

Interpreting marine benthic ecosystem
functioning in coastal waters:

VALIDATING THE
BIOLOGICAL
TRAIT CONCEPT

ANNA TÖRNROOS

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Till Fammo, Faffa och Brynka

“Yes I love it! The sea is everything.
It covers seven-tenths of the terrestrial globe.
Its breath is pure and healthy.
It is an immense desert, where man is never lonely, for he feels life stirring on all sides.”

- **Captain Nemo** -

Twenty thousand leagues under the sea by **Jules Verne** (1870)

ABSTRACT

Coastal areas harbour high biodiversity, but are simultaneously affected by rapid degradations of species and habitats due to human interactions. Such alterations also affect the functioning of the ecosystem, which is primarily governed by the characteristics or *traits* expressed by the organisms present. Marine benthic fauna is involved in numerous functions such as organic matter transformation and transport, secondary production, oxygen transport as well as nutrient cycling. Approaches utilising the variety of faunal traits to assess benthic community functioning have rapidly increased and shown the need for further development of the concept. In this thesis, I applied biological trait analysis that allows for assessments of a multitude of categorical traits and thus evaluation of multiple functional aspects simultaneously. I determined the functional trait structure, diversity and variability of coastal zoobenthic communities in the Baltic Sea. The measures were related to recruitment processes, habitat heterogeneity, large-scale environmental and taxonomic gradients as well as anthropogenic impacts. The studies comprised spatial scales from metres to thousands of kilometres, and temporal scales spanning one season as well as a decade.

The benthic functional structure was found to vary within and between seagrass landscape microhabitats and four different habitats within a coastal bay, in papers I and II respectively. Expressions of trait categories varied within habitats, while the density of individuals was found to drive the functional differences between habitats. The findings in paper III unveiled high trait richness of Finnish coastal benthos (25 traits and 102 categories) although this differed between areas high and low in salinity

and human pressure. In paper IV, the natural reduction in taxonomic richness across the Baltic Sea led to an overall reduction in function. However, functional richness in terms of number of trait categories remained comparatively high at low taxon richness. Changes in number of taxa within trait categories were also subtle and some individual categories were maintained or even increased. The temporal analysis in papers I and III highlighted generalities in trait expressions and dominant trait categories in a seagrass landscape as well as a “type organism” for the northern Baltic Sea. Some initial findings were made in all four papers on the role of common and rare species and traits for benthic community functioning. The findings show that common and rare species may not always express the same trait categories in relation to each other. Rare species in general did not express unique functional properties.

In order to advance the understanding of the approach, I also assessed some issues concerning the limitations of the concept. This was conducted by evaluating the link between trait category and taxonomic richness using especially univariate measures. My results also show the need to collaborate nationally and internationally on safeguarding the utility of taxonomic and trait data. The findings also highlight the importance of including functional trait information into current efforts in marine spatial planning and biomonitoring.

Keywords: functional diversity, Biological Trait Analysis, categorical traits, community, zoobenthos, Baltic Sea

SAMMANFATTNING (Swedish abstract)

Kustområden hyser generellt en hög biodiversitet men samtidigt förekommer en snabb förlust av arter och habitat som en följd av mänsklig påverkan. Detta påverkar ekosystemets funktion som styrs av de förekommande arternas ekologiska särdrag eller *egenskaper*. Den marina bottenlevande faunan är involverad i olika ekosystemfunktioner bland annat nedbrytning av organiskt material, sekundärproduktion, transport av syre och cirkulation av näringsämnen. Studier där arternas egenskaper används för att analysera bottenfaunasamhällets funktion har ökat snabbt i betydelse och påvisat behovet av att utveckla egenskapskonceptet. I denna avhandling har jag tillämpat metoden biologisk egenskapsanalys (eng. *biological trait analysis*), i vilken en mängd olika kategoriska egenskaper används för att undersöka flera funktionella aspekter samtidigt. I denna metod delas egenskaperna in i olika kategorier och arterna kodas i förhållande till i vilken grad de uttrycker en viss egenskapskategori. Jag utvärderade den funktionella strukturen, mångfalden och variationen av Östersjöns kustnära bottenfaunasamhällen. Dessa mått relaterades till rekryteringsprocesser, habitatheterogenitet, storskaliga miljö- och taxonomiska gradienter, samt antropogena effekter. Studierna omfattade rumsliga skalor från några meter till flera tusen kilometer och berörde tidsmässigt både en säsong och ett årtionde.

I arbete I respektive II varierade den funktionella strukturen av bottenfaunasamhället inom och mellan olika mikrohabitat i ett sjögränslandskap, liksom mellan fyra habitat i en vik. Huruvida en egenskap uttrycktes eller ej varierade inom habitat, medan individtäthet styrde den funktionella skillnaden mellan habitat. Resultaten i arbete

III påvisade en hög rikedom av egenskaper i finska kustnära bottenfaunasamhällen (25 egenskaper och 102 kategorier), trots att skillnader mellan områden med hög och låg salinitet och mänsklig påverkan förekom. I arbete IV resulterade den naturliga minskningen i taxonomisk rikedom i Östersjön i en generell minskning i bottenfaunasamhällets funktion. Förutom denna reduktion, förblev den funktionella rikedomens i fråga om antal kategorier av egenskaper jämförelsevis hög vid låg taxonomisk rikedom. Analyserna i tid, i arbete I och III, åskådliggjorde egenskaper som dominerade i ett sjögränslandskap och illustrerade en "typorganism" för norra Östersjön. I arbetena gjordes några inledande iakttagelser gällande betydelsen av vanligt förekommande och sällsynta arter samt egenskaper för bottenfaunasamhällets funktion. Dessa visade att vanligt förekommande or sällsynta arter inte nödvändigtvis uttrycker samma egenskaper. I allmänhet uttryckte sällsynta arter dock inga unika funktionella särdrag.

För att kunna utveckla förståelsen av tillvägagångssättet utvärderade jag även några förbehåll gällande egenskapskonceptet som sådant. Detta gjordes genom att med univariata metoder utvärdera länken mellan kategori och taxonomisk rikedom. Ur mina resultat framgår även behovet av att samarbeta nationellt och internationellt för att ta tillvara taxonomiskt och egenskapsrelaterat data. Observationerna lyfter även fram betydelsen av att inkludera egenskaper om funktionell information i marin områdesplanering och övervakning.

Nyckelord: funktionell diversitet, Biologisk egenskapsanalys, kategoriska egenskaper, faunasamhälle, zoobenthos, Östersjön

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LIST OF ORIGINAL PAPERS

This thesis is based on the following original publications referred to with their roman numerals in the text:

- I Boström C., **Törnroos A.**, Bonsdorff E. (2010) Invertebrate dispersal and habitat heterogeneity: Expression of biological traits in a seagrass landscape. *Journal of Experimental and Marine Biology and Ecology* 390:106-117
- II **Törnroos A.**, Nordström M.C., Bonsdorff E. (2013) Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. *PLoS ONE* 8(10):e78910
- III **Törnroos A.**, Bonsdorff E. (2012) Developing the multitrait concept for functional diversity: Lessons from a system rich in functions but poor in species. *Ecological Applications* 22: 2221-2236
- IV **Törnroos A.**, Bonsdorff E., Bremner J., Blomqvist M., Josefson AB., Garcia C., Warzocha J. Marine benthic ecological functioning over decreasing taxonomic richness. *Manuscript* (Submitted November 2013)

OWN CONTRIBUTIONS TO THE INDIVIDUAL PAPERS

- I Conceived and designed the experiments: CB EB. Performed the experiments: CB. Analysed the data: AT CB. Wrote the manuscript: CB AT EB.
- II Conceived and designed the study: AT MCN EB. Performed the field sampling: AT MCN. Analysed the data: AT MCN. Wrote the manuscript: AT MCN EB.
- III Conceived and designed the study: AT EB. Analysed the data: AT. Wrote the manuscript: AT EB.
- IV Conceived and designed the study: AT EB JB MB ABJ JW. Analysed the data: AT JB EB. Contributed trait material: AT CG ABJ. Wrote the manuscript: AT EB JB MB ABJ CG JW.

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ADDITIONAL PUBLICATION NOT INCLUDED IN THE THESIS

Aarnio K., Mattila J., **Törnroos A.**, Bonsdorff E. (2011) Zoobenthos as an environmental quality element: the ecological significance of sampling design and functional traits. *Marine Ecology* 32:58-71.

1. INTRODUCTION

Coastal areas form the interface between land and sea, which provides high habitat heterogeneity and supports diverse communities of flora and fauna. Despite covering less than 10 % of the surface of the Earth, coastal seas still harbour the highest marine biodiversity (MEA 2005). Humans also appreciate the coastal areas as they provide a variety of goods and services such as coastal protection against erosion, production of food and recreational activities (Worm et al. 2006, Barbier et al. 2011). In numerical terms, these areas deliver about 30 % of marine production and 90 % of the fisheries (MEA 2005). Moreover, nearly 70 % of the human population now live within 60 km off the coast. As a result, coastal cities have expanded and 75 % of those with >10 million inhabitants are now located in the coastal zone (Widdicombe & Snelgrove 2012). Consequently, the coastal areas experience the largest threats to marine biodiversity (Gray 1997, Lotze et al. 2006). Our continued exploitations of the coastal systems have led to rapid degradation and loss of habitats and consequent reductions in species diversity (MEA 2005). These large-scale and long-term effects have implications for the stability and resilience of the coastal area (Lotze et al. 2006). Therefore, it is of the utmost importance to safeguard the richness and diversity of organisms, as they are the ones who perform many functions sustaining the coastal system and in turn enable human-wellbeing (Cardinale et al. 2012). Simultaneously, there is an urgent need to understand how these systems function and improve assessments and analysis tools that allow effective interpretation of the functional changes.

Important ecological components of the coastal zone are the many habitats associated

with the sediment. The wide variety of biota associated with the sediment is commonly called *benthos* and both plants and animals are known to be involved in numerous processes affecting the entire coastal ecosystem. Particularly the benthic animals play important roles in organic matter transformation and transport, oxygen transport, nutrient cycling, secondary production, physical structuring and benthic-pelagic coupling (Graf 1992, Snelgrove 1999, Giller et al. 2004, Mermillod-Blondin 2011). Focusing research efforts on understanding functioning of benthic faunal communities is thus essential.

This thesis summarises four papers focused on broadening the understanding of benthic ecosystem functioning in coastal waters. The summary briefly introduces the concept of biological traits and outline the main issues addressed in this thesis for further developing the approach. It also discusses some implications for the conceptual framework and management based on the research findings.

1.1. BIODIVERSITY AND ECOSYSTEM FUNCTIONING - THE STUDY OF TRAITS

The importance of biological diversity (Biodiversity) for ecosystem function (EF) is widely recognised today, both in terrestrial (e.g. Cardinale et al. 2002, Hooper et al. 2005, Balvanera et al. 2006) and marine systems (e.g., Covich et al. 2004, Solan et al. 2004, Stachowicz et al. 2007). BEF theory states that functioning of an ecosystem is not governed by the phylogeny of the biota, but by the characteristics, i.e. *traits*, of the organisms present in a system and their distribution (Naeem 2002). Species interact with and respond to their physical and chemical environment in various ways depending on their

ability to do so. The maintenance and regulation of functions in an ecosystem is thus essentially dependent on the ecological roles and traits of the taxa present. A trait in its simplest form is thus described as a proxy of organismal performance (Violle et al. 2007, following Darwin 1859). In essence, a higher diversity of organisms denotes a higher diversity of traits, which in turn have a greater effect on ecosystem functioning (Naeem 2002, Ieno et al. 2006). Ecosystem function and functioning are still variously defined (Jax 2005). Although function is often used as a synonym for ecosystem process and refers to biogeochemical cycling and production, functioning is the more generally used term. This incorporates, in addition to the processes, the properties (e.g. pools of organic matter) as well as the goods and services (food, medicine, climate regulation) of the ecosystem (de Groot et al. 2002, Giller et al. 2004, Hooper et al. 2005, Beaumont et al. 2007). In short, functioning denotes the overall performance of the ecosystem (Jax 2005). The BEF-framework has also been adopted in management and conservation policies and strategies under the Ecosystem Approach (FAO 2003, ICES 2005, BSAP HELCOM 2007). The Ecosystem Approach is defined by the Convention for Biological Diversity (CBD 2000) as “a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way...”.

