DISTRIBUTION, TROPHIC ECOLOGY, AND FUNCTIONAL ECOLOGY OF THE BENTHIC MACROINVERTEBRATE FAUNA IN THE ELBE ESTUARY, GERMANY

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1 Preliminary note

Throughout the following text, the first person singular is used. However, it should be noted that each article of this thesis is the work of more than one person. In accordance with the applicable doctoral regulations, the author contributions are given in a separate document.

2 Summary

Estuaries are characterized by a longitudinal salinity gradient. This gradient is one of the main environmental factors responsible for the distribution of organisms. Distinguishing salinity zones is of crucial importance, e.g., for the development of tools for the assessment of ecological quality. The methods most often applied for classifying water according to salinity are the Venice System and the method of Bulger et al. (1993), both of which determine zone boundaries using species occurrences relative to mean salinity. However, although these methods were developed for homoiohaline waters, they have also been routinely applied to poikilohaline systems. I tested the applicability of both methods using salinity and macroinvertebrate data for the poikilohaline Elbe Estuary (Germany). My results showed that the mid-estuary distribution of macroinvertebrates is determined by variation in salinity rather than by mean salinity. Consequently, neither of the two methods is applicable for defining salinity zones in the Elbe Estuary. Cluster analysis combined with a significance test, by contrast, was a better tool for identifying the boundaries of salinity zones in poikilohaline systems.

In many estuaries, such as the Elbe Estuary, a maximum turbidity zone (MTZ) develops, where suspended matter accumulates owing to circulation processes. It is assumed that the MTZ is a stressful environment with an excess of organic matter, high deposition rates, large variations in salinity, and dredging activities. Under such harsh conditions, populations might remain below the carrying capacity, and it is assumed that competition is of little importance, as predicted by the stress gradient hypothesis. I tested whether competition for food is important in the MTZ of the Elbe Estuary using stable isotope analysis of the macroinvertebrate community. The isotopic niches of no two taxa within a feeding group overlapped, which indicated different resource use and the absence of competition. The main reasons for the lack of overlap of isotopic niches were differences in habitat, feeding behavior, and migration behavior.

The Elbe Estuary is nowadays highly industrialized and has long been subjected to a plethora of human-caused alterations. However, it is largely unknown what changes occurred in benthic communities in the last century. Hence, I considered taxonomic and functional aspects of macrobenthic invertebrates of the Elbe Estuary given in data from 1889 (most natural state), 1985 and 1986 (highly polluted state), and 2006 (recent state) to assess benthic community shifts. Beta-diversity analysis showed that taxonomic differences between the sampling dates were mainly due to species turnover, whereas functional differences were predominantly a result of functional nestedness. Species number (*S*), functional richness (FRic), and functional redundancy reached minimum values in 1985 and 1986 and were highest and rather similar in 1889 and 2006. The decline in FRic from 1889 to 1985/1986 was non-random, consistent with habitat filtering. FRic, functional beta diversity, and *S* data suggested that the state of the estuary from 1889 was almost re-established in 2006. However, the community in 1889 significantly differed from that in 2006 owing to species replacement. My results indicate that FRic and FR in 1889 could have promoted ecosystem resilience and stability.

3 Zusammenfassung

Ästuare sind charakterisiert durch einen longitudinalen Salinitätsgradienten. Der Salzgehalt ist einer der wichtigsten Umweltparameter, der die Verteilung der Arten bestimmt. Heute werden Grenzen von Salinitätszonen vor allem mit Hilfe des Venedig-Systems und durch eine von Bulger et al. (1993) entwickelte Methode festgelegt. Beide Systeme wurden in homoiohalinen Gewässern entwickelt und die Einteilung in Zonen erfolgt anhand der Verteilung von Arten in Abhängigkeit vom mittleren Salzgehalt. Sie werden jedoch auch regelmäßig in poikilohalinen Systemen angewendet. Ich habe, basierend auf Langzeitdaten von Salinität und Makrozoobenthos (MZB), untersucht, ob die beiden Methoden im poikilohalinen Elbeästuar (Deutschland) anwendbar sind. Meine Ergebnisse zeigten, dass die Variabilität der Salinität und nicht die mittlere Salinität für die Verteilung der Arten in den mittleren Bereichen des Ästuars bestimmend ist. Folglich ist die Anwendung von keinem der beiden getesteten Verfahren in poikilohalinen Gewässern sinnvoll. Ich empfehle die Anwendung von Clusteranalyseverfahren zur Festlegung signifikant unterschiedlicher Salinitätszonen in poikilohalinen Systemen.

