Nestedness of trophic links and biological traits in a marine food web

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Abstract. To understand the consequences of changes in diversity we need to consider the functional characteristics (traits) of species, as well as the trophic setting the taxa are part of. These two approaches have rarely been conducted in an integrated manner, although we know that trophic structure is an important driver of community functioning, and that biological traits, in particular body size, in turn determine which species interact. In this study, we assessed how structural food-web attributes (nestedness, generality, vulnerability) relate to multiple biological traits of interacting taxa. We found that the inherent complexity of a shallow subtidal trophic network of benthic macroinvertebrates and fish in the northern Baltic Sea contained identifiable and specific patterns: the feeding interactions were highly nested, both in terms of prey taxonomy and biological traits, suggesting trophic redundancy rather than trophic complementarity. Both trait diversity and trait redundancy of interacting species increased as a function of predator generality and prey vulnerability. These central food-web metrics, predator generality and prey vulnerability, were dependent on body size, which emerged as a fundamental trait. Body size, environmental habitat and body design were the relatively most important prey traits distinguishing between diets of smaller vs. larger predators, revealing morphological and spatial dimensions of predator trophic niches in the study community. We suggest continued development of an approach integrating functional diversity with the food web to effectively assess community structure, function and species interactions, and ultimately identify ecological impacts in communities undergoing environmental change in the Anthropocene.

Key words: Baltic Sea; benthos; complementarity; functional diversity; predator-prey interactions; redundancy; trophic interactions.

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INTRODUCTION

Global threats to, and reductions in biodiversity have stimulated considerable research efforts to establish a relationship between biodiversity and ecosystem functioning. It is now recognized that assessments of diversity effects on ecological processes require knowledge of the functional characteristics of taxa as well as the multitrophic setting that the species are part of (Diaz and Cabido 2001, Thébault and Loreau 2003, Duffy et al. 2007). Further, as species traits are likely to influence trophic interactions as well as functioning, there is a need for integrating trait-based approaches with the food-web framework (Reiss et al. 2009, Thompson et al. 2012).

Trophic structure is an important driver of processes in food webs, with feeding interactions mediating the effects of biodiversity changes (Duffy et al. 2007, O’Gorman and Emmerson...
The concept of trophic complementarity has been proposed as a general mechanism behind functioning in multitrophic networks (Poisot et al. 2013). Trophic complementarity is an estimate of the level of originality of dietary niches of species, based on the identity of species that interact with each other in the food web. Networks with higher trophic complementarity show higher functioning, estimated as consumer net biomass production, than webs with more overlapping trophic niches (Poisot et al. 2013). Trophic nestedness describes webs with such overlapping interactions, where specialist consumer diets are subsets of generalist consumer diets. This type of non-random interaction pattern combining dimensions of predator generality and prey vulnerability, is common for food webs (Kondoh et al. 2010), and frequently driven by body size, which is a key biological trait structuring trophic interactions (Woodward et al. 2005a, Brose et al. 2006). However, these network structural attributes have so far not been explicitly connected to multiple biological trait characteristics of species in complex food webs. For example, multi-trait information for prey could reveal whether generalist predators interact with a biologically diverse prey assemblage, or simply a larger number of different prey species, compared to more specialist predators.

Body size is a central trait of organisms, linking to biological rates of respiration, growth, reproduction and mortality (Brown et al. 2004). By extension, body size is an important determinant of a multitude of ecological traits that influence the structure and dynamics of food webs (Brose et al. 2006, Eklöf et al. 2013). Body size is often used as a measure that both captures and simplifies biological information for interacting taxa in assemblages, providing metrics to describe community structure, function, and response to environmental change (Woodward et al. 2005a, Boukal 2014). However, multiple biological traits (spanning morphological, physiological and phenological characteristics measurable at the individual level, sensu Violle et al. 2007) are increasingly used in studies of changing biodiversity along environmental gradients (Törnroos and Bonsdorff 2012; Törnroos et al. 2015) or following perturbations (Tillin et al. 2006, Villnäs et al. 2013) with the general aim of assessing the functional consequences of altered community structure (Lavorel and Garnier 2002, Solan et al. 2004, Suding et al. 2008).