Within the BEF-framework, early studies examined the effects of biodiversity on ecosystem functioning by investigating number of species (species/taxon richness). An analogue used to explain the theory of how species richness is linked to functioning is that of rivets in an airplane or boat. As more rivets (species) are lost, wings and steel plates will pop and decrease the ability of the plane to fly (ability of the species to uphold functions) and losing too many will cause the plane (ecosystem) to collapse (Lawton 1994). Related to this is

another theoretical concept that states that two species may complement each other in the functions they perform and therefore one of them might be redundant (Loreau & Hector 2001, Loreau 2004). Hence, knowledge about redundancy is also important for predicting changes in functioning due to environmental changes. Current approaches to interpret and assess the functioning and functional diversity of systems in time and space rely specifically on the traits of the species. Trait-based approaches that include a number of traits, also allow for simultaneous assessments of several functions, i.e. multifunctionality (Hector & Bagchi 2007, Gamfeldt et al. 2008, Villnäs et al. 2013). In this thesis, traits chosen reflect components of functioning and were used as proxies for ecological processes such as transport of oxygen within and between the sediment, cycling of nutrients in the sediment and between the sediment and water column, physical modification, organic transport between and within the system, secondary production and energy transfer (Bremner et al. 2006a,b, Frid et al. 2008, Table 1 in paper III).

1.2. THE TRAIT CONCEPT AND DEFINITIONS

The trait concept has evolved in a number of ways from the first studies discussing its wider application for vegetation classifications (Grime 1974), habitat heterogeneity (Southwood 1977) and trophic structure (Pearson & Rosenberg 1978, Fauchald & Jumars 1979) (Fig. 1). The concept developed in two different directions for the terrestrial and marine realm from these seminal papers (Fig. 1). The trait-based approaches in plant ecology have since been successfully applied on ever-higher organisational levels such as community (Petchey & Gaston 2002, McGill et al. 2006) and ecosystem (Lavorel & Garnier 2002) scales. Trait terminology has varied, but obtained

a completely new meaning with the introduction of the expression “functional trait” (Diaz & Cabido 2001, Petchey & Gaston 2006). This term accompanied the emergence of the ecological discipline “functional ecology” (Keddy 1992). Following this concept, a rapid increase in studies occurred focusing on functional classifications (Lavorel et al. 1997) and assessments of functional diversity in communities (Walker et al. 1999, Petchey & Gaston 2002, McGill et al. 2006). A functional trait has been defined as: “a component of an organism’s phenotype that

determines its effect on processes and its response to environmental factors” (Reiss et al. 2009). The trait is thus specifically linked to a function. The functional trait concept today is being used particularly for calculating functional indices (Petchey & Gaston 2006, Villéger et al. 2008, Mouillot et al. 2013a). Within the community and ecosystem level of functioning, two additional and more specific trait terms have emerged, namely response and effect traits (Suding et al. 2008) (Fig. 1).

Trait approaches in marine benthic

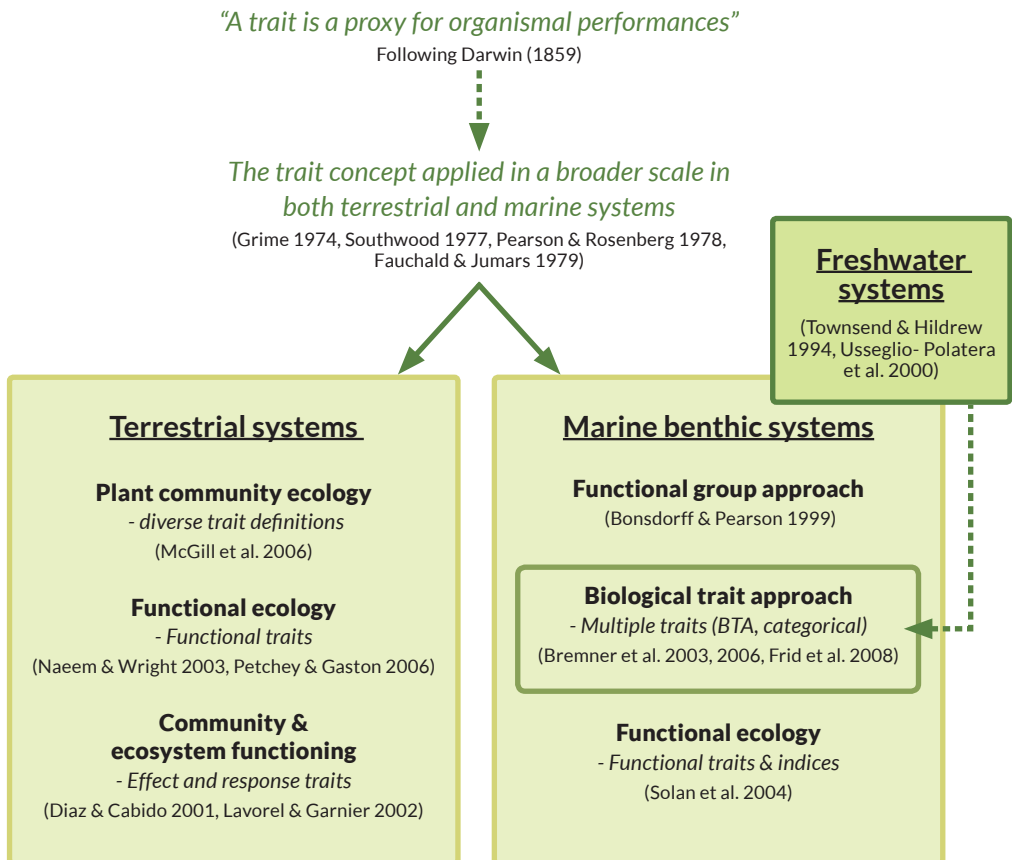


Figure 1. A summary of the major trait-based approaches and terminology that has shaped analysis and concepts in marine benthic systems. The influences are primarily from plant ecology, but the biological trait approach in the marine realm has largely been inspired by freshwater studies. Solid arrows indicate the more pronounced split in approaches and theoretical frameworks. Dotted arrows illustrate the advances, exchanges of concepts or methods between the research disciplines at various times.

systems focused primarily on community ecology following the trophic or functional group approach (Pearson & Rosenberg 1978, Fauchald & Jumars 1979, Pearson & Rosenberg 1987, Bonsdorff & Pearson 1999, Pearson 2001). The biological trait approach, BTA, was introduced to the marine system by Bremner et al. (2003a,b, 2006a,b). The approach was applied on benthic soft-bottom fauna in the North Sea (Fig. 1). This method extends the functional group approach as a multitude of taxon characteristics across entire faunal communities are used (Bremner et al. 2003a, Bremner et al. 2006a, Bremner 2008). It was primarily developed in freshwater systems for describing characteristics of invertebrate communities in streams, and as a tool for biomonitoring (Townsend & Hildrew 1994, Usseglio-Polatera et al. 2000) (Fig. 1). Marine studies have used this analytical approach to assess various effects of human-induced impacts on benthic functional structure, such as fishing (Bremner et al. 2003a, Tillin et al. 2006, de Juan et al. 2007), pollution in terms of eutrophication (Oug et al. 2012) and effects of organic enrichment related to aquaculture (Dimitriadis & Koutsoubas 2011, Villnäs et al. 2011). Functioning has also been assessed in relation to habitat heterogeneity (Hewitt et al. 2008), an estuarine gradient (van der Linden 2012) and marine management efforts (Verissimo et al. 2012). The approach has also been developed in relation to bioturbation and included into a functional index (Solan et al. 2004).

As a response to the general variability in trait terminology, Violle et al. (2007) summarised definitions of a trait from the various disciplines and provided an integrative framework that could be applied from individual scales to ecosystems. Violle et al. (2007) theoretically defines a trait as “any morphological, physiological or phenological feature measurable at the individual level”. This has been accepted widely (Reiss et al. 2009) and forms the base for the definition that I

use in this thesis. When using multiple traits as in the biological trait analysis, traits are applied on the community level. The biological trait analysis also includes behavioural characteristics other than phenological ones, such as sediment movement habit.

In the terrestrial realm, measuring trait such as ‘plant height’, ‘leaf area’, ‘seed mass’, etc. is relatively easy to conduct for each individual plant in a community. Traits are thus often measured on a continuous scale and represent real-value traits. Below the water surface, this becomes more challenging, especially for marine animals living in the sediment or moving in the water column. Hence, traits used for studying functioning in benthic communities are discrete, i.e. of a categorical or discontinuous type. A categorical trait is divided into *a priori* defined categories or modalities. An example of this type of categorical trait is ‘living habit’, which can be divided into categories such as *tube dweller*, *burrow dweller* and *case builder*. The trait value, although related to individual variability, is often not measured in a study *per se* but applied based on various previously published sources (Bremner et al. 2003a). In the biological trait approach, a continuous trait is used as a categorical one. In such cases, a category denotes a standardised range along the continuous trait axis. For example, the trait ‘size’ is divided into the categories: 1-5 mm, 5mm -1cm, 1-3 cm etc. Using categorical traits requires that some sort of coding must be used to link the species to the trait. Coding of taxa to trait categories has been done using two different approaches. In most freshwater and marine studies, a fuzzy coding approach has been used (Chevenet et al. 1994) while only presence/absence (expression or not) of a category can also be applied. The biological trait concept enables the quantification of trait categories using for example abundance or biomass (Bremner et al. 2003a). This has been highlighted as an important feature for scaling up from individuals to

populations, communities and ecosystems (McGill et al. 2006, Violle et al. 2007).

1.3 DELIMITATIONS OF THE BIOLOGICAL TRAIT CONCEPT

The use of categorical traits in trait-based analysis has both theoretical and practical advantages, apart from a number of limitations. The primary reason for choosing the categorical over the continuous trait approach is that it allows for a broader spectrum of characteristics to be analysed, and thus multiple aspects of functioning (Usseglio-Polatera et al. 2000, Bremner et al. 2003b). The set of traits may also span many different taxonomic groups, which provide for generality in both application and theory. Another benefit is that qualitative information can be utilised by transformation into numerical values by different coding methods (Chevenet et al. 1994). On the other hand, this is also one of the major drawbacks with the approach. Converting the information, which is usually of a linguistic type (e.g. 'living habit'), is subjective as the numerical value given is based on information found in research articles and other types of literature sources. The fact that the number of trait categories or values that the species can express is fixed and pre-determined is another disadvantage. By fixed, I refer to the fact that the set of species included in the study can only be coded for the pre-determined range of categories. The number cannot be as variable as would theoretically be possible using continuous trait variables. Hence, calculations of certain indices are not appropriate using categorical traits (Schleuter et al. 2010). Moreover, theoretically one needs to evaluate the results of for example trait richness against the total number of categories included. In addition to the issue of converting linguistic information, the actual choice of traits to be included in an analysis needs to be carefully

considered. The traits selected for a particular study should be linked to the processes or functions and environmental factors studied (Diaz & Cabido 2001).