In vielen Ästuaren bildet sich eine Zone maximaler Trübung (ZmT), in der suspendiertes Material durch Zirkulationsprozesse akkumuliert. Im Elbeästuar ist diese Zone deckungsgleich mit der Zone höchster Salinitätsvariabilität und weist zudem den höchsten organischen Anteil im Sediment sowie hohe Sedimentationsraten und organische Belastungen auf. Die Stress-Gradienten-Hypothese besagt, dass unter starkem äußerem Druck wie diesem, Populationen oft unter der Kapazitätsgrenze bleiben und Konkurrenz nur von geringer Bedeutung ist. Ich habe mittels stabiler Isotopenanalyse getestet, ob Nahrungskonkurrenz in der ZmT des Elbeästuars für die häufigsten Makroinvertebraten relevant ist. Innerhalb eines Ernährungstyps zeigten die artspezifischen Isotopennischen keine oder nur eine geringe Überlappung. Folglich ist Konkurrenz um Nahrung in der ZmT nur von untergeordneter Bedeutung. Ursachen für getrennte Isotopennischen waren vor allem bedingt durch Unterschiede in Habitat (Korngröße) und Migrationsverhalten der Makroinvertebraten.

Ästuare gehören heute auf Grund anthropogener Einflüsse zu den am stärksten gefährdeten Gewässern. Das Ausmaß der Veränderungen in deren Artengemeinschaften während des letzten Jahrhunderts ist jedoch weitgehend unbekannt. Ich habe anhand historischer und aktueller Daten (1889, 1985, 1986, 2006) taxonomische und funktionale Veränderungen des MZB im Elbeästuar untersucht. Taxonomische Unterschiede zwischen den Untersuchungsjahren waren vor allem auf das Verschwinden von Arten und Auftreten anderer Arten (turnover) zurückzuführen. Funktionale Unterschiede entstanden hauptsächlich dadurch, dass Arten mit bestimmten Traits (Morphologie, Reproduktion, Entwicklung, Ernährung, Habitat) verschwanden, ohne dass diese Arten von anderen Arten mit gleichen Traits ersetzt wurden (nestedness). Artenzahl und funktioneller Reichtum waren 1985 und 1986 am niedrigsten. In den Jahren 1889 und 2006 waren sie am höchsten und nahezu gleich. Dies impliziert, dass die vom MZB im Ästuar von 1889 bereitgestellten Ökosystemfunktionen im Jahr 2006, jedoch unter veränderter taxonomischer Zusammensetzung, wieder vorhanden waren. Meine Ergebnisse verdeutlichen die hohe Relevanz von funktionaler Redundanz und funktionalem Reichtum für die Resilienz und Stabilität von Ökosystemen.

