Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species

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Abstract. Studies focusing on the linkage between numerical and functional trait diversity frequently consider functional diversity indices but rarely evaluate them empirically or evaluate the use of other than continuous traits such as body size. Here, we present an extensive compilation on functional knowledge of benthic macrofauna using the categorical trait approach and scores of both common and rare species for 25 biological traits, including 102 modalities. We empirically quantify functional trait richness, within-trait species richness (redundancy), and trait variability on a large regional scale (>1000 km), in three environmentally different areas (basins of a sea), over a long time-span (10 years). To develop further the usage of multiple categorical traits as an analysis tool, we examine the effect of sampling effort for the understanding of the functional properties of the benthic meta-assemblages. We also evaluate the relationship between species richness and trait richness in order to understand co-variation between trait modalities and how traits are packaged within species. Results show that the biological diversity in terms of traits could be distinguished between areas of higher and lower salinity, higher and lower anthropogenic stress, and higher and lower species richness. A considerably lower number of samples are needed to portray the functional structure of an area in relation to the taxonomic structure, thereby demonstrating the advantage of using traits when considering management and conservation issues. Using categorical traits empirically requires, as shown within this study, an understanding of the relationship between species richness and expression of traits, co-variation of traits at different species richness and composition levels, acknowledgment of differences in trait expressions between common and rare species, and variability in abundance of species. Empirical trait-based analysis can reveal large-scale differences and insights into complexities between assemblage structure and function, and simultaneously be a valid tool for finding generalities.

Key words: biological traits; common and rare species; multiple environmental stressors; spatial scale; trait co-variation; trait richness and redundancy; zoobenthos.

Introduction

Understanding functioning of ecosystems in relation to biodiversity has become a central research theme in both aquatic and terrestrial ecology during the recent decade (Hooper et al. 2005, Solan et al. 2006). The core issue in understanding the role of biodiversity for ecosystem functioning ultimately comes down to knowing what organisms do within the constraints of their environment (Hooper et al. 2005). Through their diverse abilities to coexist and interact on multiple levels, organisms affect ecosystem processes and influence ecosystem functioning (Tilman 2000). Human activities affect this diversity and functioning by changing the environment in both aquatic and terrestrial systems, on scales from local to global and immediate to long term (Millennium Ecosystem Assessment 2005, Worm et al. 2006).

Functional diversity today is about measuring the richness and diversity (evenness and divergence) of functional traits (Schleuter et al. 2010). Functional traits are components of an organism’s phenotype that influence ecosystem level processes (Violle et al. 2007, Reiss et al. 2009). Traits can be morphological, physiological, reproductive, or behavioral aspects of an organism and may directly mediate energy and material fluxes or alter abiotic conditions that govern rates of functions (Symstad et al. 2003). Two different approaches to measuring this diversity, using multiple traits, have emerged during recent years. On the one hand, functional diversity indices have evolved rapidly, comprising of indices of functional richness, evenness, and divergence (Petchey and Gaston 2006, Laliberté and Legendre 2010, Mouchet et al. 2010, Schleuter et al. 2010). Recommended at the moment is that indices should only include traits that can be measured on a continuous scale, (i.e., real-value traits such as body size), rather than splitting a trait into a priori categories (i.e., categorical or discontinuous traits). Real value traits allow for direct use of species information...
(measured values) rather than requiring grouping or coding of species to the categories. On the other hand, the use of categorical traits has received interest especially in empirical studies, such as macro-ecological studies (Webb et al. 2009, Tyler et al. 2012). Also studies assessing anthropogenic impacts on functioning and studies evaluating functional aspects for conservation and management purposes have benefitted from using an approach based on categorical traits (de Juan et al. 2007, Frid et al. 2008). In marine and freshwater studies, this approach has often gone under the name biological trait analysis (Townsend and Hildrew 1994, Usseglio-Polatera et al. 2000, Bremner et al. 2003). In this approach, all traits are divided into sub-categories or modalities. Thus, the trait mobility can be divided into three modalities; sessile, semi-mobile, and mobile. This approach, in comparison to the other, does not measure functional diversity per se, give absolute insight into the distribution or variability of traits, or provide a direct link to functions. However, categorical traits are the present day substitutes for the data that would enable the sole use of continuous traits in measurements. For many functional aspects in space and time, this type of information is often the best available knowledge we have about species (Tyler et al. 2012) if no artificial data is used, as is often the case in simulation and theoretical studies. As it is a group-based approach, it still differs from the trophic or functional group approach (Fau-chald and Jumars 1979, Bonsdorff and Pearson 1999, Cardinale et al. 2006) in that more traits are used, not only related to feeding interactions and trophic structure but also environmental gradients. This increases the potential for identifying functional differences between assemblages on different scales (Bremner et al. 2003).

Although theoretical and experimental studies have outlined the relationship between species and functions on small scales (from petri dishes to several square meters; Naeem and Li 1997), empirical large scales (hectares to square kilometers), and long-term studies (years), scales relevant for marine ecosystems are scarce. Evidence of the connection between habitat or small-scale environmental heterogeneity and functional trait diversity in marine systems is robust (Bremner et al. 2003, Hewitt et al. 2008). However, the importance of this linkage at large scales and long term is less clear (Hooper et al. 2005). Scaling up from local processes to regional and larger scales is potentially more difficult, nevertheless critical, in taxonomically diverse, environmentally variable, and highly impacted systems such as estuaries and coastal seas (Lotze et al. 2006, Worm et al. 2006). To do so, using traits, and particularly categorical traits as we will focus on from here onward, still requires empirical testing and understanding of the procedures and pitfalls for quantifying trait diversity in comparison to species diversity and composition. Whereas, for example, trait composition has been said to be more stable than taxonomic composition over extensive biogeographic gradients in both freshwater (Charvet et al. 2000) and marine systems (Bremner et al. 2003), there is a lack of knowledge in how sampling effort influences the functional interpretation. Also, to develop and properly utilize the trait concept for understanding functional community dynamics on regional scales, quantifying not only the number of traits but also within-trait richness of species and variability as well as the functional role of common and rare species is urgent (Ellingsen et al. 2007, Hewitt et al. 2008).

The general objective of this paper is to develop the use of categorical traits by exploring the relationship between traits and traditional community variables, such as species number and composition, under different environmental conditions. More specifically, we (1) ask how trait richness in relation to species richness is affected by sampling effort in a set of environmentally different areas; (2) ask how trait composition, trait richness, as well as species richness and variability within traits differ on a large regional scale (>1000 km), in different areas (basins of a sea), over a long time-span (10 years); (3) evaluate the relationship between species richness and trait richness in order to understand covariation between traits and how traits are packaged and distributed within species to extend the scope of the functional approach; (4) evaluate trait differences between areas and depths considering abundances of species in order to allow for some generality.