Recent work at the intersection between functional ecology and food web ecology has shown that approaches employing multiple biological traits are successful in predicting network structure (Eklöf et al. 2013), as well as in determining the strength of individual trophic links (Klecka and Boukal 2013). In particular, matching empirical characteristics of consumers and resources, such as the length of a moth’s proboscis to the depth of a flower’s corolla, offer an effective way of identifying probable feeding links (Eklöf et al. 2013). Whereas some single traits, such as body size, provide a high level of predictability of feeding interactions (Petchey et al. 2008), multiple traits are needed for more complete descriptions of interactions (Eklöf et al. 2013, Boukal 2014). In experiments using aquatic insects, Klecka and Boukal (2013) found that the strength of individual feeding links, measured as prey mortality, was jointly affected by the body size of interacting taxa as well as their foraging traits and vulnerability traits (e.g., predator foraging mode, prey activity). Whereas initial descriptions of biological traits of prey in predator diets are beginning to emerge in the scientific literature (Klecka and Boukal 2013, Boukal 2014, Green and Côte 2014, Spitz et al. 2014), patterns of trait diversity in relation to the structure of trophic interactions have not previously been explored. Assessments of prey trait composition in diets can help identify functional differentiation among predator groups.

Functional and trophic attributes need to be evaluated in an integrated manner for more accurate assessments of the consequences of changing community structure (Thompson et al. 2012, Boukal 2014). With many of the recent advances in this area stemming from modeling work (Eklöf et al. 2013, Poisot et al. 2013), we set out to assess whether there are interlinked patterns of food-web structure and biological traits of species in a natural community. To meet this primary objective, we performed an analysis in two steps: First, we constructed a detailed connectance web for a benthic community in the northern Baltic Sea. Using this binary information, we quantified the degree of nestedness (and by extension trophic complementarity) focusing on predator-prey interactions in the community.
Second, we determined the expression of biological traits within the food web. We hypothesized that the food web would be size-structured, and that body size would influence linkages; for example, that larger predators would show higher generality (number of prey taxa in diet). Building on body size as a key trait, we explored patterns of biological trait diversity against a set of fundamental size-related metrics, i.e., predator generality, prey vulnerability, and nestedness of interactions. If larger predators truly represent higher functional generality, we would expect an increase in prey trait diversity with higher prey species richness in the diet. A case of increasing prey trait diversity with predator generality, further warrants assessment of the composition and relative importance of different prey traits in predator diets in relation to predator size, i.e., assessment of functional differentiation. Our descriptive approach builds on the niche hypothesis explaining positive relationships between biodiversity and rates of ecological processes (Loreau et al. 2001), and thus lastly, we discuss the potential implications of the observed patterns for ecological functioning.

**METHODS**

**Quantification of benthic macrofauna and predators**

Our study site (Hinderbengtsviken, 60°10’ N, 19°32’ E) is located at the Åland Islands, northern Baltic Sea. This is a shallow and productive environment where littoral processes are important (Kautsky and Kautsky 1995). Of coastal fish in the area, 50% of the different species depend on benthic prey during at least part of their life cycle. These benthically feeding species make up >95% of total fish abundance, and, hence, benthic macroinvertebrates constitute a major trophic pathway (Snickars et al. 2015). Our study site is an exposed bay with a mean depth of 2.5 m and sandy substrate (organic matter content 0.1%, as we determined through loss on ignition at 500°C for 4 h). The deeper part of the bay hosts vascular plant meadows among the otherwise bare sandy substrate that dominates the site.