1.4 RECENT ADVANCES WITHIN MARINE BIOLOGICAL TRAIT STUDIES

The use of multiple traits in marine studies has expanded rapidly in recent years. A search on ISI web of Science and Google Scholar, combining in various ways the terms: *traits*, *biological traits*, *functional traits*, *biological trait analysis*, *functioning*, *marine* and *community*, resulted in a total of 106 peer-reviewed published articles within the last 10-years, from 2003 to 2013 (Fig. 2). In the search, I restricted the selection of articles to only include studies analysing more than one trait and one species. There is a clear increase, especially during the last three years, in marine research using traits and trait analyses (Fig. 2a). Most efforts have through the last decade been on assessing traits of benthic communities (68%; 72 of 106 publications), followed by analysis on fish assemblages (Fig. 2b). A longer tradition of collecting quantitative samples and knowledge of taxon characteristics in general is probably a reason for the larger amount of studies on benthos. The potential of using traits to study functioning in microbes, aquatic plants or algal systems is clearly demonstrated although number of studies within these groups is not yet large (Fig. 2b). This also indicates that there may be important knowledge to be gained by making use of novel analysis methods and theoretical frameworks. For example, recent efforts using plankton has proven valuable for scaling-up trait analysis to global scales, describing large-scale biogeography of plankton characteristics (Barton et al. 2013).

One of the general issues argued to be important for advancing the knowledge of marine ecosystem functioning, is the need to

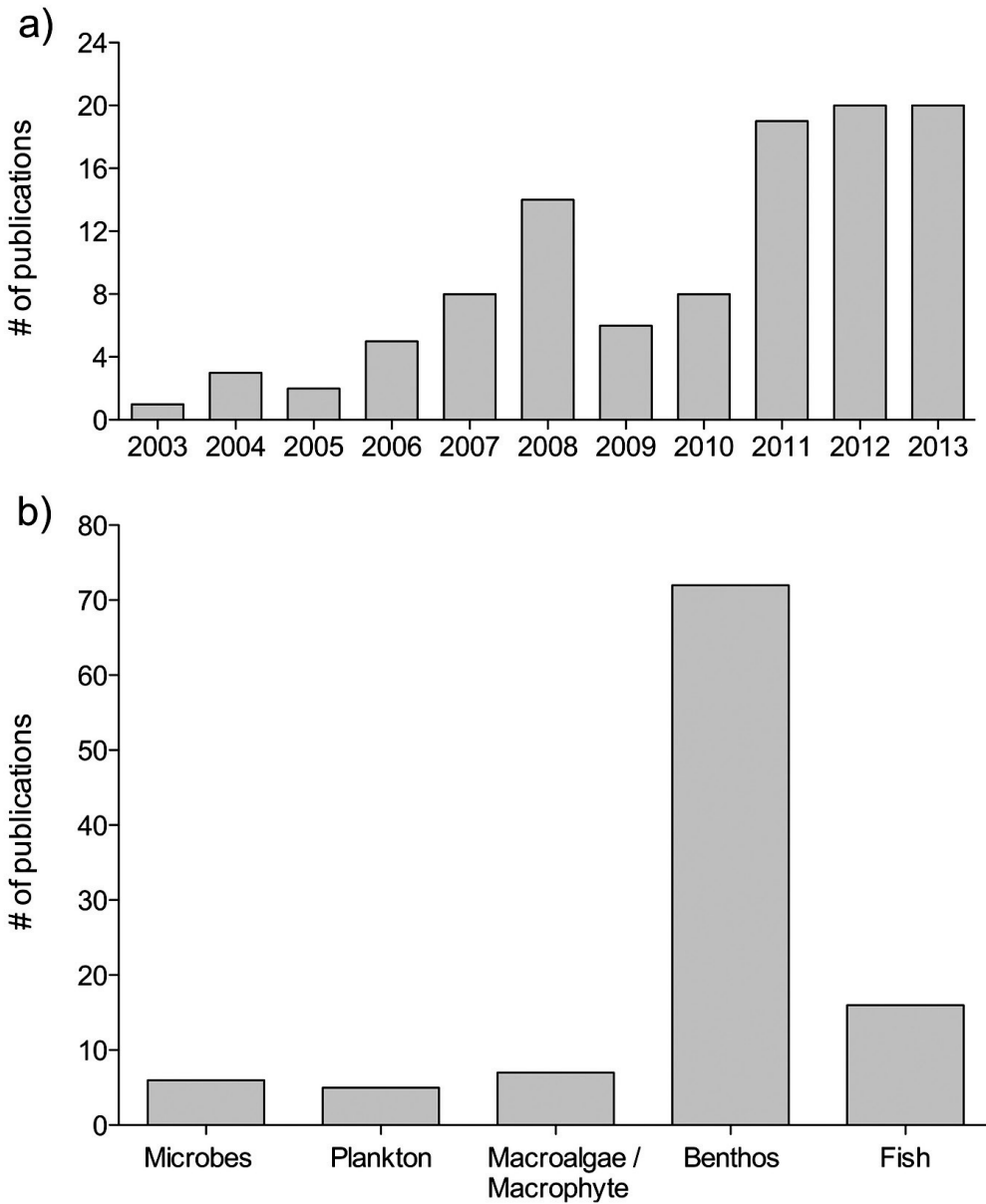


Figure 2. Results of a search on ISI web of Science and Google Scholar using combinations of the terms *traits*, *biological traits*, *functional traits*, *biological trait analysis*, *functioning*, *marine* and *community*. The a) number of publications within a 10-year period 2003-2013 (in total 106 publications), and b) number of publications within different taxonomic entities are illustrated. The search was restricted to studies using more than one trait and more than one species.

scale up from smaller to larger spatial and temporal scales (Crowe et al. 2012, Thrush & Lohrer 2012). The intention of this thesis has also been to fill parts of this gap.

1.5 AIMS OF THE THESIS

The general aim of this thesis was to validate and continue the development of the concept of biological traits for interpretation and assessment of benthic community functioning (Fig. 3). More specifically, I determined the functional structure, diversity

and variability of benthic coastal communities on four different spatial scales and over two time-periods, addressing the following specific questions:

Landscape/habitat scale:

- *How does recruitment and dispersal affect the functional structure of benthic communities in a seagrass landscape?* (paper I)
- *Do the functional structures of communities match a priori defined habitats and how does this compare with taxonomic and trophic measures of benthic community structure?* (paper II)

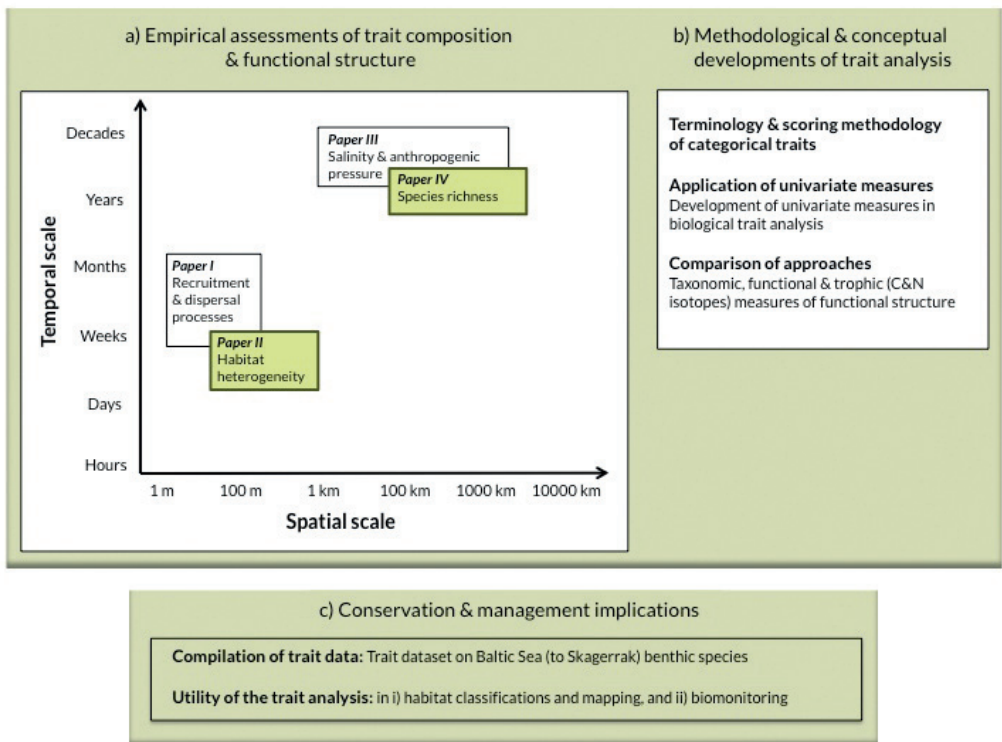


Figure 3. A conceptual illustration of how this thesis and the specific papers it is based on provide insights into a) spatial and temporal aspects of marine benthic functioning, b) development of the biological trait concept and c) utility of traits and trait analysis for conservation and management of coastal areas. The length and width of the boxes (a) indicate the spatial and temporal scales covered in each paper. Shaded boxes denote papers in which temporal aspects were not assessed *per se*. The lengths of these boxes show the temporal scale in terms of the time-period relevant for measures used (paper II) or for collected data (paper IV).

Regional scale:

- *How does the functional structure of benthic communities vary in the northern Baltic Sea, over time and between areas differing in salinity and degree of human pressure? (paper III)*
- *Is function affected by reductions in taxonomic richness and how is this portrayed along a natural gradient in taxon richness? (paper IV)*

The objective to develop the trait approach, revolved around i) methodological and conceptual investigations into terminology and scoring of traits, ii) assessments of univariate categorical trait measures, and iii) comparisons to other more traditionally used measures (Fig. 3b). Although the aim was not specifically to analyse functional effects or aspects of management efforts, implications for these is highlighted based on the findings (Fig. 3c).

In addition, within the specific papers, special attention has been paid to the role of common and rare species and traits for benthic community functioning. Although not specifically assessed, the findings from all papers are summarised in order to pinpoint gaps and future research directions.

1.6 MAKING USE OF THE TAXONOMI- CALLY LOW-DIVERSE BALTIC SEA

The *Baltic Sea* is the world's largest brackish water area, comparatively shallow (on average 53 metre deep), young and still evolving (present stage are about 3000 years old). The sea has a drainage basin comprising 14 countries and about 85 million people (Bonsdorff 2006, Leppäranta & Myrberg 2009). Hence, the Baltic Sea is a special case in many perspectives. However, it also shares generalities with other types of water bodies. The fact that the Baltic Sea is semi-enclosed with

limited water exchange and driven primarily by salinity and temperature, classifies it oceanographically as a marginal sea, such as the Black Sea and the Mediterranean Sea (Chen 2010). In addition, although the Baltic Sea is non-tidal, it is often compared with the structure and function of an estuary or a fjord, because of its steep gradients in salinity and consequent change in taxonomic richness and composition (Elmgren & Hill 1997).

The topological structure of the Baltic Sea, with a number of basins and three pronounced thresholds (the Danish straits, the Archipelago Seas of Sweden and Finland, and the northern Quark), together with the strong inflow of fresh riverine water, contribute to the strong salinity decrease from south to north (Bonsdorff 2006). Along this geographical gradient, salinity in surface waters changes from fully marine, about 36 psu, in the narrow and shallow Danish straits that opens into the North Sea via Kattegatt and Skagerrak, to 6-8 psu in the central Baltic Sea and to as low as 1 psu in the northernmost part of the Gulf of Bothnia. Therefore, there is also a strong gradient in species/taxon- richness and to some degree a compositional change in species resulting in a mixture of marine and freshwater species (Bonsdorff 2006). The young age of the Baltic Sea, implies that an adaption of species to the variable environment is still ongoing (Ruhmor et al. 1996).

Benthic community structure in the coastal areas of the Baltic Sea shares similarities with the patterns of the open sea, particularly in terms of salinity as a primary structuring factor (Bonsdorff 2006). The coastal areas, on the other hand, show a richer flora and fauna than the open sea areas, due to the higher environmental heterogeneity (Bonsdorff & Pearson 1999). In addition, the shallow areas do not suffer from permanent hypoxia, which is the

case for a large part of the open Baltic Sea, south of the Gulf of Bothnia (Karlson et al. 2002). In addition to salinity and climate (ice cover), the aquatic communities are structured by depth and food availability in the coastal zone (Bonsdorff 2006). Human activities are also having a significant effect on the coastal areas. Of the anthropogenically-driven changes, eutrophication and habitat destruction constitute for the most severe threats (Lundberg 2014).