As a base, we present an extensive compilation of soft-bottom macrofaunal traits for the brackish water northern Baltic Sea. Utilizing one of the most studied areas in the world, the coastal system of the Baltic Sea, relatively species-poor by nature due to its short post-glacial history and strong structuring environmental gradients (Bonsdorff 2006, Leppärantu and Myrberg 2009), allows for a precise and comprehensive functional assessment with high taxonomic resolution. Thus, this data provides us the possibility to include both common and rare species as species diversity is naturally low and the natural history of most species is well known.

**Materials and Methods**

**Distribution and abundance data**

In order to develop a base for the analyses and compile a species and trait data set, we used data on soft-bottom macrobenthic fauna from the Finnish National Coastal Monitoring Program, available in the Environmental Information System (HERTTA) database, maintained by the Finnish Environmental Institute. The data spanned a time period of 16 years (1988–2004) and spatially covered the entire Finnish coastline, in total about 1250 km. Altogether 782 stations and 1941 sampling visits were included and distributed across the four main basins of the northern Baltic Sea; from the northernmost basin of the Bothnian Bay and the Bothnian Sea, to the southern basins of the Archipelago Sea and the Gulf of Finland (65–59° N, 19–27° E; Fig. 1). The purpose of including data from all sub-basins in this first stage was to allow for describing...
functioning in terms of traits along the entire coast, a natural gradient of environmental and human-induced stress. The stations were separated into two depth groups: 0–10 m (hereafter shallow) and 10–55 m (hereafter deep). The divisions of sub-basins and water bodies follow the common national and international typology and division of the Baltic Sea and Finnish coastal areas (Perus et al. 2004). Benthic samples included were all obtained in a standardized way, using an Ekman-Birge grab sampler ($225-289 \text{ cm}^2$) and a 0.5-mm mesh sieve. Only visits with three replicate grab samples were included. Taxonomic resolution was set at species level when possible, and in accordance with resolution of trait information available. A thorough taxonomic quality assurance included verification of taxonomy and scientific names following the European Register of Marine Species, World Register of Marine Species, and the Integrated Taxonomic Information System (ITIS) (databases available online). Based on this large data set, we randomly compiled a smaller data set that was used for all analyses. This subset combined data from shallow and deep areas in three selected basins along the coast: the Bothnian Bay, the Archipelago Sea, and the Gulf of Finland (Fig. 1). To include a temporal aspect, data were included from six years within a 10-year period (1994, 1996, 1998, 2000, 2002, 2004). Five visits were randomly selected per year, per depth stratum and area, altogether 30 visits per depth, i.e., 60 visits (180 samples) per basin in total. An exception had to be made for the deep stratum in the Gulf of Finland, where not enough visits from 2002 could be found in the monitoring data. Thus, for this depth strata and area, a total of 25 visits were included. The three basin areas in the subset were chosen to maximize the contrasts in climate and environmental forcing and represent the “end points” in salinity and anthropogenically induced stress. As for the whole of the Baltic Sea, the strongest environmental factor in the northern Baltic Sea is salinity, decreasing gradually from 5–7 psu in the southwest, the Archipelago Sea, to 1–6 psu in the Gulf of Finland in the east, and 1–4 psi in the almost limnic Bothnian Bay in the north (Fig. 1; Rönning and Bonsdorff 2004, Leppäranta and Myr-
berg 2009). The northern basin differs from the two southern basins in annual light, temperature and riverine discharge dynamics, affecting the input of organic material and nutrient flow to zoobenthos. Not only the deep bottoms, but also the coastal sedimentary areas and zoobenthic assemblages are heavily affected by eutrophication and oxygen deficiency, specifically in the southern basins (Karlson et al. 2002, Conley et al. 2011). A higher cumulative pressure and impact is found in the Archipelago Sea and specially in the Gulf of Finland, compared to the Bothnian Bay, which is the least impacted area in the whole of the Baltic Sea (HELCOM 2010) (Fig. 1). Hence, the three areas differ largely in background environmental conditions, providing a setting for functional analysis, comparable to other estuarine environments.

**Trait data**

The principle for gathering information on species characteristics was to include as wide a range of traits as possible in order to be able to describe the trait diversity and general functioning of the assemblages in the most comprehensive way. Therefore, trait information was gathered on the lowest possible taxonomic level, and only later adjusted to appropriate higher taxonomic levels. Adjustments were done using all information for the species on the accepted taxonomic level, and when differing trait expressions between species/genera was found, the taxon was assigned equal probabilities. This was generally an issue affecting number of modalities rather than the scoring within a modality. Species were assigned to 25 traits and 102 sub-categories or modalities (Table 1). The traits reflect key components of functioning and proxies for ecological processes (Table 1; see also Frid et al. 2008). Scoring of species to traits was done using the fuzzy coding procedure (Chevenet et al. 1994), with a scoring range of 0 (no affinity) to 3 (total affinity). Some species are known to display plasticity in certain traits, and to overcome this on a large scale when information on, e.g., sediment characteristics for each sample was scarce, species were assigned equal probabilities to express the different potential trait modalities. We also acknowledged the fact that traits differ in how many modalities individual species can be assigned to within a trait, in three ways. First, traits for which a species can only express one modality of a number of possibilities, e.g., maximum size, we categorize as a discrete trait (Table 1, Supplement). Second, for a combinatory trait, species can be assigned to one, several, or all of the modalities, for example the trait reproductive technique, as some species can reproduce both sexually and/or asexually. The third possibility is a binary trait, where species can be assigned to only one modality or, if not to that specific modality, to any combination of the others. For example the trait living habit for which some species can only be attached and coded only for this modality, but other species may be both free-living and burrow dwellers to certain degrees, hence coded for several modalities (Table 1, Supplement). Consequently, the maximum number of scores, i.e., number of species expressions, within any modality, can only be the total number of species, though different modalities may display differing total numbers of score inputs. The maximum number of scores within the whole trait may thus differ depending on if species can express one or several modalities within a trait. Hence traits are not equal in the implication of a modality per se. This difference is an important issue specifically when trait richness and trait redundancy are discussed.