Community quantification was conducted during the height of the benthic secondary-production period, which occurs in July and August. Sediment-dwelling macroinvertebrates (e.g., polychaetes, crustaceans, bivalves, gastropods and insect larvae) were sampled by SCUBA diving and using a core (10 cm diameter and 15 cm height) at about 1.5 m depth. Five replicate samples were taken, once in July and once in August 2010, at each of 6 stations evenly positioned along the shoreline. The collected sediment was sieved (500-µm mesh) and retained material was preserved in 70% ethanol until sorted in the lab. Species were identified to the lowest taxonomic level possible.

Epibenthic and benthic-pelagic predators (e.g., flatfishes, gobies, brown shrimp) were quantified using a beach seine with a mesh size of 2 mm. Each haul sampled an area of 40 m². Predators were sampled during three days in July and three days in August, with 6–8 hauls along the shoreline per sampling day. The fishes and epibenthic crustaceans were euthanized, put on ice, and identified to species level and counted back in the laboratory. We also measured and recorded each individual’s body length (to the closest millimeter) and weight (to 0.01-g accuracy). The predators were stored in 70% ethanol for gut content analysis, during which prey were identified to the lowest possible taxonomic level and counted. We analyzed a total of 1,065 individual guts (at least 30 guts per predator species) for documentation of feeding links to be complemented by the literature review (see below).

**Construction and analysis of the connectance web**

A total of 36 taxa were identified at the site (Appendix: Table A1), which is a representative number of species for the habitat and area (Nohrén et al. 2009, Törmroos and Bonsdorff 2012). For each taxon, we conducted a literature review for information on feeding links. Summary connectance webs usually include links reported over larger spatial areas and over time, which tends to overestimate the broadness of diets (O’Gorman et al. 2012). We were conservative in our approach and only included links for which there was evidence of direct consumption, i.e., food items were found in the guts analyzed in this study, or from gut content analyses, preference trials or direct observation reported in peer-reviewed literature (sensu Byrnes et al. 2011).

Based on the binary link data, we calculated a
set of metrics describing food-web diversity and complexity, namely species richness (S), number of links (L), linkage density (L/S), directed connectance (C = L/S²), which gives the proportion of possible trophic links that are realized, as well as the fractions of top, intermediate and basal taxa (Dunne 2006, Dunne et al. 2013). We then evaluated trophic complementarity in the community by quantifying the nestedness of interactions by calculating NODF (nestedness based on overlap and decreased fill), which takes values between 0 (perfectly non-nested, full trophic complementarity) and 100 (perfectly nested; Almeida-Neto et al. 2008). The significance of nestedness was tested using null model analysis; more specifically an incidence proportion model constraining both resources and consumers (Gotelli 2000, Ulrich et al. 2009, Kondoh et al. 2010).

Biological trait analysis
Each faunal taxon was assigned a set of seven traits reflecting foraging characteristics of the species, as well as aspects of their morphology and location in the habitat (Table 1). These traits do not provide an exhaustive representation of the multifunctionality of the community, but are central in determining the presence and strength of predator-prey interactions, encompassing dimensions of size-dependent foraging, spatial-temporal overlap of predator and prey niches, as well as predator foraging traits and prey vulnerability traits (Eklof et al. 2013, Klecka and Boukal 2013, Boukal 2014, Green and Côte 2014). In Table 1, we outline some examples of predicted relationships between traits and prey vulnerability or foraging relationships. However, we do not assume simple and general relationships, as there may be interactions between traits. For example, Klecka and Boukal (2013) found an interactive effect of predator foraging mode and prey escape ability, so that prey mortality was higher for active prey, but only when exposed to ambush predators (compared to searching predators).