The question that arises is then *what makes this study system valuable for empirical trait studies*. There are three principal reasons for this: first, the amount of knowledge of the physical and biological characteristics of the area is considerable and an advantage when a multitude of species and their characteristics are used in analysis. The Baltic

Sea is often regarded as the most studied sea area in the world (Chen 2010). This is a result of the well-known history of human exploration of the sea and in modern times, well-coordinated collaborative monitoring and legislative efforts (HELCOM 2010). Secondly, and coupled to the previous statement, is the fact that species diversity is comparably low and thus, knowledge of the species characteristics, trophic interactions and status is in general well-known (Ojaveer et al. 2010). Thirdly, although the system has a low species diversity compared to fully marine areas, the resemblance with many different types of water bodies and aquatic environments with high species diversity makes it valuable for case studies testing more general ecological theories.

2. MATERIALS AND METHODS

The objectives of this thesis were met by focusing on the coastal ecosystem and in the first two studies particularly on a number of key habitats for soft bottom benthic organisms. In general, the ambition has been to comprise the whole taxonomic spectrum of each dataset used and assign traits to all taxa to assess functioning on a community level. In papers I and II, faunal data was collected through field sampling, while monitoring data from national databases was used in papers III and IV. Both univariate and multivariate statistical analysis were used.

2.1 STUDY AREA, HABITATS AND ORGANISMS

The northern Baltic Sea and Finnish coastal areas were the focus of papers I-III (65-59° N, 19-27° E), while paper IV considered seven coastal areas from the Skagerrak region to the Bothnian Bay in the northernmost parts of the Baltic Sea (Fig. 4). In general, the habitats studied throughout this thesis were primarily soft-bottom benthic faunal habitats such as bare and vegetated sand and mud or mixtures of sediments. In paper II, vegetated hard bottom was also included as a habitat. These habitats are common in shallow coastal areas worldwide and are especially important for primary and secondary production and as nursery habitats for fish (Rönnbäck et al. 2007).

More specifically, the study site in paper I was located in the Gulf of Finland at the Hanko Peninsula (Ryssholmen: 59°60'N, 23°05'E). **The study focused on the microhabitats in a seagrass landscape and included the seagrass meadow, seagrass patch and bare sediment.** Sampling was conducted in the seagrass landscape, consisting of a 7 ha *Zostera marina* meadow (primarily

Z. marina but also *Potamogeton* spp.) with isolated seagrass patches in the more exposed areas south of the meadow, and in the bare sand area. Paper II was conducted in a moderately exposed shallow bight in the Åland Islands (60°10'N, 19°32'E). In this paper, in addition to assessing the structure of the benthic community in bare sand and seagrass meadow, the canopy-forming algae (predominantly *Fucus vesiculosus*) on a rocky shore was also included as a habitat. In this study, the seagrass habitat was further divided into a belowground and an aboveground seagrass habitat, dominated by *Z. marina* and interspaced with e.g. *Potamogeton* spp., *Nitella* sp and *Ruppia* sp. Papers III and IV did not focus on any particular habitat but covered various sediment types from sandy mud to mud with clay content. Instead, the larger scale studies both covered the salinity gradient that is primarily structuring the benthic communities in respective study area. Salinity ranged from 7-1 psu in paper III, along the Finnish coastline, and in paper IV from fully marine in Skagerrak to almost limnic in the northernmost part of the Baltic Sea, 36-1 psu respectively. Additionally, the data in paper III was chosen to represent areas differently affected by anthropogenic pressure, according to the HELCOM pressure index (HELCOM 2010).

The aim in all four studies was to include the entire taxonomic spectrum of the sampled or collected benthic macrofaunal invertebrates. To summarise, the number of taxa included in the studies varied from 36 to 221 taxa in total and covered no fewer than 9 higher taxonomic entities (in total 12) and represented all major phyla in the marine benthos (Table 1). Taxonomic quality assurance has included verification of taxonomy and scientific names following the European

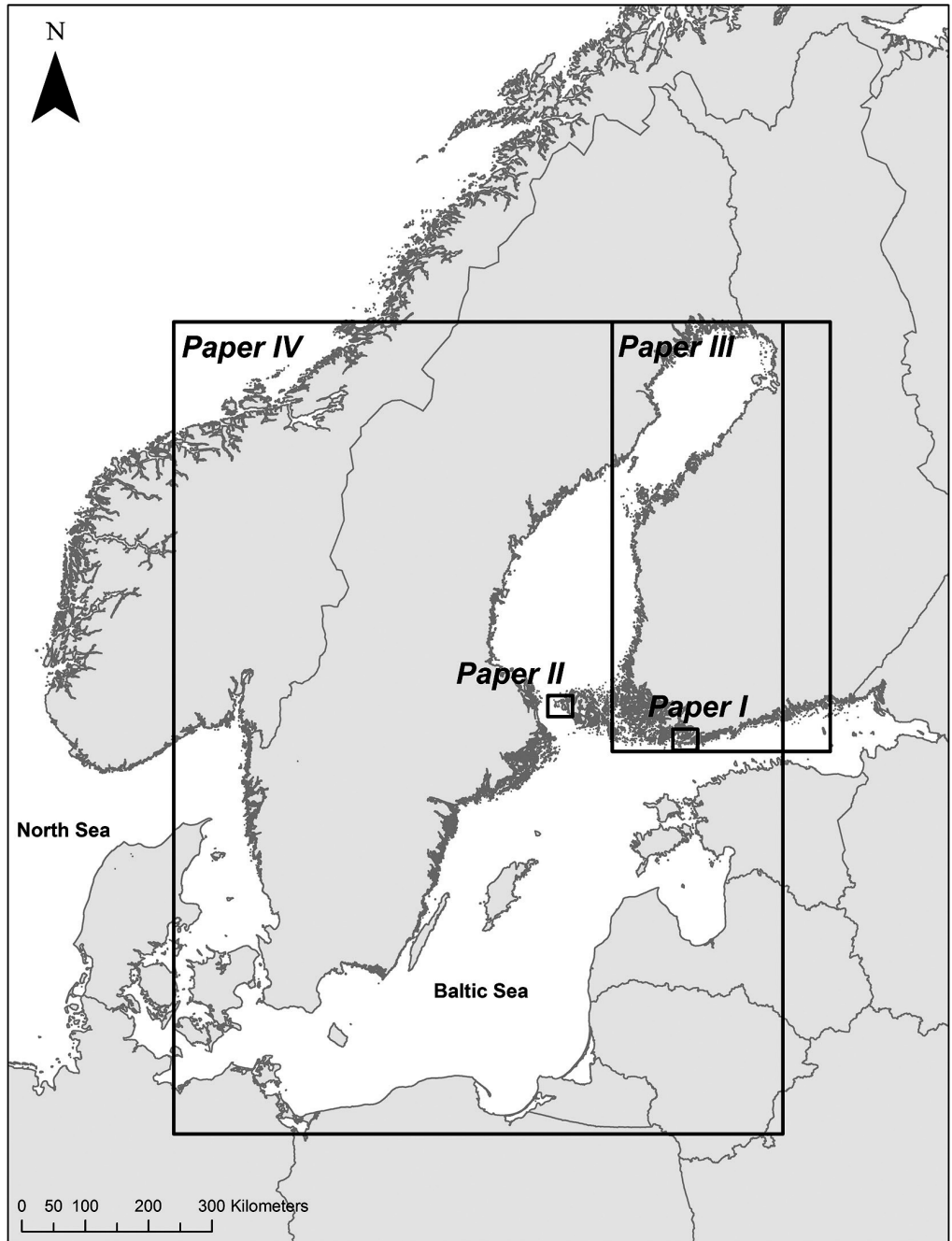


Figure 4. Map of the study system, the Baltic Sea, and geographical position of individual studies. Papers I-III were conducted in Finnish coastal areas, while paper IV spanned an area from the Skagerrak region and Swedish west coast to the Bothnian Bay.

Table 1. List of main taxonomic entities and total number of species/taxa included in respective study.

Phylum/Class	Paper I	Paper II	Paper III	Paper IV
Nemertea	1	1	2	1
Priapulida	1	1	1	2
Sipuncula	-	-	-	2
Polychaeta	2	6	7	96
Hirudinea	1	1	5	-
Polyplachophora	-	-	-	2
Bivalvia	4	4	7	32
Gastropoda	3	5	8	19
Crustacea	11	13	17	50
Anthozoa	-	-	-	4
Echinodermata	-	-	-	9
Insecta	2	3	6	1
Other	11	2	3	3
Total no. of taxa	36	36	56	221

Register of Marine Species (ERMS: www.marbef.org/dataerms.php), World Register of Marine Species (WoRMS: www.marine-species.org) and the Integrated Taxonomic Information system (ITIS: www.itis.gov), especially in study III and IV where I used monitoring data.

2.2 SAMPLING DESIGNS AND DATA COLLECTIONS

In the two field studies (I and II) all sampling was done by SCUBA, while in papers III and IV pre-collected monitoring data was used. In paper III, Finnish national monitoring data from the HERTTA database (maintained by the Finnish Environmental Institute) was utilised. In paper IV, in addition to this data source, national and regional monitoring data from Sweden (national data host Swedish Meteorological and Hydrological

institute SMHI), Poland (Benthic database maintained by the National Marine Fisheries Research Institute) and Denmark (ODAM database maintained by the Danish Centre for Environment and Energy, Aarhus University) were also used.

In paper I, sampling was conducted to assess invertebrate settlement and resuspension with traps constructed of a tube equipped with a removable jar, filled with azoic sand and covered with a mesh. Three replicate traps were established in bare sand, isolated seagrass patches and in continuous meadows at a depth of 2-3 m. The tubes containing the traps were pushed into the sediment leaving the opening of the traps at the same height as the upper part of the leaf canopy (30cm). The design was replicated spatially ($n=2$) and temporally ($n=5$, from June to August) and the traps clustered in each habitat were treated as subsamples

and averaged in the statistical analysis. At each sampling occasion, jars were closed, retrieved and replaced by new jars with azoic sediment. In the laboratory, samples were conserved until animals were separated from the sediment by rinsing and identified to the lowest taxonomic level possible as well as enumerated under a microscope.

In the other field study focusing on functioning in habitats (paper II), macrofauna was quantitatively sampled at five locations with three replicates in each of four habitats: sand, canopy-forming algal belt, seagrass below- and aboveground, at a depth of 0.5–2.5 m. Epi- and infauna were both sampled in a 25 cm × 25 cm area, epifauna with a net-bag and infauna with a sediment core. The two sampling techniques required faunal densities to be standardized to volume for each replicate rather than to area, to enable comparison between the different types of habitats. Faunal samples were sieved, conserved and animals counted, measured, weighed and identified to lowest taxonomic level possible or in accordance with resolution of trait information. To assess trophic structure of the benthic communities, stable isotopes ($\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$) were used. For the analysis, sediment organic matter, suspended organic matter, primary producers (macrophytes and associated flora) as well as primary consumers (macrofauna) were collected within three days of the quantitative sampling. For a detailed description of field collections and laboratory preparations, see paper II. Samples were sent to the Stable Isotope Facility, UC Davis (USA), for the analysis.

The dataset in paper III consisted of in total 782 stations (1941 sampling visits) from two depth groups, shallow (0–10m) and deep (10–55m), and was used to compile a benthic species and trait dataset for the Finnish coastal areas. For the statistical analysis, a smaller dataset was randomly compiled from the large one, combining data from shallow and deep areas in three

basins spatially distinct along the coast: the Bothnian Bay, the Archipelago Sea and the Gulf of Finland. The temporal aspect in this study was assessed by including data, 30 visits per depth group and basin, from every second year within a 10-year period from 1994 to 2004 ($n=6$).