Information on species traits was obtained, supplemented, and reported here using (1) peer-reviewed, published sources (articles, books, etc.), (2) information based on the species phenotype, e.g., body design, or based on other traits, and (3) expert knowledge or unpublished sources (Supplement). The information was primarily collected from studies conducted in the region in order to appropriately include region-specific characteristics. Species in the Baltic Sea might express other ranges of modalities compared to their conspecifics in fully marine areas. Specific to this region is the presence of insect larvae as a significant component of the zoobenthos community and thus we included these based on their larval characteristics. Still, most traits and modality divisions were based on other studies (Bremner et al. 2003, 2006, Frid et al. 2008), and thus kept comparable with other regions outside the Baltic Sea.

To reach our fourth aim of evaluating trait differences between areas considering abundances of species, we weighed the functional trait expressions with the abundances of the species in the randomly assembled subset. This weighting procedure was done through multiplying the trait scores of the species with the abundances of the species, producing a sample-by trait matrix. Prior to this step, abundances were square root transformed, in order to down-weight abundant species (Anderson et al. 2003, 2006, Frid et al. 2008), and trait scorings standardized to one within a trait for a species (Boström et al. 2010).

**Data analysis**

To illustrate the effect of sampling effort (visits) on the functional richness in relation to species richness, sample-based species rarefaction curves for the three selected areas and two depth strata were calculated using EstimateS (Version 8.2; available online). In order to examine the trait richness in relation to area, we performed the same analysis using trait modalities instead of species, utilizing presence/absence of trait modalities in the randomly assembled data set. This analysis method randomly permutes (50 permutation) the order of species or trait modalities considered in an analysis.