The only continuous trait, body size (body mass), was determined for each species during laboratory work described above. The remaining traits made up a total of 25 sub-categories and were based on peer-reviewed information (e.g., Törnroos and Bonsdorff 2012) and publicly available databases (e.g., MarLIN 2006). In a matrix, we listed all 25 categories as columns and each row represented a prey species. For each prey, the expression of trait categories was denoted as presence/absence (1/0). We allowed for multiple categories to be expressed within a trait, e.g., under ‘feeding habit,’ omnivorous taxa were denoted as expressing both herbivorous and carnivorous feeding (Törnroos 2014). Including the 10 most abundant predators within the quantified community, we then created a matrix, which was based on the diet composition of each predator, giving the number of different prey species for each trait category in the predator’s diet. This ‘predator by prey traits’ matrix was then used to calculate prey trait richness and prey trait redundancy for each predator. We also created a predator trait matrix for corresponding calculations for prey taxa (i.e., a ‘prey by predator traits matrix’).

Statistical analysis
To determine whether predator-prey interactions were size-structured, we constructed a predation matrix (e.g., Hall and Raffaelli 1991, Yodzis 1998, Petchey et al. 2008) with species in rows and columns. Rows contained species denoted as resources (ordered by body size, increasing from top to bottom), and columns contained species denoted as consumers (ordered by body size, increasing from left to right). Dots indicate feeding links between resources and consumers. We then conducted a proportion test (McLaughlin et al. 2010) to assess if a significant fraction of data points or links were located in the upper right triangle of the predation matrix, i.e., instances were the consumer was larger than the resource. Linear regressions were calculated for log₁₀ body mass of predators vs. generality (the number of prey taxa included in diet), and generality vs. trait richness (the number of traits included in diet) and trait redundancy (the average number of prey taxa per trait category). Corresponding analyses were performed for log₁₀ body mass of prey vs. vulnerability (the number of predators feeding on the prey), and vulnerability vs. predator trait richness and trait redundancy. We adopted a data-driven approach to identify patterns in trait composition of predator diets using a posteriori group classification of hierarchical clustering followed by
random forest analysis to determine the relative importance of different traits for the clusters observed. Random forest analysis is a classifying procedure that estimates variable importance by combining multiple classification trees through bootstrap sampling and model averaging (Cutler et al. 2007, Darling et al. 2012). The clusters were verified using permutational multivariate ANOVA, and standard metrics, such as out-of-bag error rates, were used to assess model accuracy for classification trees and random forests (stratified sampling did not affect the results and was not included in the analysis). All analyses were run in R (R Development Core Team 2014) using the Cheddar (Hudson et al. 2013), vegan (Oksanen et al. 2013) and randomForest (Liaw and Wiener 2002) packages.

Table 1. Biological traits with subcategories characterizing multiple dimensions of trophic interactions, including size-dependent foraging, spatial-temporal overlap of predator and prey niches, as well as foraging attributes and vulnerability attributes for the taxa studied.