To meet the aim of paper IV, to analyse functioning along a natural reduction in taxonomic richness, data was compiled into seven sub-sets representing a gradient from Skagerrak to Bothnian Bay. As the data was compiled from four different countries and different sampling schemes, sampling stations and replicates varied in number. In total 81 stations (11.6 ± 0.7 per sub-set) constituted the data at an average depth of 28.0 ± 0.4 m.

Benthic samples in both paper III and IV were obtained in a standardised way, in paper III with an Ekman-Birge grab sampler (225–289cm²) and sieved on a 0.5 mesh size and in paper IV with a van Veen (1m²) and a 1mm mesh size.

2.3 TRAIT INFORMATION AND ANALYSIS

The rationale for choosing traits, and categories in particular, has throughout the thesis been that the traits included are relevant for answering the specific questions and aims of each study (Diaz & Cabido 2001). This has also been the approach in other studies using the biological trait concept (Bremner et al. 2003a,b, Bremner 2008, Frid et al. 2008). Number of traits as well as types of traits and trait categories has varied in my studies. In total 26 different traits and 118 trait categories have been used in the four studies (Supplement table). Out of these, seven traits were used in all studies, and these were: 'size', 'reproductive frequency', 'developmental type/ larval type', 'environmental position', 'feeding position/ feeding habit', 'mobility' and 'movement habit' (Supplement table). Trait and category

names as well as the general classification structure have as far as possible been kept the same between studies and in accordance to other biological trait studies. A trait category not expressed by the taxa in a study, is consequently not included in the analysis. For example the trait 'size,' has in all four studies been divided into a set number of trait categories based on the size range of the species pool in each study.

To summarise, traits chosen in papers I and II were linked to species movement, reproduction and community dynamics in general. In addition, feeding traits were also included in the analysis of Paper II, as the functional and trophic structures were compared. The aim in paper III was to study the functioning of the benthos along the Finnish coastline and to create a trait data set as a base for future studies. Therefore, as broad a set of traits as possible was compiled in this paper. The taxonomically broader dataset used in paper IV meant primarily that more categories within traits were included, but not particularly any new traits. The reasons for choosing traits in this study was to include several different traits related to specific functions rather than describing the overall trait diversity of the communities, as in paper III.

The principle for collecting trait information has throughout the thesis been to concentrate on lowest taxonomic level, and only later adjust it to appropriate higher levels. Information has been obtained from i) peer-reviewed published sources such as articles, books, taxonomic keys, or ii) expert knowledge and unpublished sources, including information drawn from species phenotypes or knowledge linked to other traits. The focus has been on including primarily sources of information from the region studied, so for paper I-III from the northern Baltic Sea (Fig. 4). Since parts of the taxa in paper IV occurred in fully marine areas, data on species characteristics was

included from the North Sea or corresponding environments in Northern Europe in addition to the Baltic Sea collection.

Species were scored to trait categories using two different coding procedures. In paper I-III, scoring was based on the standardised fuzzy coding approach (Table 2). This approach is based on fuzzy logic that can be used to express approximate data in numerical terms (Zadeh 1965). Using this logic, an object has a degree of membership in a category (group/set) between 0 and 1, rather than being a member of the category or not (presence/absence, 1/0). Hence, using the fuzzy coding approach a species is scored to the degree that it expresses a trait category on a scale from usually 0 (no affinity) to 3 (total affinity) (Chevenet et al. 1994, Bremner et al. 2003a,b, Table 2). For example, a benthic species may primarily burrow in the sediment but also crawl on the sediment surface. The same species may also occasionally swim above the sediment and drift in the open water (Table 2). The species would then be scored with a 3 for the movement category burrower, a 2 for crawler and a 1 for swimmer and rafter/drifter. To standardise the trait expressions between species, values are then summarised within a trait to 1, which is what I refer to as standardized fuzzy coding (Table 2). In paper IV, the crisp coding procedure, based on the Set theory, was applied i.e. using either trait expression or not (1/0). The rationale for choosing the latter in paper IV was that the trait information collected did not warrant the other, more refined type of coding for all of the species in the study. In addition, benthic species have the potential to show plasticity in certain trait categories, for example depending on grain size or other environmental variables. When there was no such abiotic information to allow for such scoring, species were assigned equal probabilities to express the different categories.

Table 2. Different types of coding approaches used to score species to traits. The table also shows the outcome (total sum within a trait) of the coding approaches for the three different types of traits (discrete, combinatory and binary trait type) and for two different hypothetical species (Sp. X and Sp. Y).

Trait (Type of trait)	Category (or modality)	Fuzzy coding (0-3)		Standardized fuzzy coding (0-1)		Crisp coding (1 or 0)	
		Sp.X	Sp.Y	Sp.X	Sp.Y	Sp.X	Sp.Y
Size (Discrete)	1-5mm	0	0	0	0	0	0
	5mm-1cm	3	0	1.00	0	1	0
	1-3cm	0	3	0	1	0	1
	3-5cm	0	0	0	0	0	0
	>5cm	0	0	0	0	0	0
SUM		3	3	1	1	1	1
Movement method (Combinatory)	Swimmer	1	0	0.14	0	1	0
	Rafter/drifter	1	2	0.14	0.40	1	1
	Crawler	2	0	0.29	0	1	0
	Byssus	0	3	0	0.60	0	1
	Tube-builder	0	0	0	0	0	0
	Burrower	3	0	0.43	0	1	0
SUM		7	5	1	1	4	2
Living habit (Binary)	Attached	0	3	0	1.00	0	1
	Tube-dweller	0	0	0	0	0	0
	Burrow dweller	3	0	0.50	0	1	0
	Case builder	0	0	0	0	0	0
	Free living	3	0	0.50	0	1	0
SUM		6	3	1	1	2	1

The use of coding approaches on a mix of categorical and continuous traits theoretically means that traits differ in how many categories within a trait individual species can be assigned to (Table 2). There are three possibilities in which the traits can differ, i.e. three different types of traits, as I refer to in paper III. For a discrete trait, such as 'size', species can only express one category of a number of possibilities. A combinatory trait means that species can be assigned to one, several or all of the modalities. An example of this type of trait is 'movement method' for which one species can express a number of different trait categories. The third trait type is called a binary trait and species can be assigned to only one category or, if not to

that specific category, to any combination of the others. The trait 'living habit' is an example of this type as some species can only live attached and coded only for this category, while others may be both *free living* and *burrow dwellers* (Table 2). Consequently, the maximum number of scores (i.e. number of expressions or inputs) within a trait category can only be the total number of species present. Because of this, the maximum number of scores within the whole trait may thus differ depending on if species can express one or several categories within the trait (Table 2).

The data used in the functional analysis consisted in general of three data matrices: an ordinary *Species x Site matrix* (abundance

values), a *Species x Trait matrix* (trait scores) and a *Site x Trait matrix* (abundance-weighted trait scores), which is a combination of the other two (Fig. 5). To produce the third matrix, each species' abundance value at a site (replicate or station) is multiplied with the trait score of the species. The scores are then summed over all species at the station to produce the *Site x Trait matrix*. Consequently, the two trait based matrices include different types of trait information and can be used to answer different questions. Abundance-weighted trait data was used in all papers, but the *Species x Trait matrix* was only used in a separate analysis in paper III, for assessing differences in trait expressions of rare and common species (Fig. 5). The matrices contain multivariate data *per se*, but utilising the *Site x Trait* data and calculating a total number of expressed trait categories or total/ average number of species per trait category per station, mean that the data can also be analysed univariately (Fig. 5).

The trait dataset and trait codings used in paper III are available as a supplement to the paper III (*Ecological Archives* A022-120-S1). For the other studies, the data is available upon request.

2.4 STATISTICAL ANALYSIS

A broad set of different types of parametric and non-parametric univariate analysis as well as multivariate analysis has been used to analyse the functional properties of the benthic communities (Fig. 5). A short summary of the statistical analysis specifically for traits and some general remarks are given below:

PAPER I

Univariate analysis (repeated measure ANOVA) was only applied on the traditional community variables, species richness

(number of taxa) and abundance, as well as abundance of the two dominating species. Habitat and time were used as independent variables. To quantify and compare differences in the temporal turnover in different parts of the seagrass landscape, Whittaker's measure Bw (Whittaker 1960) was used. To analyse trait expressions in each habitat over time, abundance-weighted trait expressions were analysed using a Fuzzy Correspondence Analysis (FCA, Chevenet et al. 1994) based on Euclidean distance.

PAPER II

Generalized linear models (nested design) were used to investigate between and within habitat differences on the dependent variables: species/taxon richness, abundance, number of categories (modalities) and mean number of species/taxa per modality. Poisson and gamma distributions were chosen for taxon richness and abundance as best match for the model fit (ratio of the deviance to its degrees of freedom), while normal distribution was used for the functional data. Nested PERMANOVA was run on traditional species abundance and abundance-weighted trait expressions. One-way analyses were used to assess principal habitat differences in consumer isotopic niches, organic matter, primary producers and abundance-weighted isotopic values of primary consumers. Abundance-weighted data was illustrated using nMDS (Bray-Curtis similarity).

PAPER III

Univariate analysis in terms of non-parametric sample based species rarefaction curves were used to assess effect of sampling effort on taxon richness and number of categories. The same analysis was used to evaluate species/taxon richness effects on number of trait categories based on i) all species, ii) all common species, iii) all

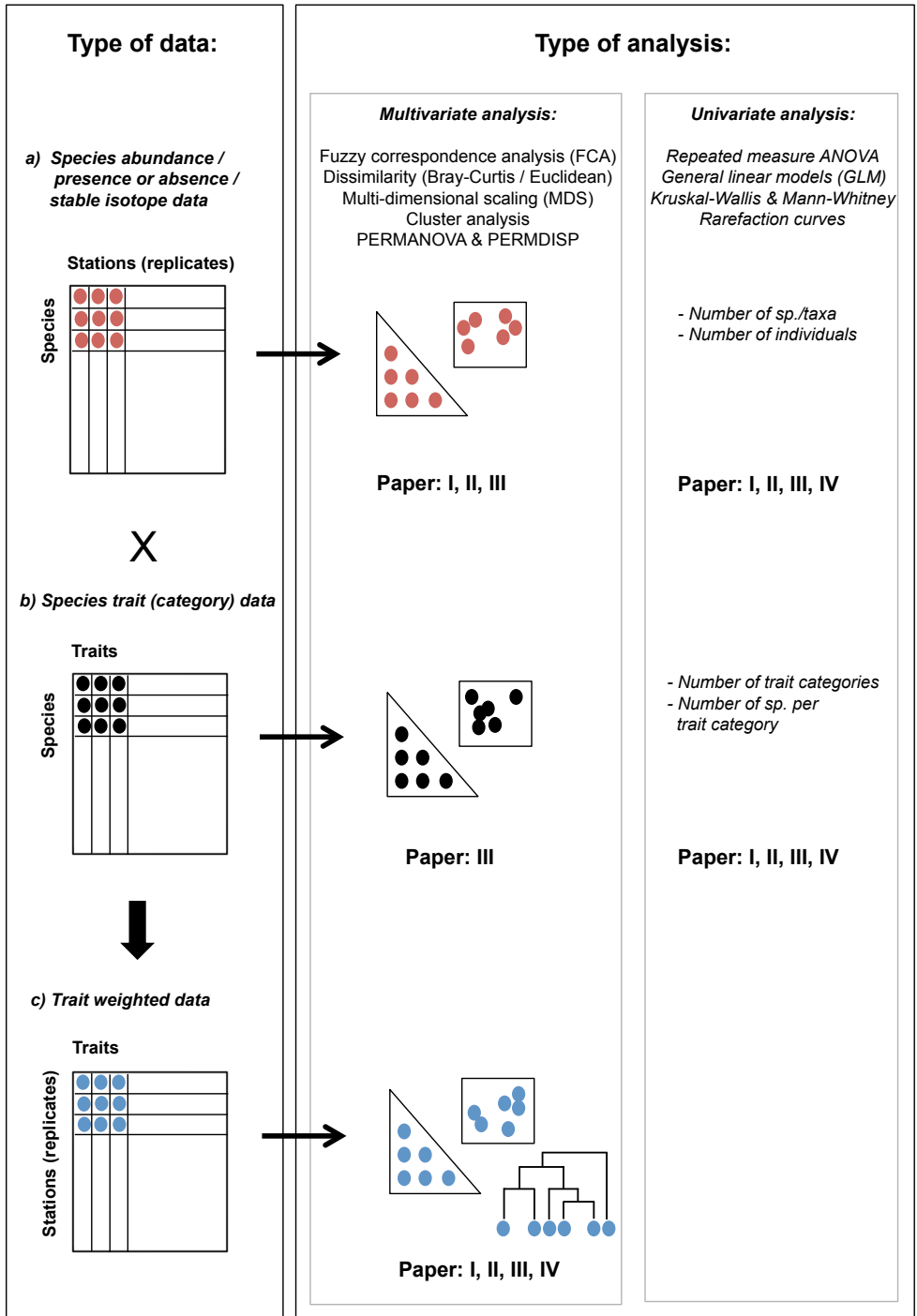


Figure 5. Schematic diagram of different types of data and corresponding multi- and univariate analyses methods used in trait analysis.