5 http://viceroy.eeb.uconn.edu/estimates
Table 1. List of biological traits and modalities (subcategories).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Modality</th>
<th>Explanation</th>
<th>Key mechanisms of functions</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morphology/physiology</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum size†</td>
<td>1–5 mm</td>
<td>small</td>
<td>rate of production</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>5 mm–1 cm</td>
<td>small–medium</td>
<td>amount of exchange,</td>
<td>elemental cycling</td>
</tr>
<tr>
<td></td>
<td>1–3 cm</td>
<td>medium</td>
<td>facilitation</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3–5 cm</td>
<td>medium–large</td>
<td>respiration</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;5 cm</td>
<td>large</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body design†</td>
<td>vermiform, unsegmented</td>
<td>wormlike, lacking true segments</td>
<td>rate of production</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>vermiform, segmented</td>
<td>wormlike, divided into semi-independent units</td>
<td>proxy for litter quality</td>
<td>decomposition</td>
</tr>
<tr>
<td></td>
<td>bivalved</td>
<td>a shell of two calcaceous valves joined by a</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>flexible ligament</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>articulate</td>
<td>joined, arthrous (composed segments)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protection†</td>
<td>no protection tube</td>
<td>no protection at all</td>
<td>proxy for palatability</td>
<td>elemental cycling</td>
</tr>
<tr>
<td></td>
<td>burrow</td>
<td>uses a built tube as protection</td>
<td>decomposition</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>case</td>
<td>uses loose burrows as protection</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>soft shell</td>
<td>an exoskeleton or hard cuticula</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>hard shell</td>
<td>a hard protective shell, such as, e.g., a mussel</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body flexibility†</td>
<td>non-flexible</td>
<td>&lt;10 degrees</td>
<td>proxy for palatability</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>very flexible</td>
<td>&gt;45 degrees</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>flexible</td>
<td>10–45 degrees</td>
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</tr>
<tr>
<td></td>
<td>jointed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fragility†</td>
<td>fragile</td>
<td>likely to crack as a result of physical impact</td>
<td>proxy for palatability</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>intermediate</td>
<td>liable to suffer minor damage</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>robust</td>
<td>unlikely to be damage by physical impact (e.g.,</td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>hard, leathery</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Degree of dependency†</td>
<td>low</td>
<td>totally free above sediment</td>
<td>transport</td>
<td>elemental cycling</td>
</tr>
<tr>
<td></td>
<td>temporary</td>
<td>temporary in/on sediment</td>
<td></td>
<td>(pelagobenthos)</td>
</tr>
<tr>
<td></td>
<td>permanent</td>
<td>permanent in/on sediment</td>
<td></td>
<td>(within benthos)</td>
</tr>
<tr>
<td>Reproduction/development</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Longevity†</td>
<td>&lt;1 yr</td>
<td>lives less than one year</td>
<td>energy fixations,</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>turnover, prod. rate</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1–2 yr</td>
<td>lives between one to two years</td>
<td></td>
<td>elemental cycling</td>
</tr>
<tr>
<td></td>
<td>2–5 yr</td>
<td>lives between two to five years</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>5–10 yr</td>
<td>lives between five to ten years</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time to maturity†</td>
<td>&lt;20%</td>
<td>takes &lt;20% of lifetime to reach maturity</td>
<td>proxy for turnover</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>20–50%</td>
<td>takes one-half (50%) of lifetime to reach maturity</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;50%</td>
<td>takes more than one-half (50%) of lifetime to</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>reach maturity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductive technique‡</td>
<td>asexual</td>
<td>budding/fragmentation, non-fertilized eggs laid</td>
<td>proxy for turnover</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td></td>
<td>by mother/individual</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sexual differentiation‡</td>
<td>sexual</td>
<td>having separate sexes capable of producing both</td>
<td>rate of production</td>
<td>proxy for turnover</td>
</tr>
<tr>
<td></td>
<td>gonochoristic</td>
<td>ova and spermatozoa either at the same time</td>
<td></td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>hermaphrodite</td>
<td>the ovum develops without fertilization (a form</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fertilization type‡</td>
<td>nonfertile</td>
<td>e.g., parthenogenetic</td>
<td>proxy for turnover</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>external</td>
<td>fertilization outside body</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>internal</td>
<td>fertilization inside body</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Developmental</td>
<td>asexual</td>
<td>asexual both fragmentation and budding</td>
<td>proxy for turnover</td>
<td>production</td>
</tr>
<tr>
<td>technique‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trait</td>
<td>Modality</td>
<td>Explanation</td>
<td>Key mechanisms of functions</td>
<td>Function</td>
</tr>
<tr>
<td>-----------------------------</td>
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<td>------------------------------------------------------------------------------</td>
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</tr>
<tr>
<td>oviparous</td>
<td>non-fertilized eggs (hermaphrodite, parthenogenetic) or fertilized eggs laid or spawned</td>
<td>proxy for recruitment success</td>
<td>elemental transport production</td>
<td></td>
</tr>
<tr>
<td>ovoviviparous</td>
<td>egg layer/brooder</td>
<td>develop within and nourishment from the maternal body, parental or no care</td>
<td></td>
<td></td>
</tr>
<tr>
<td>viviparous</td>
<td>develop within and nourishment from the maternal body, parental or no care</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Larval type†</td>
<td>planktotrophic</td>
<td>feeding on material captured from the plankton</td>
<td>proxy for recruitment success</td>
<td>elemental transport production</td>
</tr>
<tr>
<td></td>
<td>lecitotrophic</td>
<td>nourished on internal resources, yolk</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>direct development</td>
<td>direct development of mini adults</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductive frequency‡</td>
<td>semelparous</td>
<td>breeding only once then dying breeds every year in desolate periods</td>
<td>proxy for turnover production</td>
<td></td>
</tr>
<tr>
<td>annual episodic</td>
<td>annual protracted</td>
<td>breeds every year over an extended or drawn out period</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Living</td>
<td>attached</td>
<td>adherent to a substratum (95% of adult time)</td>
<td>ability to perform transport and extent</td>
<td>elemental cycling (pelagobenthos)</td>
</tr>
<tr>
<td></td>
<td>tube-dweller</td>
<td>builds and dwells in a tube(s)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>burrow dweller</td>
<td>builds and dwells in a burrow(s)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>case builder</td>
<td>builds and dwells in a case (more pronounced “housing” than a tube)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>free living</td>
<td>in or on sediment, in water column</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Environmental position‡</td>
<td>infauna (&gt;5 cm)</td>
<td>living within the substrate, deeper than 5 cm</td>
<td>susceptibility to cropping/predation</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>infauna (2–5 cm)</td>
<td>living within the substrate between 2–5 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>infauna (top 2 cm)</td>
<td>living within the top 2 cm of the substrate</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>epibenthic</td>
<td>living on the surface of the substrate</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>benthopelagic</td>
<td>living in the water column but (primarily/occasionally) feeds on the bottom</td>
<td>elemental cycling (pelagobenthos)</td>
<td></td>
</tr>
<tr>
<td>Feeding</td>
<td>suspension feeder</td>
<td>obtaining food by actively sweeping or by holding out a filter</td>
<td>production</td>
<td></td>
</tr>
<tr>
<td></td>
<td>surface feeder</td>
<td>obtaining food from the surface of the substratum</td>
<td>transport from pelagous</td>
<td>elemental cycling (pelagobenthos)</td>
</tr>
<tr>
<td></td>
<td>sub-surface feeder</td>
<td>obtaining food from within the substratum</td>
<td>transport within sediment</td>
<td>elemental cycling (within benthos)</td>
</tr>
<tr>
<td></td>
<td>selective particle feeder</td>
<td>obtaining food by targeting prey or items (in sediment or water column)</td>
<td>facilitation/provision of material</td>
<td>decomposition</td>
</tr>
<tr>
<td></td>
<td>miner</td>
<td>obtaining food through mining in, e.g., woody material</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>detritivore</td>
<td>feeds on detritus</td>
<td>energy fixation/rate of transfer</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>omnivore</td>
<td>feeds on mixed diet of plant and animal material</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>herbivore</td>
<td>feeds on plants</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>carnivore</td>
<td>feeds on animals (predator)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>scavenger</td>
<td>feeds on dead organic material</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>parasite</td>
<td>obtaining food from another animal (host)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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Ecological Applications
Vol. 22, No. 8
### Table 1. Continued.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Modality</th>
<th>Explanation</th>
<th>Key mechanisms of functions</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resource capture method (How they feed)†</td>
<td>jawed</td>
<td>jaws, mandibles</td>
<td>consumption</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>siphon</td>
<td></td>
<td></td>
<td>elemental cycling</td>
</tr>
<tr>
<td></td>
<td>tentacular</td>
<td>using tentacles</td>
<td></td>
<td>decomposition</td>
</tr>
<tr>
<td></td>
<td>pharynx</td>
<td>both jawed and not jawed</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>radula net</td>
<td>rasping</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>build nets for capturing food particles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Movement</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mobility ‡</td>
<td>sessile</td>
<td>temporary (e.g. <em>Mytilus edulis</em>)</td>
<td>turnover</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>semi-mobile</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Movement method ‡</td>
<td>swimmer</td>
<td>movement with fins, legs, appendages via undulatory movements</td>
<td>facilitation of materials</td>
<td>elemental cycling (pelagos-benthos)</td>
</tr>
<tr>
<td></td>
<td>raftier/driver</td>
<td>rafting on, e.g., drifting algal mats, drifting</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>crawler</td>
<td>movement on the substratum via muscles, legs, appendages</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>byssus</td>
<td>acknowledged occasional movement by byssus threads</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>tube-builder burrower</td>
<td>moves when in a tube</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>moves in a burrow</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Migration (seasonal, reproductive)§</td>
<td>non-migratory vertical</td>
<td>migratory between sediment and water column</td>
<td>turnover</td>
<td>production</td>
</tr>
<tr>
<td></td>
<td>horizontal</td>
<td>migratory from shallow to deep (vice versa)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dispersal§</td>
<td>non-dispersal</td>
<td>resident</td>
<td>movement of resources</td>
<td>decomposition</td>
</tr>
<tr>
<td></td>
<td>local</td>
<td>frequent movement within habitat (10–1000 m)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>long distance</td>
<td>frequent movement out of habitat (km)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Behavior</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sediment transport§</td>
<td>no transport</td>
<td></td>
<td>transport, extent of bioturbation</td>
<td>elemental cycling (within benthos) decomposition</td>
</tr>
<tr>
<td></td>
<td>diffusive mixing</td>
<td>vertical diffusive transport (e.g., reworking, excavating)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>surface deposition</td>
<td>surface deposition of particles (e.g., defecation or egestion)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>conveyor belt transport</td>
<td>translocation of sediment within the sediment, deep-top (e.g., feeding, excavation)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>reverse conveyor belt transport</td>
<td>subduction of particles from surface to some depth (e.g., feeding, defecation)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sociability ‡</td>
<td>solitary</td>
<td>living alone</td>
<td>consumption rate</td>
<td>elemental cycling</td>
</tr>
<tr>
<td></td>
<td>gregarious</td>
<td>living in groups (aggregated together) occasionally (e.g., mussels)</td>
<td></td>
<td>decomposition</td>
</tr>
<tr>
<td></td>
<td>aggregated</td>
<td>living in groups, growing in clusters, schooling</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Notes:** Labels and explanations are included as well as examples of mechanisms and linkages to functions. Traits (25 in all), modalities (102 in all), and explanations are adopted from trait literature (see biotic glossary under the MarLin network: http://www.marlin.ac.uk/biotic/upload.php). Examples of traits linked to key mechanisms and functions are based on Bremner et al. (2003, 2006) and Frid et al. (2008).