<table>
<thead>
<tr>
<th>Traits and categories</th>
<th>Examples of potential relationships</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body size</td>
<td>Smaller prey body size increases prey vulnerability</td>
</tr>
<tr>
<td>Body design</td>
<td>A more linear body form increases prey vulnerability, e.g. veriform &gt; bivalved</td>
</tr>
<tr>
<td>Vermiform</td>
<td></td>
</tr>
<tr>
<td>Bivalved</td>
<td></td>
</tr>
<tr>
<td>Turbine</td>
<td></td>
</tr>
<tr>
<td>Articulate</td>
<td></td>
</tr>
<tr>
<td>Pisciform</td>
<td></td>
</tr>
<tr>
<td>Protection</td>
<td>Protection decreases prey vulnerability, e.g. with spines &lt; no protection</td>
</tr>
<tr>
<td>No protection</td>
<td></td>
</tr>
<tr>
<td>Tube or Case</td>
<td></td>
</tr>
<tr>
<td>Burrow</td>
<td></td>
</tr>
<tr>
<td>Soft shell</td>
<td></td>
</tr>
<tr>
<td>Hard shell</td>
<td></td>
</tr>
<tr>
<td>Spines</td>
<td></td>
</tr>
<tr>
<td>Feeding habit</td>
<td>Feeding habit indicates role in trophic pathway</td>
</tr>
<tr>
<td>Detritivore</td>
<td></td>
</tr>
<tr>
<td>Herbivore</td>
<td></td>
</tr>
<tr>
<td>Carnivore</td>
<td></td>
</tr>
<tr>
<td>Environmental position</td>
<td>Spatial overlap of predator and prey niches increases prey vulnerability</td>
</tr>
<tr>
<td>Infauna deep (&gt;5 cm)</td>
<td></td>
</tr>
<tr>
<td>Infauna middle (2–5 cm)</td>
<td></td>
</tr>
<tr>
<td>Infauna top (&lt;2 cm)</td>
<td></td>
</tr>
<tr>
<td>Epifauna</td>
<td></td>
</tr>
<tr>
<td>Benthic-pelagic</td>
<td></td>
</tr>
<tr>
<td>Mobility</td>
<td>Mobility may increase prey vulnerability, alt. decrease if strong escape response</td>
</tr>
<tr>
<td>Sessile</td>
<td></td>
</tr>
<tr>
<td>Crawler</td>
<td></td>
</tr>
<tr>
<td>Facultative swimmer</td>
<td></td>
</tr>
<tr>
<td>Obligate swimmer</td>
<td></td>
</tr>
<tr>
<td>Metabolic category</td>
<td>Organisms generally feed on organisms with the same, or lower, metabolic type</td>
</tr>
<tr>
<td>Invertebrate</td>
<td></td>
</tr>
<tr>
<td>Ectotherm vertebrate</td>
<td></td>
</tr>
</tbody>
</table>

RESULTS

Food-web topology and nestedness of interactions by taxonomy

The summary connectance web (Fig. 1) for the shallow subtidal community contained 36 taxa, of which 5 were basal resources and 14 were primary consumers (herbivores or detritivores). The remaining 17 were categorized as carnivores or omnivores. Intermediate-level taxa made up the bulk of the web (67% of nodes), with basal resources constituting 14% of the nodes, and top consumers 20%. The nodes were connected by 168 links, resulting in a linkage density of 4.67 and a connectance of 0.13 (see Appendix: Table A1 for full species list).

The trophic complementarity was low in the studied community, as the predator-prey interactions in fact were highly nested (NODF = 69.69, z = 7.234, P = 0.0001). This means that the diets of more specialized predators were direct subsets of
the diets of more generalist species, rather than consisting of small sets of prey that few other predators utilize. Regarding uniqueness of node linkages, there was only a marginal effect of an aggregation to trophic species, which reduced the network by no more than two elements (grouping together the basal resources macroalgae with vascular plants, and the gastropods *Potamopyrgus antipodarum* with *Theodoxus fluviatilis*). This would suggest that taxonomic richness, or the taxonomic identity of the nodes, is important for the topology of this particular food web. However, although they did not show completely identical sets of links, many of the primary consumer macroinvertebrate species relied on the same resources and also shared predators, as shown by the high nestedness.