4 General introduction

Ecology as a subdiscipline of biology first emerged in 1866, when Ernst Haeckel defined it in a broad sense of the term as the science of the relationships of organisms to their environment (Haeckel, 1866). Between then and now, ecology has developed from purely descriptive studies (e.g., Dahl, 1891) to studies using complex models to explain species–environment interactions (e.g., Bizzi et al., 2013). To date, ecology publications cover nearly all conceivable habitats, such as forests (e.g., Morin et al., 2014), deserts (e.g., Fleishman et al., 2003), oceans (e.g., Kortsch et al., 2015), freshwater environments (e.g., Calizza et al., 2012), and estuaries (e.g., Ysebaert et al., 2003). Ecological studies also cover a multitude of species on different trophic levels, e.g., phytoplankton (e.g., Roubeix et al., 2016), macrozoobenthos (e.g., Austen et al., 1989), and mammals (e.g., Gouveia et al., 2014). Within ecology, different subdisciplines have evolved, all of which could help to clarify the sophisticated changes in species compositions that are caused by environmental alterations. Trophic ecology, for instance, focuses on feeding relationships of organisms under different environmental conditions (Gaston et al., 1998) and can reveal shifts in feeding habits and changes in trophic positions in the food web along gradients (e.g., Davias et al., 2014; Doi et al., 2005). Functional ecology, on the other hand, seeks to understand the relationships between species traits and the environment (Keddy, 1992) and enables analysis of how ecosystem functioning and ecosystem services provided by species traits change along gradients within a community (e.g., Díaz et al., 2008; Mouillot et al., 2014).

Lotic waters are an important environment for ecological studies. They are vital for humans because they can serve as drinking water resources, provide water for irrigation, enable energy production, and provide food, e.g., fish (Jürging and Patt, 2005). However, most studies dealing with ecology of lotic waters to date have been conducted in freshwater and marine waters; the transition zone between freshwater and seawater has been studied to a much lesser extent. Nevertheless, the first studies in brackish waters (i.e., waters with salinity lower than that of saltwater and higher than that of freshwater; Elliott and McLusky, 2002) date back to the early 20th century (e.g., Alexander et al., 1936; Redeke, 1922; Remane, 1934). The part of the transition zone that reaches from the inlet of the sea to the upper limit of the tidal rise is called an estuary (Fairbridge, 1980). The origin of the English word ‘estuary’ dates back to the 16th century and is derived from the Latin word ‘aestuarium’ (channel, marsh), which is derived from ‘aestus’ (billowing movement, tide) (Collins, 1979). Estuaries are characterized by a strong longitudinal salinity gradient resulting from river and seawater inflow, with salinity concentrations increasing seaward (Elliott and Whitfield, 2011). Salinity in estuarine waters varies in space and time owing to the twice-daily rhythm of the tides, river discharge, and tidal range (McLusky and Elliott, 2004). It is thought that salinity is the environmental factor with the strongest influence on biota in estuaries because of the large differences in the physiological ability of organisms to deal with changing salt concentrations in the environment (Basset et al., 2012; Telesh and Khlebovich, 2010). Organisms, such as benthic macroinvertebrates, are known to structure their communities along natural estuarine gradients like the salinity gradient (Ysebaert et al., 2003). Indeed, as early as 1922, brackish waters were divided into different salinity zones based on the organisms present to foster a better understanding of the underlying ecological processes (Redeke, 1922). Later, other methods to define the salinity zones were proposed (e.g., Dahl, 1956; Remane, 1940; Välikangas, 1933). The most widely used and accepted method for classifying waters according to salinity today is the Venice System, which was introduced and proposed for universal application (Venice System, 1959). However, it has often been criticized as being static and descriptive (e.g., den Hartog, 1974), and consequently, an alternative method was introduced by Bulger et al. (1993). The authors determined salinity zones of the Chesapeake Bay and Delaware Bay (both USA) based on salinity tolerances of fish and invertebrates using a multivariate method. However, both of these methods only consider mean salinity, even though it is assumed that also variation in salinity influences species occurrences (Attrill, 2002). The degree of variation in salinity can differ greatly between brackish environments. For instance, the Baltic Sea is an enclosed non-tidal aquatic system and is thus characterized by relative stable isohalines, i.e., it is a homoiohaline system (Zettler et al., 2007), like Chesapeake Bay and Delaware Bay (Bird, 2010; Boesch, 1977). By contrast, aquatic systems like the Elbe Estuary (Germany; Fig. 1) are likely to lack stable isohalines due to the tide and thus exhibit pronounced salinity variations. Such an aquatic system is called a poikilohaline system. In the Elbe Estuary, long-term salinity conditions and variability are largely unknown, and it is not clear whether the Venice System or the method of Bulger et al. (1993) are applicable in this and other poikilohaline estuaries. Nonetheless, particularly the Venice System is regularly applied in the Elbe Estuary and other systems with high salinity variations (e.g., ARGE ELBE, 1998; Gómez and Defeo, 2012; Krieg, 2006) and has even found its way into the European Water Framework Directive (European Parliament, 2000), in which the Venice System boundaries are used for the characterization of types of surface water bodies (Annex II, 1.2.3. Transitional Waters, System A).

