing a fourth-corner approach using a more restrictive algorithm that maintains column and row totals (e.g., the 'Curveball' algorithm, Strona et al., 2014).

Feeding output from fourth-corner analysis into an ecological network linking biological traits revealed that the trait web preserved the overall hierarchy of food webs: primary producers being eaten by ectotherm invertebrates, themselves being preyed upon by ectotherm vertebrates. This is not surprising as the functional structure of communities seems to constrain food web structure (Laigle et al., 2018), which further controls functioning of ecosystems (e.g., metabolism, production and productivity, Maureaud et al., 2020). However, we also found that, within their own networks, consumer-resource trait interactions tend to structure within modules, which implies that sets of consumer traits interact more strongly with certain sets of resource traits than they will with other traits. Such modules of consumer-resource trait interactions could potentially portray profiles of interactors: what does the consumer of a particular resource type look like, or what will a consumer with certain characteristics most likely feed on? Using profiles of interacting consumer-resource traits could help identify trophic interactions for species with similar trait profiles, similarly to how 'recommenders' algorithms suggest products given the preferences of other customers with similar profiles (Desjardins-Proulx et al., 2017). Commonly used inference techniques for species interactions involve regression, which search for the best combination of traits out of all possible combinations. Consumer-resource trait profiles may help make a priori decisions about the types and numbers of traits to include.

Biological traits present several benefits to food web ecology and ecological network approaches: they (i) require less extensive sampling than comprehensive ecosystem and diet surveys, (ii) can be collated using local literature on single species (always more numerous than diet studies in the literature), and (iii) can provide—through response-effect traits and trait-matching rules— information on whether two species are likely to meet in space, time, and be able to interact with one another and at what rates. Therefore, the use of consumer-resource trait profiles could advance in several directions. First, when testing causality between trait associations and trophic interactions, trait profiles may help constrain generalized linear models when testing a high number of consumer-resource trait associations (Pomeranz et al., 2019). Second, traits and advanced statistical techniques such as machine learning have shown increasing potential in accurately reproducing trophic interactions (Pichler et al., 2020); combined with consumer-resource trait profiles, they may help predict contextual trophic interactions. Finally, trait profiles may help aggregate taxa into more realistic trophospecies than based on ad hoc choices or morphological similarities alone. Previously, food web aggregation studies have found algorithms based on shared taxonomy or trophic similarity to perform best at grouping taxa without altering the food web structure (Olivier and Planque, 2017). Taxonomically related species often share similar traits, which supports the findings in Olivier and Planque (2017). The results from the present study further support the use of trophic similarity as a suitable aggregation criterion, as traits describing fundamental trophic characteristics of species (metabolic category, foraging strategy) were found to strongly associate in the food webs. In conclusion, joint collection of trait and trophic link information can help refine, produce and even simplify food

web models, helping to build more realistic food webs that are adaptable to the environmental and spatiotemporal context (Albouy et al., 2014; Poisot et al., 2015; Beukhof et al., 2019a; Fortin et al., 2021).

5. Concluding remarks

Understanding the fundamental role of traits structuring trophic interactions is essential if we are to construct realistic representations of food webs, especially under global change. In this study, we investigated the structure of local food webs across multiple habitats through a network approach that link food web structure and species traits. Our "trait web" approach showed that (i) certain trait interactions are unique to habitats whereas others occur across habitats, in particular habitats that share structural elements (e.g., the hard substrate in rocky areas and *Fucus* habitats), and (ii) trait interactions structure into modules, providing profiles of interacting consumers and resources. Such interactor profiles may help identify consumers with certain ecological characteristics that interact more frequently with resources with specific characteristics.

CRediT authorship contribution statement

P.E.N. Olivier: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **M. Lindegren:** Methodology, Writing – review & editing. **E. Bonsdorff:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **M.C. Nordström:** Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

None.

Availability of data and material

The habitat-specific food webs and trait data are available at https://github.com/PierreENOlivier/traitwebs

Appendix A. Supplementary data

Appendix A-C. Tables associated with Appendix B are available at https://github.com/PierreENOlivier/traitwebs. Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2023.e00333.

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