† Discrete trait (species can only express one modality of the trait).
‡ Combinatory trait (species can be assigned to one, several, or all of the modalities in the trait).
§ Binary trait (species can be assigned to only one modality, or if not to that one modality to any combination of the others in the trait).
To determine the functional composition in the three different end-point areas, we calculated trait richness as the number of modalities expressed (presence/absence) and functional redundancy as number of taxa per modality (taxa richness within modalities) over time for each area and depth. Redundancy is here simply used as shorthand for species richness within trait modalities. The definition is not a strict one, since any functional effect, in space and time, of removing a species is not measured per se, and thus it is not known if a function remains exactly the same after the removal (Walker 1992). As a measure of the stability in functional redundancy, variability in number of species per modality was calculated using the coefficient of variation (CV) for each area and depth over time.

For further evaluating how species richness affect the functional understanding, using categorical traits, we calculated the cumulative number of trait modalities expressed by (1) all species, (2) all common species, and (3) all rare species found in the randomly assembled subset, irrespective of area or depth. We defined common and rare species as species occurring in 50% and 10% of the visits, respectively. This definition implies that a species is, e.g., not necessarily rare in all areas. Since species number differed greatly between common (10) and rare species (38), we also randomly drew 10 species out of the rare species pool to be able to compare these properly. To relate this to the empirical data we randomly drew ten species per area and depth from the data subset. These different compilations were analyzed using rarefaction curves in the EstimateS program, based on the trait expressions of species in terms of presence/absence of a trait modality. In comparison to only looking at presence/absence of a trait modality. In contrast to the community structure and trait assignment

A comprehensive benthic species list for the Finnish coastal region with a grand total of 143 species/taxa is presented based on the national quantitative monitoring data and notes of species occurrence in other literature references (Supplement). For trait assignments, we only used the quantitative monitoring data and a division into 56 taxa was done. This division was inevitable due to inconsistency in taxonomic resolution of the monitoring data and the level of trait knowledge found for the macrofauna. The 56 taxa expressed on average 29 trait modalities per species, indicating that species, in general, express more than one modality per trait, which highlights the different trait types (Supplement). Out of the 25 traits, 11 belonged to the discrete trait type, 10 to the combinatory type, and 4 to the binary type of traits. In general, the total number of taxa scores for single modalities varied from 1 (four modalities: less than one-half lifetime to maturity, attached living habit, sessile mobility though movement with byssus threads), to the maximum of 53 scores (one modality: sexual reproductive technique) (Supplement).

Effect of sampling effort on species and trait richness

In total, 53 of the 56 species/taxa signed to traits based on the quantitative data set were found in the randomly assembled data set, representing all functional important species. The species-accumulation curves demonstrated differences in species richness between the three geographical areas and the two depth strata, for which Archipelago Sea shallow had the highest richness (37 species/taxa; Fig. 2a). The different line curvatures showed the higher number of visits required to sample the species-rich Archipelago Sea (higher sampling effort) compared to the other two areas, or the shallow areas compared to the deep. The trait accumulation curves showed an analogous pattern in relation to differences between areas for species accumulation curves (Fig. 2b). The curves leveled off in each area and depth, but all possible modalities, i.e., the predetermined 102, were found only in the shallow area of the Archipelago Sea. A marked difference between the number of species and the number of trait modalities gained by sampling a similar area (number of visits) is noteworthy (Fig. 2). Considering all areas and depths, a minimum between 17 and 25 visits were needed to obtain 90% of the species, compared to only two to six visits to acquire 90% of the trait modalities (Fig. 2).

Trait richness, composition, and redundancy

The two extremes in the salinity gradient, the Archipelago Sea and the Bothnian Bay, differed functionally by 13 trait modalities (Table 2). When moving from the south to the north, the identity of the modalities revealed a loss in small, flexible organisms with a very long longevity but short (less than one-half of lifetime) maturity, a parthenogenetic sexual differentiation and both planktoto- and leucotrophic larval types. Lost were also modalities such as attached, tentaculate, sessile, movement by byssus threads, and sediment transport characteristics such as conveyor belt- and reversed conveyor belt transport. These
latter modalities are expressed by, e.g., the blue mussel, *Mytilus edulis*, or polychaete worms, both lost when moving in the south-north gradient (Supplement). In the most anthropogenically stressed area, the Gulf of Finland, six modalities were absent compared to the Archipelago Sea (Table 2). Aside from the differences in absence of traits, the three areas had 72 trait modalities in common, i.e., these constitute the common functional pool in the region (Table 2).

Richness of taxa within trait modalities, or redundancy, revealed a different pattern compared to the one found for the number of modalities expressed. In total, 48 modalities (47% of all) displayed a median of over two taxa per modality over the 10-year period (Table 3). The area with most modalities and also overall highest redundancy was the Archipelago Sea. In this area a total of 34 modalities had a median over two species/taxa, and the maximum number of taxa found within one such modality was eight (sexual reproductive technique; Table 3). The area displaying the lowest redundancy was the most stressed area, the Gulf of Finland, with 12 modalities corresponding to only about 12% of the total number of 102 modalities (Table 3). The variability across years, measured as CV, was similar and low for all areas varying between 0.21 and 0.63 (Table 3). A group of 12 modalities, with a median over two species/taxa was found to be general to all areas over time, hence representing the typical functional characteristics and reveals a “type organism” of the region (Table 3). Based on these modalities (shown in boldface type in Table 3), the typical northern Baltic Sea benthic organism is of medium size, reproduces sexually and is gonochoristic (separate sexes), has larvae that are direct developers, and lives as an adult permanently in or on the sediment, both in the top 1 cm of the sediment and epibenthically. It is further a mobile detritivore with local dispersal and diffusively mixes the sediment as it lives solitarily.