**Patterns of biological traits of interacting species in the food web**

The observed nestedness was linked to the size of the predators and their prey, and also revealed patterns of biological traits of interacting species. We found that the feeding interactions were size-structured, as hypothesized ($P < 0.0001$; upper triangularity in the predation matrix; Fig. 2A). The consumers were not only larger than their prey, but also occurred in lower densities; with energy flowing from smaller, abundant taxon to larger, less abundant predators (overall body mass-abundance relationship $y = -1.18x - 1.33$, $r^2 = 0.55$; Fig. 2B). With increasing predator body size, there was an increase in generality, i.e., diet breadth or the number of taxa used as prey ($y = 0.20x + 1.08$, $r^2 = 0.70$, $F = 18.25$, $P = 0.0027$; Fig. 3A). With this increase in generality, through larger predator body size, there was higher trait diversity, measured as the number of prey traits included in consumer diets ($y = 0.27x + 1.02$, $r^2 = 0.76$, $F = 25.98$, $P = 0.0009$; Fig. 3C). Predators with higher generality also showed a higher trait redundancy in their diet, i.e., a higher number of prey taxa per trait category ($y = 0.66x - 0.18$, $r^2 = 0.95$, $F = 141.80$, $P < 0.0001$; Fig. 3E). Corresponding patterns were evident for prey vulnerability and predator traits. Smaller prey were fed upon by a higher number of predator species ($y = -0.11x + 0.50$, $r^2 = 0.24$, $F = 4.84$, $P = 0.0438$; Fig. 3B), and with this increase in prey vulnerability came a higher trait diversity ($y = 0.29x - 3.07$, $r^2 = 0.26$, $F = 5.23$, $P = 0.0372$; Fig. 3D) as well as trait redundancy in the interacting predator assemblage ($y = 0.47x + 0.06$, $r^2 = 0.69$, $F = 32.91$, $P < 0.0001$; Fig. 3F).

Just as for prey identities in diets, there was a significant nestedness of feeding interactions when considering the traits of prey taxa (NODF = 75.11, $z = 6.475$, $P = 0.0001$), showing that there is a basic set of prey traits found in the diets of more specialist as well as more generalist predators. This translates to low trait complementarity between predator diets, and a potential for redundancy directed by predator body size. To identify the relative importance of prey traits in different predator diets, we created predator clusters based on the dissimilarity of the trait composition of their prey (Fig. 4). The highest order split corresponds with a grouping into ‘smaller’ predators (*Halicryptus spinulosus*, *Hediste diversicolor*, *Cyanophthalma obscura*, *Pungitius pungitius*) and ‘larger’ predators (*Ammodytes tobianus*, *Pomatoschistus minutus*, *Crangon crangon*, *Gasterosteus aculeatus*, *Platichthys flesus*, *Scophthalmus maximus*), and the trait composition of diets...
differed significantly between the two clusters (PERMANOVA $F_{1,9} = 10.484$, $P = 0.0037$), indicating some functional differentiation between predator groups. The top three relatively most important prey traits distinguishing the two predator groups were body size, environmental habitat, and body form, as revealed by random forest analysis. In our study food web, the smallest consumers were found among the infauna, feeding on mainly sediment-dwelling vermiform invertebrates, whereas the larger consumers were found at the sediment surface or in the benthic-pelagic habitat, feeding also on bivalved, turbinate and pisciform prey. This confirms the general importance of body size we found in the analyses of food-web topology, but also includes dimensions of morphology and space. As the larger predators fed on the smaller consumers as well as their prey, the results identify trophic transfer from benthos to the pelagic, indicating an additional, spatial dimension (vertical habitat) in the nestedness of interactions (again following body size).

**Discussion**

The complexity of ecosystems challenges our ability to predict the consequences of changing species assemblages. Accounting for the presence and strength of interactions among species promotes a better understanding of the effects of altered community structure. Studying a shallow-water, soft-sediment community, we found that the inherent complexity of the multi-trophic assemblage contained identifiable patterns; a nestedness of interactions, and that this nestedness was mirrored in the fundamental biological characteristics of interacting predators and prey species in the web.

**Body size and nestedness of interactions**

We hypothesized that our study food web would be size-structured, and the consumers in our community were indeed generally larger than their prey, confirming well-established patterns of size-structured feeding interactions (Woodward et al. 2005a, Brose et al. 2006, Riede et al. 2011). The numerical abundance across trophic levels scaled as $M^{-1.18}$, which is a steep relationship, close to the predicted slope of $y = -1.18x - 1.33$, $r^2 = 0.55$.