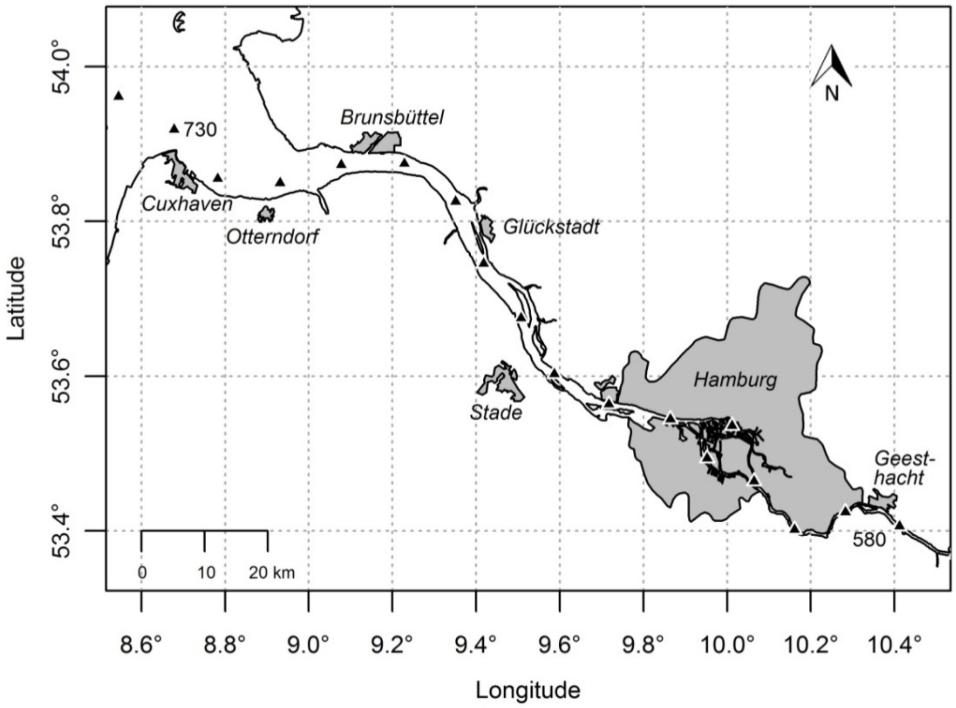

Fig. 1 The Elbe Estuary (river-km 585 to 727). River-kilometer marks are shown every 10 km as triangles. City limits are shown in gray.

In addition to pronounced spatial and temporal salinity variations, another important feature of many estuaries is the so-called maximum turbidity zone (MTZ). An MTZ develops because, besides saltwater and freshwater inputs, also sediment is carried into the estuary from both the sea and river (McLusky and Elliott, 2004); fine sediment can accumulate in the estuary, and transport of particles upstream is balanced by the seaward transport (Little, 2000). The existence and magnitude of the turbidity maximum depends on various factors, e.g., the amount of suspended matter in the riverine and tidal inflow, estuarine circulation, and settling velocity (McLusky and Elliott 2004). Elevated levels of turbidity can reduce primary production (and subsequently oxygen production) and negatively impair the growth of filter feeders and the performance of visual predators

(Essink, 1999). Along with the sediments, biologically relevant nutrients such as calcium, magnesium, sulfur, potassium, and trace elements enter the estuary with the tide. Nitrogen and phosphorus, which are the two main limiting factors for primary production in marine ecosystems, enter the estuary with the river inflow (Correll, 1978). As a result, estuaries are one of the most productive environments worldwide, with an exceptionally high mean net primary production comparable to that of tropical rainforests (Whittaker and Likens, 1973).