Covariation of traits and “trait packaging” within species

The accumulation curves based on all 53 species found in the subset shows that as more species are added more trait modalities are expressed, hence, trait richness is determined by species richness (Fig. 3a). The fact that the curve for all 53 species levels off before reaching the predetermined limit of 102 modalities shows that traits are also packaged into species, since a new species does not necessarily add a new trait modality. This follows theory (Schleuter et al. 2010) and is also illustrated in the calculations above of trait richness and redundancy.
This raises the question of covariation of trait modalities, i.e., that there are sets of traits that covary or to certain degrees accompanies others so that if, e.g., the trait modality bivalved (body design) is present then the modality hard shell (protection) is also. Loosing one or a few species might, depending on species composition, result in a sharp loss in trait modalities, as the lost species are the only ones expressing particularly those modalities. The curve implies that this might be true when species are few (the beginning of the curve), this will be less likely when there are more species. This loss is not easily deduced at low species level, as shown for the accumulation curves for 10 randomly drawn species from the species pool of the different areas and depths (Fig. 3b). Archipelago Sea shallow still showed the highest trait richness but the maximum number of trait modalities that the 10 randomly drawn species expressed differed from what was expected based on the trait accumulation curves for the areas (Fig. 2b). Archipelago Sea showed a lower number (higher loss) of trait modalities than expected (89 compared to 99), while Bothnian Bay showed a higher number (lower loss) of modalities (73 compared to 79).

Complicating this further, the result of the accumulation curves for the common and 10 randomly drawn rare species differed. Common species showed a higher number of species per modalities than did the rare species and, hence, expressing more modalities independently of species richness (Fig. 3a). Common and rare species had 78 trait modalities in common, 13 trait modalities were only expressed by common species, and eight modalities only by the rare species. These results suggest that number of modalities can also depend on the number of common and rare species included in the analysis, though this still requires further testing. A distinction between common and rare species could also be seen using the trait scores, which portray relevant ecological variation and not only expression or not, of a trait modality (Fig. 4).

Table 2. Traits and modalities present (X) and absent (blank) in the different areas (AS, Archipelago Sea; GF, Gulf of Finland; BB, Bothnian Bay; S, shallow, 0–10 m; D, deep, 10–55 m).

<table>
<thead>
<tr>
<th>Traits</th>
<th>Modalities</th>
<th>ASS</th>
<th>ASD</th>
<th>GFS</th>
<th>GFD</th>
<th>BBS</th>
<th>BBD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum size†</td>
<td>small</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>medium, large</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Body design†</td>
<td>bivalved</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>turbinate</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Protection†</td>
<td>burrow</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>case</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>hard shell</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Body flexibility†</td>
<td>non-flexible</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Longevity†</td>
<td>very long</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time to maturity†</td>
<td>less than half lifetime</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sexual differentiation‡</td>
<td>parthenogenetic</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Larval type‡</td>
<td>planktotrophic</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>lectotrophic</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Reproductive frequency†</td>
<td>annual episodic</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
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<tr>
<td>Living habit§</td>
<td>attached</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Environmental position‡</td>
<td>benthic pelagic</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>parasite</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>scavenger</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feeding habit‡</td>
<td>parasite</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>scavenger</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feeding position‡</td>
<td>siphon</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>tentaculate</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resource capture method‡</td>
<td>radula</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mobility†</td>
<td>sessile</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>semi mobile</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Movement method‡</td>
<td>byssus</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sediment transport§</td>
<td>conveyor belt transport</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>reverse conveyor belt transport</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sociability†</td>
<td>aggregated</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other traits (19–25)</td>
<td>other modalities (31–102)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total traits 18 (max. 25) for sub-areas</td>
<td>total modalities 30 (max. 102) for sub-areas</td>
<td>0</td>
<td>4</td>
<td>8</td>
<td>11</td>
<td>15</td>
<td>26</td>
</tr>
<tr>
<td>Total traits 18 (max. 25) for areas</td>
<td>total modalities 30 (max. 102) for areas</td>
<td>0</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: Modalities in boldface type are absent in all areas but the Archipelago Sea. The last two rows indicate the total number of traits and modalities displayed in the table. Out of the total number of traits (18 out of 25 possible) and modalities (30 out of 102 possible) displayed in the table, the first row indicates the number of traits displayed per sub-area (e.g. ASS, ASD, etc.). The second row indicates the number of traits displayed per area (i.e., AS [Archipelago Sea], GF [Gulf of Finland], and BB [Bothnian Bay]).