rare species, iv) 10 randomly drawn rare species irrespective of area and depth, as well as v) 10 randomly drawn species per area and depth. The analyses were run on EstimateS version 8.2. (<http://viceroy.eeb.uconn.edu/estimates>), which uses a technique that randomly permutes the order of the data. To assess variability of trait categories over time, the coefficient of variation (CV) was calculated for number of species per trait category. To compare trait expressions of common and rare species an nMDS (based on Euclidean distance) was used. Traditional species abundance patterns and abundance-weighted trait expressions were analysed for differences in area and depth using two-way PERMANOVA and illustrated using nMDS.

PAPER IV

Non-parametric univariate analysis, Kruskal-Wallis and multiple comparisons using Mann-Whitney, were used on taxon richness, number of trait categories and functional diversity (FD). The FD index was

calculated *sensu* Petchey & Gaston (2002, 2006). Number of taxa per trait categories per sample was analysed using one-way PERMANOVA (based on Euclidean distance) and PERMDISP.

GENERAL REMARKS

Prior to all parametric univariate analysis, dependent variables were tested for normality and homogeneity of variances and transformed when necessary (square-root, log). For the Generalized linear models a logarithmic, power of two or an identity link function was used. Prior to the repeated measure ANOVA data was also tested for sphericity using the Mauchly's test of sphericity and when violated Huynh-Feldt epsilon was used to adjust F values and probabilities. Where possible, I used Bonferroni-corrections on multiple comparisons of within-variable effects. PERMDISP analyses were run alongside all PERMANOVA analyses to test for homogeneity in average dispersion of samples from group centroids (Anderson et al. 2008).

3. RESULTS AND DISCUSSION

In this thesis, I assessed and interpreted benthic ecosystem functioning by applying the biological trait analysis to coastal benthic communities, an approach using multiple categorical characteristics of taxa. Specifically, I determined the functional trait structure, diversity and variability of coastal zoobenthic communities in the Baltic Sea. The measures were related to recruitment processes, habitat heterogeneity, large-scale environmental and taxonomic gradients as well as anthropogenic impacts. The studies comprised spatial scales from metres to thousands of kilometres, and temporal scales spanning one season to a decade.

The benthic functional structure was affected by habitat heterogeneity and did vary between and within seagrass landscape microhabitats (paper I) and four different habitats within a coastal bay (paper II). An analysis of trait expressions of Finnish coastal benthos showed high trait richness (in total 25 traits and 102 categories) although this differed between areas high and low in salinity and human pressure (paper III). The natural reduction in taxonomic richness across the Baltic Sea led to an overall reduction in function, although the relative change was smaller functionally than taxonomically. Changes in number of taxa per category showed, that the change over the gradient was subtle and individual categories were maintained or even increased (paper IV). A *type organism* for the northern Baltic Sea was described based on zoobenthic data spanning a 10-year period (paper III).

In order to advance the understanding of the approach, I also assessed aspects of the limitations of the concept. This was conducted by evaluating the link between category and taxonomic richness using

especially univariate measures. The role of rare and common species was assessed in relation to the functional understanding of the coastal benthic system as well as the theoretical implications for the biological trait concept.

3.1 FUNCTIONAL (TRAIT) STRUCTURE IN COASTAL WATERS - EFFECTS OF HABITAT HETEROGENEITY

The findings in papers I and II suggest that habitat heterogeneity affects not only the taxonomic, but also the functional and to some degree the trophic structure (based on stable isotopes signals, $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$) of the benthic communities. The functional structure was surprisingly similar between habitats whether considering microhabitats in the seagrass landscape (paper I) or *a priori* defined habitats in a bay (paper II). It is important to notice that the functional structure in terms of trait expression varies both within and between habitats but is reflected in different ways. The variability in univariate measures such as number of trait categories was determined primarily by small-scale environmental heterogeneity. This was evident especially in paper II where almost all trait categories were expressed in all habitats, but where the presence or absence of a trait category varied between locations within habitats.

Abundance of species (density of individuals) was found to drive the functional differences between habitats. In paper I, the between-habitat functional differences also varied in time due to the physical disturbance by wind and waves and consequent variations in transport and redistribution of individuals. Over the season trait expressions differed between the seagrass meadow

and the other two habitats. This corresponded to the abundance pattern of the benthic fauna, which was constantly higher for sand and patch habitats compared to the meadow. This pattern illustrated the presence of a settlement shadow from the outer areas to the inner less hydrodynamic seagrass meadow (Orth 1992).

The approach of using abundance-weighted data also proved valuable for comparing the taxonomic, functional and trophic structures of benthic communities in relation to different habitats (paper II). Benthic community structure varied in how well the structure matched the four *a priori* defined habitat units (sand, canopy-forming algae, seagrass below- and aboveground). The taxonomic and the functional structures of the benthic communities did comply with all four habitats, but the habitats were considerably more similar functionally than taxonomically. When all four habitats were identified as separate units in terms of the taxonomic structure, only two groups were functionally distinguished, namely the bare sand and a cluster including the three other habitat units. The taxonomic dissimilarity within habitats was 60 % when four units were identified, in comparison to a functional dissimilarity of only 35 %. The trophic structure did only identify a division into an epifaunal and an infaunal habitat unit. The contrasts between the measures of benthic structures and the mismatch with the habitats and the measures showed that pre-defined habitat units, such as the ones used in this study, which are easily identified in nature, might not correspond to all types of measures of community structure. This is ecologically interesting as it relates to how habitats are defined, but also from a management perspective as habitat classification and spatial planning activities are becoming increasingly more common (Davis et al. 2004, Borja et al. 2010). The biological trait approach has previously been evaluated by Bremner et al. (2003b) against the traditional

taxonomic approach and the trophic group approach. In my study, the analysis of the trophic structure differed as stable isotopes were used rather than trophic groups.

As a conclusion, it is important to recognise that the functional structure is affected by habitat heterogeneity in different ways, depending on if within- (α) or between (β) habitat variability are considered. This may also be important for understanding distributions of traits and functions across temporal scales. The results found in my studies are in accordance with results found in fully marine areas (Bremner et al. 2003b, Hewitt et al. 2008) and in freshwater systems (Charvet et al. 2000). The results also suggest that although these variations across scales pinpoint the need and potential to scale up trait analysis, focusing experimental work on small within habitat scales (cm to metres) may still fill important gaps in knowledge. The smaller scales may be important for understanding the mechanisms that drives trait presence or absence and how this affects specific functions (Hewitt et al. 2008, Villnäs et al. 2012).

3.2 TRAIT VARIABILITY ALONG LARGE-SCALE ENVIRONMENTAL GRADIENTS

Applying the trait analysis on larger spatial scales enabled identification of more general functional patterns. The spatial gradient, in both papers III and IV, also reflected the salinity gradient primarily driving the Baltic Sea system. In paper III, the functional patterns were also indirectly related to the general difference in anthropogenic pressure in the Finnish coastal areas, while in paper IV the natural decrease in taxon richness along the spatial gradient of the whole of the Baltic Sea was utilised.

Benthic trait category richness in Finnish coastal waters varied between areas differing in salinity, anthropogenic stress and taxonomic richness (paper III). A total of 102

categories were expressed in the southern Archipelago Sea, the richest area in terms of both species and category richness. In comparison, 89 categories were found in the northernmost Bothnian Bay. Hence, along this spatial gradient a number of categories were lost, such as *plankto*- and *lecitotrophic* 'larval types', *tentaculate* 'feeding type', two different sediment transport characteristics *conveyor*- and *reverse conveyor belt transport*, *sessile* movement as well as movement by *byssus*. Six categories differed between the Gulf of Finland, the area most anthropogenically stressed, and the Archipelago Sea. Higher numbers of categories were expressed in the shallow photic areas (0-10 metres) (paper III). Despite these differences, 72 trait categories were expressed in all areas and thus constituted the common functional trait pool in the region. As discussed above, relating the trait expressions to the abundance of taxa provides a more nuanced picture of the variations than only presence or absence of trait categories. In this study, however, the multivariate analysis only confirmed the differences found in the univariate analysis and the taxonomic pattern.

The effect of loss of species on function and trait expression, addressed briefly in paper III, was specifically assessed in paper IV. The bulk of the knowledge of how taxonomic richness affects functional richness and functioning has derived from theoretical modelling, simulation-studies or small scale-experimental work (Savage et al. 2007). The advantage of these types of studies is that species and traits can be manipulated in a controlled way. However, the species compilations are often unnatural or only partial (Solan et al. 2004). The observational nature of paper IV helped overcome these issues and made use of the natural reduction in taxon richness from 151 to 6 taxa along the gradient from Skagerrak/Danish Straits to the Bothnian Bay. The findings showed that drastic reductions in taxon

richness (96%) lead to an overall reduction in function, but that functional richness remained comparatively high (66 % of the total 51 trait categories expressed) even at the lowest taxon richness (6 taxa). To significantly affect and reduce trait category richness, an 86 % reduction in taxonomic richness was needed (151 to 21 taxa), which equalled only a 12 % reduction in trait categories (50 to 44). In addition to this, there was no significant turnover in terms of loss and gain in categories, which meant that all (but one) categories expressed at low taxon richness (6 taxa) were expressed in the taxon rich ones. Functional diversity (FD) followed the reduction in taxonomic richness, which implied that similarity in trait values increased when taxon richness decreased. The analysis of changes in trait categories, in terms of number of taxa per category, illustrated the effects of taxon reductions more in depth as the whole range of selected trait categories was assessed (see Table 3 in paper IV). Although most of the trait categories did decline (49 % of the categories), there was also a gradual increase for 8 % of the categories, as well as either idiosyncratic effects (whereby the number of taxa per category both decreased and increased, 35 % of the cases) or no changes (8 % of categories). Investigations into the potential meaning of the changes in individual trait categories showed that reductions in taxonomic richness could possibly have an effect on the way carbon is moved through the system. Categories indicating bioturbation were not altered significantly. To conclude, this study particularly showed the value of using traits rather than species for ecological understanding of changes in systems as well as the importance of considering multiple traits (multifunctionality) (Gamfeldt et al. 2008, Mouillot et al. 2011).