![Fig. 2. (A) Predation matrix showing size-structured feeding interactions as upper triangularity. Points indicate a trophic link between predator and prey (arranged by increasing body mass from left to right and top to bottom). The line with a slope of −1 illustrates instances where the biomass of consumers and resources is equivalent (cannibalism). (B) Trivariate relationship between abundance (N), body mass (M) and food-web structure with energy flowing from small, more abundant taxa to larger, less abundantly occurring species. Regression line shown in black; $y = -1.18x - 1.33$, $r^2 = 0.55$.](image-url)
Not only were predators larger than their prey but there were also size-related patterns in interactions; predator generality and prey vulnerability, together constituting a hierarchical nestedness of the food web.

We found an increasing generality with predator size, which is a pattern occurring in terrestrial, marine, lake and stream ecosystems (Digel et al. 2011). Smaller predators had overall narrower diets; usually diets of smaller predators do consist of fewer prey taxa and show more...
narrow prey body-mass spectra (Yvon-Durocher et al. 2008). As our consumers increased in size, the breadth of their diets grew as smaller prey taxa were still consumed but progressively larger prey species were included in the diet. Our findings (based on binary data) do thereby not suggest allometrically constrained feeding, where the predator diet shifts according to an optimal size niche with most efficient exploitation of certain sized prey and decreasing interaction strength to smaller and larger prey, respectively (Brose 2010, Schneider et al. 2012). In fact, our food web resembles e.g., the well-studied Broadstone Stream macroinvertebrate food web in that the largest predators included most prey taxa in their diets and feeding links of smaller predators were subsets of those of larger consumers (Woodward et al. 2005b), which is consistent with the hierarchical structuring central to several ‘niche models’ (Williams and Martinez 2000, Cattin et al. 2004). A nested hierarchy of dietary niches, like the one we found in our study, is widely observed in nature (Kondoh et al. 2010) and has potential implications for the functioning of the community (e.g., lower trophic complementarity reduces biomass production; Poisot et al. 2013). However, simply using taxonomic information to describe these types of trophic niches holds limited information on potential functional complementarity among predators. In the following paragraphs we discuss patterns of trait diversity, redundancy,
and composition against this backdrop of nested trophic transfer, more specifically in relation to body size and principal food-web metrics of generality and vulnerability.

**Trait richness of interacting predators and prey**

With an increasing number of interacting species, such as more predators feeding on a certain type of prey, or more prey taxa in a predator’s diet, increases in trait richness are expected to follow. We did, indeed, find such patterns of diversity for interacting taxa. The most vulnerable (smallest) prey organisms were susceptible to the highest number of predator traits, and the most generalist (largest) predators had highest prey trait richness. Through their higher generality, larger predators interacted with a biologically more diverse prey assemblage, indicating "true" functional generalism.

Our findings are in line with recent research showing strong connections between body sizes and effects on ecological processes. Size-spectra across taxa and within species greatly influence functioning, for example rates of decomposition, net primary production or nutrient fluxes at the sediment-water interface (Dossena et al. 2012, Norkko et al. 2013, Rudolf and Rasmussen 2013), through both trophic and non-trophic mechanisms. The relationship between large body size and high contribution to functioning is particularly important considering the association between large body size, high trophic level, low population density and an increased vulnerability and risk of extinction (Purvis et al. 2000). It would be informative to determine to what degree generalist consumers maintain a qualitatively stable trait composition in their diet, in spite of temporal and spatial variation in realized feeding links. Assuming that changes in the traits of a prey assemblage indicate an altered environment (response traits), generalist feeding may suggest predator adaption potential (Clavel et al. 2011).