In the Elbe Estuary, the MTZ is characterized by exceptionally high concentrations of suspended particulate matter (Kappenberg and Grabemann, 2001), high sedimentation rates (as indicated by coincidence of the locations of most turbidity peaks and the locations of elevated dredging volumes; Bergemann, 2004), and, compared to the rest of the estuary, particularly high concentrations of some organic pollutants in the sediment (e.g., organo-tin compounds and organo-chlorine pesticides; Wetzel et al., 2013). It can be assumed that together with variations in salinity, which in the Elbe Estuary are highest within the MTZ, these special environmental conditions exert significant stress on the inhabitants of this zone. Such harsh conditions often keep populations below carrying capacity (Connell, 1980) and influence ecologically relevant processes, such as feeding behavior of benthic invertebrates, trophic interactions, resource partitioning and competition (Dauer et al., 1981; Miller et al., 1992). Generally, it is assumed that competition is of little importance in stressful environments, as predicted by the stress gradient hypothesis (Menge and Sutherland, 1987), but the magnitude of competition for food within estuarine MTZs is still largely unknown.

Feeding relationships and food-web structures are often assessed by stable isotope analysis (Layman et al., 2012). Isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are measured within organisms using an isotope ratio mass spectrometer. $\delta^{13}C$ values of consumers enable tracking of their diet (DeNiro and Epstein, 1978), and $\delta^{15}N$ values are stepwise enriched within consumers with increasing trophic level (Minagawa and Wada, 1984). In δ-space, the isotopic values represent coordinates and define an area called the isotopic niche (Newsome et al., 2007). It is believed that overlapping isotopic niches of consumers indicate comparable use of resources, whereas consumers that show separated isotopic niches use different resources, at least partially, which makes competition for food seem unlikely (Ryan et al., 2013).

In addition to natural environmental gradients, such as salinity and turbidity gradient, estuaries also exhibit pronounced pollution gradients in space and time in the wake of various anthropogenic impacts in the last centuries (Lotze et al., 2006). As a consequence, estuaries today are highly endangered aquatic systems (Blaber et al., 2000) due to the loss of estuarine habitats and species (Lotze et al., 2006). The 'human impact history' of the Elbe Estuary already began in 1840, when the Port of Hamburg was extended; levees were constructed, and the waterway was straightened and dredged to maintain the fairway. Prior to that, the estuary had been in a relative pristine state (ARGE ELBE, 2007; Li et al., 2014; Riedel-Lorjé and Gaumert, 1982). In the 19th century, also organic loads began to increase considerably because of elevated amounts of untreated sewage that were released into the estuary (Riedel-Lorjé and Gaumert, 1982). The introduction of new species was supported by the opening of the Kiel Canal in 1895, which provided a direct connection between the North Sea and Baltic Sea (Gocke et al., 2008). In 1960, the weir 'Geesthacht' was brought into service at river-km 585, creating a clearly defined boundary of the estuary and thereby drastically limiting the landward extent of the tide (ARGE ELBE, 2008). In the following decades, deepening of the fairway continued and chemical loads (e.g., heavy metals, PCBs, PAHs, pesticides, insecticides, organo-tin compounds) with high potential to affect estuarine life negatively were released into the estuary. In the 1980s, pollution in the Elbe Estuary was exceptionally high, and anoxia was an often observed phenomenon that regularly led to mass death of fish. After the German reunification in 1990, amelioration slowly began because of the decommissioning of industrial plants and the installation of waste-water plants (ARGE ELBE, 2007, 1997). However, today, structural changes and anthropogenic pressure subsist, and consequently, the estuary has ad interim been classified as a 'heavily modified water body' (ARGE ELBE, 2004) in accordance with the European Water Framework Directive (European Parliament, 2000). Our knowledge about how these long-time environmental impacts influenced the benthic fauna in the Elbe Estuary is extremely limited, and it is generally recognized that long-term ecosystem studies are urgently needed to find appropriate conservation and management measures or to provide baselines (Lindenmayer and Likens, 2009; Magnuson, 1990).