The studies by Bremner et al. (2003a,b) and Hewitt et al. (2008), are one of the first studies to compare marine benthic functioning over large areas and sites separated

geographically. No benthic studies have to my knowledge assessed trait expressions on the geographical scales used in paper III and IV. In comparison, the Finnish coastline (~1200 km) is about twice the length of the English Channel and the spatial distance in paper IV (~3200 km), from Skagerrak to the Bothnian bay, is roughly the distance between Helsinki and Lisbon.

3.3 TRAITS IN TIME

Compared to the spatial effects, investigations of functional variability over time have been less studied in marine trait research. However, a number of recent studies have assessed trait variation primarily on seasonal (Neumann & Kröncke 2010) but also on decadal (Frid 2011) and even geological time scales (Villéger et al. 2011, Caswell & Frid 2013). These studies, together with the studies in this thesis (paper I and III) illustrated the relevance of assessing community trait composition over various timescales. My results highlighted both generalities in trait expression over time and specific temporal trait patterns.

Apart from identifying effects of spatial habitat heterogeneity on the functional structure, the results in paper I also revealed some insights into changes in trait composition over a reproductive season (June to August). The temporal variability in species and traits was found to primarily be an effect of wind and hydrographical forcing but variability in species' reproductive characteristics also influenced the patterns. Temporally, the bare sand and the seagrass patch habitat showed similar trait compositions, which changed concurrently between June/July and early August. Earlier in the season, the communities were characterised by infaunal species living deeper down in the sediment (*infauna deep*, *infauna middle*), having a *semelparous* 'reproductive frequency', *low* (0.1-1m) 'propagule dispersal range' and a *burrowing* 'movement method'. The

trait composition shifted in August to trait categories such as *annual episodic* 'reproductive frequency' and *detritivore* 'feeding habit', leaving the communities still dominated by infaunal species with a *burrowing* 'movement method'. In other words, the functional (trait) structure of the communities in the habitats did change over the season. These functional differences were important for assessing the temporal role of habitats for benthic fauna as well as in relation to each other.

In addition to these habitat-specific temporal changes, the trait analysis also illustrated the general characteristics of the post-larval and redistributing fauna. Throughout the season and across all the microhabitats in the seagrass landscape, organisms expressed predominantly a *semi-mobile* level of mobility, *crawling* as primary movement method, a *detritivorous* feeding habit as well as a *direct development* of larvae. These results emphasised the importance of direct development and short distance dispersal for community assembly in coastal seagrass-sand mosaics. The minor role of planktonic life stages in the faunal source pool is supported by other recent studies in the area. For example, Valanko et al. (2010) found that 40 % of the invertebrate taxa on coastal non-vegetated soft-sediments (northern Baltic Sea) lacked planktonic larval stages. These findings are especially notable since pelagic development is thought to predominate in the marine realm, as well as the general presumption that a continuous supply of larvae shape the communities in heterogeneous landscapes (Gaines et al. 2007). My results do not contradict the latter, but highlight the importance of assessing also connectivity and dispersal of the species pool not characterised with the obvious long-term and large-scale dispersal traits. To my knowledge, this was one of the first attempts to quantify multiple traits and their distribution in relation to seagrass landscape features and over time (but see

Valanko et al. 2010 for non-vegetated soft-sediment environments).

Scaling up the time frame, from months in paper I to years in paper III, proved valuable for getting insight in to the functional (trait) variability, redundancy and potential stability of the benthic system along the Finnish coastline. The number of species per trait category provided a measure of redundancy, which reached as high as 8 taxa per category in the functionally richest area, the Archipelago Sea (paper III). Interestingly, of the categories with more than two taxa per category, the variation was relatively low (CV range: 0.21-0.63) over the studied 10-year period. In relation to findings in other ecosystems such as fish assemblages in temperate and coral reefs with average redundancy values of 2 and 1.6 taxa/category, the redundancy in the northern Baltic Sea benthos was comparable or even higher

(Micheli & Halpern 2005). The results would imply that the functional expressions are temporally stable, at least in the areas not severely affected by anthropogenic pressure (the Archipelago Sea and the Bothnian Bay). The potential for species substitutions to maintain functioning, as reflected upon here, is also supported by Frid (2011). These findings support the fact that investigations of changes in relative proportions of biological traits over time offer a reliable means to identify alterations to ecological functioning, proposed by Bremner et al. (2003a,b).

In accordance with paper I, the temporal assessment in this study also illustrated some functional generalities in the system (Table 3). A group of 12 categories expressed a median of more than two taxa in all areas over the 10-year period. These categories could be said to represent a “type organism” of the region. Two categories, *direct*

Table 3. Trait categories found to be dominant (relative expression %) over time in a seagrass landscape (paper I) or typical (median >2 taxa/category) regionally along the Finnish coastline (paper III).

Dominant trait categories in a seagrass landscape (Paper I)	“Type organism” of the Northern Baltic Sea (Paper III)
<i>Detritivore</i>	<i>Detritivore</i>
<i>Direct development</i>	<i>Direct development</i>
<i>Semi-mobile</i>	<i>Mobile</i>
<i>Crawling</i>	<i>Medium size</i>
	<i>Sexual (reproduction)</i>
	<i>Permanent (in/on sediment)</i>
	<i>Top (2cm)</i>
	<i>Epibenthic</i>
	<i>Gonochoristic</i>
	<i>Local dispersal</i>
	<i>Diffusive mixing</i>
	<i>Solitary (sociability)</i>

development of larvae and *detritivore* feeding habit, were found to be important characteristics of the benthic fauna, both on a landscape (~100 m) and a regional scale (~1000 km).

3.4 ROLE OF THE COMMON AND THE RARE

Apart from understanding generalities in functional patterns and trait expressions, it is also important to have knowledge about what is functionally rare or unique in a system. At present, the definitions of *common* and *rare* are still unclear for both the trait and the species concept (Kunin & Gaston 1993, Gaston 2011) and, therefore terminology has varied in this thesis. The roles of rare and common species in ecosystem functioning are also still debated (Lyon et al. 2005, Gaston 2011). Nevertheless, rarely expressed traits are important in regard to changes or shifts in a system, as these may give insights into how functioning might change. On the other hand, traits that are unique for example are only expressed in one habitat or by one species, might be particularly worth safeguarding on a broader scale. Within the trait concept, there are principally two ways that rarity and commonness can be studied, either i) through investigating distributions of trait categories in time and space or ii) by examining trait expression of species, particularly rare and common species.

In this thesis, both approaches have initially been investigated. Paper I and III highlighted “common traits”, which had a distribution in the whole study area and over the entire time-period (Table 3). In comparison, a number of trait categories were identified to be unique and only expressed in one habitat in paper II. For example, the category *case builder* was unique for the canopy-forming algal habitat while the ‘size’ category 3-5 mm was found only in the epifaunal habitats.

In addition, trait expressions of common

and rare species were analysed in paper III. The results showed that the two different groups of species expressed different sets of traits and that the common taxa expressed more categories than rare taxa. The latter is important to consider for calculations of trait richness, as the number of categories expressed may thus depend on the number of common and rare species included in the analysis.

In paper IV, rare species were defined as true singletons, i.e. only one individual found in one sample per region studied. According to this definition, 31 % of all 221 taxa included were rare. None of these rare taxa expressed any unique trait categories, except for two species that expressed a category specific for only one or two taxa in general. Hence, the rare species did not stand for the functional complexity or uniqueness in the system. This is in accordance with other studies, for example Ellingsen et al. (2007) that found a similar set of traits for species restricted in their spatial range (≤ 2 sites) compared with the total species pool. In comparison, Mouillot et al. (2013b) found that rare species in high diversity systems support distinct trait combinations and as a consequence, vulnerable functions. Hence, it seems that the functional roles of common and rare species needs further investigation in both high and low diverse systems. The functional role of rare species in particular requires further assessments as it is of interest both when systems do and do not change, since rare and common species will probably differ in their impacts on functioning. In general, the idea is that when systems change, function is maintained although common species that are individually most abundant may be removed, since rare ones might increase in abundance and so maintain function. On the other hand, if the systems remain unchanged, the cumulative contributions of rare species may be important if they all express similar traits (paper IV).

4. IMPLICATIONS AND FUTURE RESEARCH DIRECTIONS

The results and methodology presented in this thesis have potential implications for the development of the categorical trait concept in terms of ways to analyse traits in the future. The findings in this thesis also give some implementation of applications of the trait concept in management and conservation in general and within the Baltic Sea region specifically (Fig. 2). Future research directions using the trait analysis would be to link traits to the food web concept on a broader scale, as well as make use of techniques, such as modelling, applied initially on trait data in other disciplines.

4.1 THE CONCEPTUAL FRAMEWORK

Despite the rapid increase in the use of multiple traits in marine research (Fig. 2), the evaluation of the methodology and the categorical trait concept has not been as comprehensive. There have been theoretical discussions about differences between the uses of continuous or discrete (categorical) traits for functional diversity measures (Laliberté & Legendre 2010, Mouchet 2010, Schleuter et al. 2010). These have primarily revolved around the inclusion of traits into indices (Petchey & Gaston 2006). This has not covered other aspects relevant for the use of multiple categorical traits. Building on the work by Bremner et al (2003a, 2006b), the focus in this thesis was to develop the trait analysis by applying the concept to several different spatial and temporal scales. Apart from the ecological assessments, some initial evaluations of more theoretical and technical kind were also done. These have mainly concerned the link between species and trait richness. This is an issue, which is fundamentally different for categorical compared continuous traits. Using

the categorical approach, the number of trait values (categories) that species can express is pre-determined (Schleuter et al. 2010). This implies that an addition of a species does not necessarily mean addition of a new trait value (trait category), but an input to a trait category. Categories are thus packaged within species (paper III). This means that a species expresses a certain amount of the pre-determined set of trait categories. One species cannot express all categories, due to the fact that traits are not equal (different types of traits: discrete, combinatory and binary) for example a species cannot be *attached* and *free living* (as an adult). This will ultimately affect the total number of taxa within categories. However, these differences also reflect true ecological variation. Interpreting the categories as such rather than the trait names they are linked to is important for understanding functional aspects. Future investigations into these issues are essential if the univariate trait measures should be used in the future.

Another aspect highlighted in paper III is the potential for co-variation when using a multitude of traits. This refers to the fact that when one trait is expressed, another one is as well. For example, the 'living habit' *attached* and the 'mobility' category *sessile* will co-vary if species are very similar and there happens to be only one or two species that express these categories. The question is whether the richness of a community is exaggerated by using both categories in the analysis. If so, should both be seen as one category or should one of the traits be disregarded completely? This issue need to be further tested and included into future trait protocols.

In general, measures have been calculated in a number of different ways and

terminology has varied. Some of these measures require further assessments. To exemplify, the univariate measures that I have used in this thesis is outlined in Table 4. together with the some other components of trait diversity and the alternative ways of calculating the measures. The terminology and theory behind the calculations of the trait measures have usually been based on the equivalent measures in the species diversity literature.

The definitions and methods for calculating trait or functional diversity using categorical traits are still debated (Schleuter et al. 2010) and different indices are being used (Petchey & Gaston 2002, 2006, Villéger et al. 2008). Evenness as a trait measure also requires further investigations, particularly in comparison to the two measures of richness. Related to these methodological discrepancies is the fact that the total number of traits has to date always been presumed

to be all categories expressed, rather than the total number of trait categories possible for any species to express. A species cannot, for example, express both a *bivalve* and a *vermiform* body form. This was briefly touched upon in paper III (Supplement S1), but not elaborated further. Ultimately the choice of methodology in this case comes down to the research question.

To summarise, it is important to develop both the use of multiple continuous traits as well as categorical traits, as not all essential functional aspects can be assessed using only continuous ones. A mutual understanding of the terminology of both traits (names and categories) and measures (univariate and multivariate) is a prerequisite for advances to succeed. This is also essential if the concept is going to be successfully implemented into future management and conservation schemes.