† Discrete trait (species can only express one modality of the trait).
‡ Combinatory trait (species can be assigned to one, several, or all of the modalities in the trait).
§ Binary trait (species can be assigned to only one modality, or if not to that one modality to any combination of the others in the trait).
Table 3. Number of species and modalities displaying redundancy in the different areas.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Modalities</th>
<th>ASS</th>
<th>ASD</th>
<th>GFS</th>
<th>GFD</th>
<th>BBS</th>
<th>BBD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum size‡</td>
<td>medium</td>
<td>4 (0.37)</td>
<td>5 (0.33)</td>
<td>3 (0.31)</td>
<td>3 (0.38)</td>
<td>3 (0.34)</td>
<td>3 (0.30)</td>
</tr>
<tr>
<td>Body design‡</td>
<td>verminiform segmented</td>
<td>3 (0.45)</td>
<td>3 (0.39)</td>
<td>3 (0.37)</td>
<td>X</td>
<td>3 (0.32)</td>
<td>3 (0.21)</td>
</tr>
<tr>
<td>Protection‡</td>
<td>no protection</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Body flexibility‡</td>
<td>hard shell</td>
<td>3.5 (0.49)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Fragility‡</td>
<td>non-flexible</td>
<td>3.5 (0.49)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Degree of dependency‡</td>
<td>intermediate</td>
<td>3 (0.54)</td>
<td>4 (0.31)</td>
<td>X</td>
<td>X</td>
<td>3 (0.41)</td>
<td>3 (0.47)</td>
</tr>
<tr>
<td></td>
<td>robust</td>
<td>4 (0.48)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>temporary</td>
<td>3 (0.57)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Longevity‡</td>
<td>short</td>
<td>4 (0.45)</td>
<td>4 (0.41)</td>
<td>X</td>
<td>X</td>
<td>3 (0.42)</td>
<td>X</td>
</tr>
<tr>
<td>Time to maturity‡</td>
<td>half of lifetime</td>
<td>5 (0.45)</td>
<td>3 (0.46)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>longer than half of lifetime</td>
<td>3 (0.53)</td>
<td>4 (0.39)</td>
<td>X</td>
<td>X</td>
<td>3 (0.45)</td>
<td>X</td>
</tr>
<tr>
<td>Reproductive technique‡</td>
<td>sexual</td>
<td>8 (0.40)</td>
<td>6 (0.34)</td>
<td>4 (0.36)</td>
<td>4 (0.37)</td>
<td>4.5 (0.36)</td>
<td>4 (0.34)</td>
</tr>
<tr>
<td>Sexual differentiation‡</td>
<td>gonochoristic</td>
<td>7 (0.41)</td>
<td>6 (0.35)</td>
<td>3 (0.43)</td>
<td>3 (0.50)</td>
<td>3 (0.39)</td>
<td>3 (0.46)</td>
</tr>
<tr>
<td>Fertilization type‡</td>
<td>external</td>
<td>5 (0.45)</td>
<td>3 (0.40)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>internal</td>
<td>3.5 (0.58)</td>
<td>4 (0.45)</td>
<td>3 (0.47)</td>
<td>X</td>
<td>5 (0.38)</td>
<td>4 (0.34)</td>
</tr>
<tr>
<td>Developmental technique‡</td>
<td>oviparous</td>
<td>2.5 (0.63)</td>
<td>3 (0.40)</td>
<td>3 (0.45)</td>
<td>X</td>
<td>3 (0.42)</td>
<td>3 (0.21)</td>
</tr>
<tr>
<td></td>
<td>ovoviviparous</td>
<td>5 (0.50)</td>
<td>4 (0.47)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Larval type‡</td>
<td>planktotrophic</td>
<td>2.5 (0.59)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>direct development</td>
<td>5.5 (0.37)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Reproductive frequency‡</td>
<td>semelparous</td>
<td>3 (0.40)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>annual protracted</td>
<td>4 (0.50)</td>
<td>3 (0.57)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Living habit§</td>
<td>burrow dweller</td>
<td>3 (0.46)</td>
<td>3 (0.34)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>free</td>
<td>4 (0.53)</td>
<td>3 (0.59)</td>
<td>X</td>
<td>X</td>
<td>3 (0.57)</td>
<td>X</td>
</tr>
<tr>
<td>Environmental position‡</td>
<td>infuna middle</td>
<td>3 (0.38)</td>
<td>3 (0.32)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>infuna top</td>
<td>6 (0.33)</td>
<td>6 (0.25)</td>
<td>3.5 (0.33)</td>
<td>4 (0.35)</td>
<td>4.5 (0.31)</td>
<td>4 (0.26)</td>
</tr>
<tr>
<td>Feeding position‡</td>
<td>suspension</td>
<td>3 (0.45)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>surface</td>
<td>4 (0.40)</td>
<td>4 (0.39)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Feeding habit‡</td>
<td>detritivore</td>
<td>7 (0.39)</td>
<td>6 (0.31)</td>
<td>3 (0.44)</td>
<td>3 (0.44)</td>
<td>4 (0.39)</td>
<td>3 (0.30)</td>
</tr>
<tr>
<td></td>
<td>omnivore</td>
<td>3 (0.47)</td>
<td>3.5 (0.41)</td>
<td>X</td>
<td>X</td>
<td>4 (0.39)</td>
<td>3 (0.34)</td>
</tr>
<tr>
<td></td>
<td>carnivore</td>
<td>3 (0.50)</td>
<td>3 (0.45)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Mobility‡</td>
<td>semi mobile</td>
<td>2.5 (0.53)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Movement method‡</td>
<td>swimmer</td>
<td>6 (0.39)</td>
<td>6 (0.38)</td>
<td>3 (0.44)</td>
<td>3 (0.34)</td>
<td>4 (0.35)</td>
<td>3 (0.34)</td>
</tr>
<tr>
<td></td>
<td>rafter/drifter</td>
<td>2.5 (0.54)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>crawler</td>
<td>5.5 (0.40)</td>
<td>4 (0.52)</td>
<td>X</td>
<td>X</td>
<td>4 (0.42)</td>
<td>3 (0.34)</td>
</tr>
<tr>
<td></td>
<td>burrower</td>
<td>3 (0.47)</td>
<td>3 (0.40)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Migration§</td>
<td>nonmigratory</td>
<td>6.5 (0.46)</td>
<td>4 (0.46)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>vertical</td>
<td>3 (0.36)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Dispersal§</td>
<td>non dispersal</td>
<td>3 (0.54)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>local</td>
<td>7 (0.37)</td>
<td>6 (0.38)</td>
<td>4.9 (0.39)</td>
<td>3 (0.32)</td>
<td>5 (0.36)</td>
<td>4 (0.34)</td>
</tr>
<tr>
<td></td>
<td>long distance</td>
<td>3.5 (0.49)</td>
<td>3 (0.58)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Sediment transport§</td>
<td>no transport</td>
<td>4 (0.51)</td>
<td>3 (0.55)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>diffuse mixing</td>
<td>6 (0.35)</td>
<td>5.5 (0.29)</td>
<td>4 (0.35)</td>
<td>3 (0.38)</td>
<td>4.5 (0.31)</td>
<td>4 (0.29)</td>
</tr>
<tr>
<td></td>
<td>surface deposition</td>
<td>3 (0.48)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Sociability‡</td>
<td>solitary</td>
<td>6 (0.41)</td>
<td>5 (0.33)</td>
<td>3.5 (0.35)</td>
<td>3 (0.35)</td>
<td>4 (0.44)</td>
<td>3 (0.26)</td>
</tr>
<tr>
<td></td>
<td>gregarious</td>
<td>5 (0.40)</td>
<td>4 (0.37)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Total traits 24 (max. 25) for sub-areas</td>
<td>total modalities 48 (max. 102) for sub-areas</td>
<td>44</td>
<td>37</td>
<td>16</td>
<td>12</td>
<td>24</td>
<td>20</td>
</tr>
<tr>
<td>Total traits 24 (max. 25) for areas</td>
<td>total modalities 48 (max. 102) for areas</td>
<td>34</td>
<td>12</td>
<td>20</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Values are given only for modalities with a median of >2 species (with CV in parentheses). "X" marks modalities in that are present but with a median <2 species; other modalities are absent (see Table 2 for comparison). Boldface type indicates modalities where a median of >2 species is found in all areas and thus represent the "type organism" of the northern Baltic Sea. The only trait not represented here, i.e., with a modality displaying a median of species >2, is resource capture method. The last two rows are as in Table 2.

† Discrete trait (species can only express one modality of the trait).
‡ Combinatory trait (species can be assigned to one, several or all of the modalities in the trait).
§ Binary trait (species can be assigned to only one modality, of if not to that one modality to any combination of the others in the trait).