**Trait redundancy of interacting predators and prey**

Our results corroborate a general positive relationship between taxonomic richness and trait richness in the study food web. However, such relationships may differ greatly depending on the extent to which different species show the same biological traits (Micheli and Halpern 2005), and we did find patterns of redundancy. The most vulnerable (smallest) prey interacted with more predators, but also more species displaying the same traits. The corresponding positive, linear relationship between predator generality and prey trait diversity with a slope <1, also shows that multiple prey express similar traits. It is worth exploring the ways generality may influence the potential for trophic redundancy in the community (Peralta et al. 2014). Larger predators could be more likely to (qualitatively) match the consumption by smaller predators through broader feeding niches, both in terms of prey taxonomy and biological traits. This reasoning suggests that hierarchical nestedness of diets affects trophic redundancy in a directed manner, once more emphasizing processes structured by the size of interacting species. Interestingly, this would infer that species that contribute the most to such redundancy might be the first to be lost from communities. Generally, redundancy is thought to be more prevalent at lower trophic levels, which show higher species richness and greater abundances (Loreau et al. 2001).

The other side of the (redundancy) coin is that nestedness indicates low trophic complementarity in the food web (Kondoh et al. 2010, Poisot et al. 2013). However, there are additional dimensions of feeding (other than prey taxonomy) through which biodiversity effects can emerge. For example, consumers sharing the same resources may increase overall trophic transfer in the community through temporal separation of trophic niches (Nordström et al. 2010). Interactions are structured in time and space and predators are not expected to distinguish between prey based on taxonomy, but on characteristics affecting foraging, i.e., are of functional relevance to the predator (Woodward and Warren 2007). In our study, we saw that body size was the most important prey trait distinguishing diets of smaller vs. larger predators, followed by environmental habitat and body design. In a study on diet selection within a single genus (*Pterois*, lionfish), prey morphology and behavior affected vulnerability to predation; small, shallow-bodied, solitary fishes in the reef habitat were most vulnerable (Green and Côte 2014).
**Benthic food webs and empirical opportunities**

We focused on the benthic macroinvertebrate and benthic-pelagic fish community but there is potential to expand this network further, towards both smaller and larger food-web components. For example, meiofauna are important in the diet of many infaunal and epifaunal macroinvertebrates, such as polychaetes and crustaceans (*Crangon crangon*), and juvenile and small fishes, such as gobies (*Pomatoschistus minutus* and *Pomatoschistus microps*) and flatfishes (*Platichthys flesus* and *Scophthalmus maximus*; Pihl 1985, Aarnio et al. 1996). In the Broadstone Stream food web, including permanent meiofauna flipped the relationship to a decreasing generality with increasing macroinvertebrate predator body mass, thus revealing possibilities for both upper and lower size-refugia for prey (Woodward et al. 2005a), in comparison to our benthic community that only showed a size-refugium for larger prey. Also, parasitic feeding relationships were excluded from this study, but clearly have the potential to affect the diversity and complexity of food webs (Dunne et al. 2013).

We see potential in using readily available qualitative information on the biology of interacting taxa. Benthic macroinvertebrates are often treated as a homogenous group, e.g., in simulations of food-web reorganization due to changing climate or anthropogenic pressure (Tomczak et al. 2013). Identification of the biological characteristics of trophically important prey taxa could help in the selection of macrobenthic prey groups for modeling purposes if higher taxonomic resolution is not possible (Timmermann et al. 2012).

In conclusion, our empirical data indicate that a combination of fundamental biological characteristics and trophic linkages provides significant insight into the ecology and organization of benthic communities. In light of the ongoing global declines in diversity (i.e., a sixth mass extinction; Barnosky et al. 2011), with particular emphasis on current extinctions of interactions and the trophic downgrading of earth (Estes et al. 2011), it is imperative that we study coastal biodiversity (species/taxa) within a proper context of interactions (e.g., food webs) and functioning (species’ roles within the community) if we want to increase our chances of understanding coastal ecosystems undergoing change in the Anthropocene. The next step is therefore to assess if and how the relationship between trophic structure and biological traits of interacting species changes during community degradation (or reassembly) and what the functional consequences of this would be.

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**LITERATURE CITED**


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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix is available online: http://dx.doi.org/10.1890/ES14-00515.1.sm