Table 4. Univariate components of biological trait diversity. An outline of the measures and their definitions is presented in regard to the alternative ways of calculating them using categorical traits.

Measure	Alternative ways of calculation	Applied in this thesis
Richness of categories	No. of expressed categories	paper I, II, III, IV
Richness within a category	No. of individuals within a category No. of sp./taxa within a category No. of inputs (scores) within a category	paper II, III, IV
Diversity of categories	No. of categories expressed + either of the three evenness measures	paper IV
Evenness of categories	Evenness of individuals within a category Evenness of sp./taxa within a category Evenness of inputs (scores) within a category	

4.2 POLICY AND MANAGEMENT

The utility of the trait analysis as a tool for monitoring anthropogenic impacts on functioning of benthic systems has been proven in a number of studies, particularly in regard to fishing impacts (de Juan et al. 2007, Fleddum et al. 2013) and organic enrichment (Papageorgiou et al. 2009, Dimitriadis & Koutsoubas 2011, Villnäs et al. 2011, Oug et al. 2012). Trait analysis has also been applied to describe effects of conservation efforts, for example functional differences of fish assemblages between marine reserves and non-protected areas (Micheli & Halpern 2005) or functional changes in benthic communities after restoration (Verissimo et al. 2012). Biological trait analysis has also been used parallel to assessments of classifications of environmental quality by Aarnio et al. (2011). In this study, the approach proved valuable in revealing ecological implications for benthic sampling designs and pointed towards integrating functional assessments in monitoring efforts to achieve “good ecological status” of water bodies (*sensu* the EC Water Frame Directive, WFD). In this thesis, trait analysis has been useful in addressing functional differences of habitats in regard to the benthic faunal structure and provided knowledge that could be used for a more functional approach to habitat classifications and spatial planning (paper II). The contrasts between the functional, trophic and the traditional taxonomic measure of community structure indicate that future mapping and modelling of marine habitats should not only emphasise the taxonomic diversity of habitats but also assess distribution of functionally different units in coastal areas. As monitoring efforts are balanced against time and resources, the efforts of sampling to gain a functional understanding should not be larger than the efforts for assessing e.g. species/taxon richness. The findings in paper III regarding the reduced effort needed to obtain the bulk of the trait

modalities expressed (2-6 visits) compared to most taxa (17-25 visits) are supportive of this view.

Basic morphological, life history and behavioural information about the species are needed to be able to apply any type of trait analysis. Collecting such data and scoring species to traits, when biological trait analysis is used, is principally a one-time investment in time and resources. In practice, updating the biological information is necessary due to new research findings or adaptations of species to changes in the environments (Bremner 2008). In this thesis, two extensive data sets of trait information for benthic fauna were compiled in the Baltic Sea and Skagerrak regions (paper III and IV). Inclusion of such data into either national or international databases gives the possibility to extend the usage for both scientific collaborations but also inclusion of trait analysis in management efforts. This would require a proper structure of the database and linkages to original sources, as well as a system for crediting the author who originally submitted and compiled the data. Such efforts are currently being advanced internationally and early initiatives such as the Biological Traits Information Catalogue BIOTIC (www.marlin.ac.uk/biotic) offer good examples upon which future databases and collaborations can build.

4.3 OUTLOOK AND FUTURE DIRECTIONS

Making use of techniques applied in other disciplines, such as modelling may drive the use of multiple categorical traits in a new direction. An example of this is the simulation study by Norkko et al. (2011) demonstrating that bioirrigation by a polychaete worm may mitigate oxygen conditions in the sediment and potentially reduce hypoxia. Another example is Solan et al (2004), who simulated the effect of species loss for benthic functioning. Furthermore, incorporating the biological

trait concept into models describing biogeographical patterns will also be a valuable future research direction. Moreover, there is an almost complete lack of interaction between terrestrial and marine faunal community research. This is an opportunity for interesting collaborations in the future (Menta 2012).

In addition, linking the biological trait approach to the food web concept will give novel insights into how trophic structure link to functioning in other ways than specifically through feeding interactions (Gamfeldt et al. 2008, Harvey et al. 2013). Using multiple traits on a community level may help disentangle the multitude of processes that are to be accounted for in order to understand the complexities in empirical food webs. An application of the biological trait concept in the general food web context

has not yet been conducted. A first step towards merging the two concepts was taken in paper II.

As the roles taxa play in the system is context-dependent (Thrush & Lohrer 2012, Villnäs et al. 2012), combining observational patterns of species distribution with experimental findings will also be an essential approach for future research efforts utilising functional traits. Results from such studies would increase the information about what species do in the system and add to the general trait knowledge. Especially questions concerning which traits that drive a specific function and thus are more important than other traits could be answered. Such knowledge is essential in order to bring the understanding of ecosystem functioning further.

5. CONCLUDING REMARKS

This thesis has focused on further developing the concept of biological traits for interpretation of benthic community functioning in coastal waters. Although the approach was applied in the Baltic Sea, the various scales explored (from metres to thousands of kilometres, weeks to a decade) and multiple traits included, make the findings general and applicable in other marine environments. Biological traits as a concept and approach are thus not dependent on the context in which it is applied, a strength that is relevant for future applications and inclusion into management and conservation. The search on the ISI web of Science and Google Scholar illustrated the timeliness of this thesis, in a period of rapid increase in marine studies using multiple traits.

From an ecological perspective, the results of trait distributions in various habitats disclosed the importance of organismal densities for identifying functional differences. On a landscape scale, the faunal source-pool expressing traits such as *direct developing larvae*, *local dispersal* and *crawling* habits dominated the system. Furthermore, the discrepancies found between the functional and trophic structures to four pre-defined common habitats are important ecologically and give implications for future management efforts concerning habitat classifications and subsequent habitat mapping. On larger scales, trait assessments

of Finnish coastal benthos showed high trait richness, somewhat differing between areas high and low in salinity and human pressure. Utilising gradients in taxonomic richness, such as those found in estuaries or the ones used in this thesis, have the potential to illustrate general functional patterns. Temporal variability of trait expressions described functional dynamics of benthic communities on both small and large spatial scales. The temporal analysis highlighted two things; i) that although functional trait expressions can be similar overall in space, context-dependency might be attributed to temporal variations, and ii) that temporal analysis of traits may illustrate general sets of traits which may be useful as reference and in possible future predictions.

Using categorical traits, calculations and interpretations of univariate measures such as number of categories, must be done with the restrictions of the approach in mind. The findings in this thesis demonstrate that such measures may provide relevant understanding of functioning, in addition to traditionally used multivariate analysis. Exploring expressions of individual trait categories proved valuable for i) the different components of the species pool (common vs. rare taxa) and ii) changes over time (variation in number of taxa per category). In addition, this way of investigating functional aspects is applicable on any spatial scale.

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SUPPLEMENT TABLE

List of biological traits and categories (modalities) in the thesis and specific papers (I-IV). In total 26 traits and 118 modalities have been used in the thesis.

		I	II	III	IV
Trait (26 tot.)		9	13	25	10
Category/Modality (118 tot.)		35	55	102	51
Size*	0.1-1mm/0.10mm	X	X		X
	15mm	X	X	X	X
	5-10mm/11-20mm	X	X	X	X
	10-30mm/21-50mm		X	X	X
	30-50mm/51-100mm		X	X	X
	>50mm/>100mm		X	X	X
Adult longevity	<1yr			X	X
	1-3yrs/1-2yrs		X	X	X
	3-6yrs/2-5yrs		X	X	X
	6-10yrs/5-10yrs		X	X	X
	>10yrs		X	X	X
Reproductive technique	Asexual		X	X	
	Sexual		X	X	
Sexual differentiation	Gonochoristic		X	X	
	Hermaphrodite		X	X	
	Partenogenetic		X	X	
Fertilisation type	Nonfertile			X	
	External			X	
	Internal			X	
Reproductive frequency*	Semelparous	X	X	X	X
	Iteroparous				X
	Semi-continous				X
	Annual episodic	X	X	X	
	Annual protracted	X	X	X	
Developmental type / Larval type*	Fragmentation		X	X	X
	Direct	X		X	X
	Lecitotrophic	X		X	X
	Planktotrophic	X		X	X
	Oviparous		X	X	
	Ovoviviparous		X	X	
	Viviparous		X	X	

		I	II	III	IV
Environmental position *	Deep (>5cm)	X	X	X	X
	Middle (2-5cm)	X	X	X	X
	Top (2cm)	X	X	X	X
	Interface				X
	Epibenthic	X	X	X	X
	Benthopelagic	X	X	X	X
Living habit	Attached		X	X	X
	Tube dweller		X	X	X
	Burrow dweller		X	X	X
	Case builder		X	X	X
	Free		X	X	X
	Crevic dweller				X
	Parasite/Commensal				X
Feeding position / Feeding habit *	Suspension/filter feeder		X	X	X
	Surface feeder		X	X	
	Sub-surface feeder		X	X	
	Selective particle feeder		X	X	
	Detritivore / Deposit feeder	X		X	X
	Predator /Carnivore	X		X	X
	Scavenger			X	X
	Herbivore	X	X	X	X
	Miner/Borer		X	X	X
	Parasite	X	X	X	X
Omnivore	X		X		
Resource capture method	Jawed		X	X	
	Siphon		X	X	
	Tentaculate		X	X	
	Pharynx		X	X	
	Radula		X	X	
	Net		X	X	

		I	II	III	IV
Mobility *	Sessile		X	X	X
	Semi-mobile	X	X	X	X
	Mobile	X	X	X	X
	No movement				X
Movement method *	Swimmer	X	X	X	X
	Crawler	X	X	X	X
	Rafter/drifter/Byssus	X	X	X	X
	Tube-builder		X	X	X
	Burrower	X	X	X	X
Migration	Non-migratory			X	
	Vertical			X	
	Horizontal			X	
Dispersal	Non-dispersal/Resident	X	X	X	
	Local	X	X	X	
	Long distance	X	X	X	
Sediment transport	No transport			X	X
	Diffusive mixing			X	X
	Surface deposition			X	X
	Conveyor belt transp.			X	X
	Reverse conv. belt transp.			X	X
Sociability	Solitary			X	
	Gregarious			X	
	Aggregated			X	
Propagule dispersal range	<0.1m	X			
	0.1-1m	X			
	1-10m	X			
	10-100m	X			
	100-1000m	X			
	1000-10 000m	X			
	>10 000m	X			

		I	II	III	IV
Body design	Vermiform unsegmented			X	
	Vermiform segmented			X	
	Bivalved			X	
	Turbinate			X	
	Articulate			X	
Protection	No protection			X	
	Tube			X	
	Burrow			X	
	Case			X	
	Soft shell			X	
	Hard shell			X	
Body flexibility	Non-flexible			X	
	Very flexible			X	
	Flexible			X	
	Jointed			X	
Fragility	Fragile			X	
	Intermediate			X	
	Robust			X	
Degree of dependency	Low			X	
	Temporary			X	
	Permanent			X	
Time to maturity	<20%			X	
	20-50%			X	
	>50%			X	

Interpreting marine benthic ecosystem functioning in coastal waters:

VALIDATING THE BIOLOGICAL TRAIT CONCEPT

This thesis describes how species traits can be used to understand ecosystem functioning in terms of the functional structure, diversity and variability of faunal communities. The thesis demonstrates the utility of the concept on both small and large spatial and temporal scales as well as in relation to human impacts using coastal zoobenthic data in the Baltic Sea. The results also comprise further developments of the methodology and highlight the importance of including functional aspects in marine management and conservation.



THE AUTHOR

Anna Törnroos received her MSc in Environmental Biology from Åbo Akademi University in 2009 and has since then been working as a PhD student in Marine Biology at the university. In her research she has utilized data collected through field sampling at Husö Biological Station and data from national and regional monitoring programs. As part of her work she has also compiled an extensive dataset on traits of benthic fauna in the Baltic Sea.

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