Trait differences in relation to species abundance

The NMDS analysis for the abundance subset and for the sample-by-trait matrix was in line with the findings in the numerical analysis of differences between areas and depths (Fig. 5a and b). The PERMANOVA analysis indicated a significant difference between the species rich Archipelago Sea and the two other areas for the interaction between area and depth both in the analysis based on species abundance ($F_{2,169} = 3.6944, P = 0.0002$) and the abundance-weighted sample-by-trait matrix ($F_{2,169} = 3.2288, P = 0.0026$).
Our study identified biological traits for all functionally important species (56 taxa both rare and common) along the entire Finnish coastline. The analyses showed that the biological diversity in terms of traits could be distinguished between areas of higher and lower salinity, higher and lower anthropogenic stress, and higher and lower species richness. Using categorical traits, as is done within the biological trait analysis, require an understanding of the relationship between species richness and expression of traits, covariation of traits at different species richness and composition, and acknowledgment of both common and rare species and variability in abundance of species. However, all of these issues need further evaluation before this approach can be implemented, e.g., into management.

This study concerned the diverse shallow photic areas as an alternative to the more often investigated open sea areas in the Baltic Sea, which are known to inhabit only a handful of species (Bonsdorff 2006, Villnäs and Norkko 2011). The bulk of the species along the Finnish coast is also found in fully marine areas, making comparisons relevant over and between systems. We also included an often forgotten (see Nohrén et al. 2009), but highly interesting faunal component, namely the insects, both aquatic and terrestrial species with aquatic benthic larval stages. This group, also present in marine estuaries (Nohrén et al. 2009), was represented in this study primarily by midges (e.g., Chironomidae and Certaopogonidae) and identified as a general and important functional contributor along the entire coastal and salinity gradient. Our results reflect the common hypothesis of decreasing diversity with salinity, as noted in the southern Baltic Sea and other estuarine...
areas (Elmgren and Hill 1997, Bonsdorff and Pearson 1999), but highlight the loss, particularly of polychaetes and individual mollusc species, rather than the gain of taxa, such as insects.

Trait diversity and redundancy are, as are other measures of diversity, scale dependent (Fonseca and Ganade 2001). Since assemblages are defined for a given area at a given time, sampling a larger area means more species and thus possibly more traits. Our assessment of how sampling effect could affect trait analysis showed that considerably fewer numbers of samples are needed to portray the functional structure of an area in relation to the biotic (taxonomic) structure. Sampling a larger area may not necessarily reveal additional trait modalities. In this respect, this type of trait analysis is a cost-effective tool for the understanding of coastal soft-bottom communities, because large scale coverage may not be required in order to obtain a picture of how the systems differ in functional aspects.

We found that a species/taxa expressed on average more than one modality per trait. For one modality a total of 53 taxa scores were found, i.e., almost all 56 taxa in the analysis expressed it, possibly indicating that there is potential for redundancy across the whole region for some traits. It has been argued theoretically that functional redundancy is not expected on large scales since spatial and temporal environmental variation help maintain coexistence (Loreau 2004). For the Baltic Sea, the argument in general has been exactly this, that loss or drastic reduction of a single species most probably leads to loss of a whole functional group and thus greatly affect ecosystem functioning (Elmgren and Hill 1997, Bonsdorff and Pearson 1999). On the contrary, the ecosystem is simple with a short successional history, and hosts estuarine species with mixed origins living on the edge of their stress tolerances and hence, not co-evolved or highly specialized (Elmgren and Hill 1997, Bonsdorff 2006). This reasoning would imply that there might be open niches and that species tolerating the conditions could also be more general and similar in their trait expressions, hence give room for redundancy (Norkko et al. 2011). Though we found general differences in traits between areas, recognizing both common functional characteristics (type organism) and characteristics seldom expressed (e.g., traits specific to rare and common species) is important, especially in a rapidly changing environment. For species to withstand changes, possessing some of the common characteristics of the type organism might be enough, however to be a winner one might need e.g., traits expressed by the rare species.

Empirical studies such as ours, simultaneously investigating trait richness and redundancy, encompassing a wide range of ecosystem processes, are fragmentary and thus in demand (Fonseca and Ganade 2001). However, treating trait richness and redundancy levels with caution is important as classification schemes and scoring methods will affect the interpretation of patterns observed (Fonseca and Ganade 2001, Bremner et al. 2006). As we highlighted for the multitrait method, the types of traits chosen for the analysis will also affect the results. If a modality reflects the number of species directly, as for some types of traits where species can
only express one modality (the discrete or binary type), higher redundancy in such a modality may be important for functioning in that it directly buffers for loss of a function. In contrast, a trait for which one species can express several modalities to varying degrees, the probability of several species covering the modality and potential function is higher. Another issue that needs to be resolved is how much the correlation of traits, i.e., one trait complementing others, influences the functional understanding of a system. Based on our results, we highlight that a pre-analysis on how many and which traits that covary could be useful as a means to eliminate duplicated information. However, this is dependent on species richness and could be relevant information when species richness is low. In relation to this, our results imply that common and rare species express different traits and that this could also be important in comparing different areas and warrants further analysis, as indicated earlier (Ellingsen et al. 2007). Our results demonstrate that the multitrait method shows potential to develop theoretically and also for practical management purposes, but protocols for analyses are still needed (Bonsdorff and Pearson 1999, Bremner et al. 2006, Naeem and Bunker 2009).

We conclude that the biological trait analysis proved to be useful in describing the functional patterns on
large to small regional scales between areas differing in salinity and human impact, in a comparatively species-poor system, the Baltic Sea. The species and trait data set developed (Supplement) can hopefully aid further research on functional diversity not only in the region, but also allow for comparisons between marine areas, since the traits and modalities described are not specific, but rather applied to the Baltic Sea. We see our data set and analysis approach as an additional base and tool for management of the coastal soft-bottom areas in the region. Our study serves as a marine empirical example in the trait debate, which has to date mostly been conducted in terrestrial environments.

Acknowledgments

We thank Julie Bremner, Marie Nordström, and Katri Aarnio for providing fruitful comments, which greatly improved the manuscript. We also thank the reviewers for an in-depth examination of the analysis and manuscript. Thanks also to Jens Perus for help with data gathering and compilation. Financial support was received from the Maj and Tor Nesselö Foundation and Stiftelsen för Akademi.

Literature Cited


SUPPLEMENTAL MATERIAL

Supplement

Data on species occurrence and trait information of northern Baltic Sea coastal benthos (Ecological Archives A022-120-S1).