The first study of the benthic soft-bottom fauna in the Elbe Estuary was already conducted in 1888/1889 (Dahl, 1891), but to date these data have only been used to compare species lists in a literature review (Petermeier et al., 1996). However, understanding shifts in communities and the underlying processes requires thorough analysis of changes in species taxonomy and function (Villéger et al., 2010), whereby ‘function’ refers to species traits that influence ecosystem function and are sensitive to disturbances (Bremner et al., 2006). Taxonomic and functional changes can be investigated by beta-diversity analysis, which can provide information about the two underlying fundamental processes, namely nestedness resulting from species/function loss and turnover as a result of species/function replacement (Baselga, 2010; Villéger et al., 2013). Another important functional aspect of communities is its functional redundancy. Two or more species are considered functionally redundant if they perform similar roles in the environment, e.g., productivity or nutrient cycling (Loreau, 2004; Walker, 1992). Functional redundancy can buffer ecosystems against function loss and thus improve ecosystem resilience (Dalerum et al., 2012; Walker, 1992).

In the light of all the foregoing considerations and given that estuaries provide important services for the benefit of humans, such as filtering pollutants, serving as a nursery for many marine fish, and providing stopover points for migratory birds (Elliott and McLusky, 2002), the overall aim of this dissertation is to make a contribution to a better understanding of estuarine benthic ecology and consequently to help improve future management and conservation measures. To achieve this goal, I conducted three studies in the Elbe Estuary. In study 1, I focused on the salinity-dependent distribution of benthic organisms and tested whether the Venice System, the zonation method of Bulger et al. (1993) can be applied within the estuary. This was done by comparing the limits of the salinity zones determined by both methods to zones of significantly different benthic community compositions determined by cluster analysis. In study 2, I focused on trophic ecology, investigating the importance and magnitude of food competition within the benthos of the estuarine MTZ using stable isotope analysis. In study 3, I focused on functional ecology, studying how taxonomic and functional aspects of the benthic community changed over more than a century within the estuary.

5 Study 1

Leaving the beaten track – Approaches beyond the Venice System to classify estuarine waters according to salinity

Abstract

The Venice System is one of the best-known and most applied systems to classify waters with respect to salinity. It has often been subject to criticism because the criteria used to derive zone boundaries were not made explicit. Consequently, an alternative multivariate PCA method that aimed at identifying salinity zones by means of the salinity ranges preferred by species was introduced by Bulger et al. (1993). We tested the applicability of both methods using salinity and benthic macroinvertebrate data for the poikilohaline Elbe Estuary (Germany) from 1997 to 2012. This was done by comparing the resultant salinity zone limits from the two approaches with boundaries where significant community changes were found by means of cluster analysis. Only the Venice System polyhaline and limnetic zone boundaries, and the PCA method outer estuary zone limit, showed good agreement with the benthic community pattern. None of the other Venice System or PCA method zone limits reflected the benthic community patterns. Our findings suggest that zone limits can only be well determined from mean salinity at the inner and outer end of the estuary, where the variation of salinity is relatively low. In contrast, in the middle of the estuary variation in salinity is the better predictor of zone boundaries. Thus, application of the Venice System or the PCA method in poikilohaline estuaries, such as the Elbe, is not meaningful and their use should be limited to homoiohaline systems. For poikilohaline systems, we found cluster analysis to be a better tool to identify salinity-zone boundaries.

Keywords: salinity gradient, salinity zones, macrozoobenthos, Venice System, Elbe Estuary

Due to copyright issues, the text of this chapter was replaced by the reference information. The interested reader is kindly asked to read the published paper via the following reference:

Taupp, T., Wetzel, M.A., 2014. Leaving the beaten track – Approaches beyond the Venice System to classify estuarine waters according to salinity. *Estuarine, Coastal and Shelf Science* 148, 27-35. © 2014 Elsevier Ltd.

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6 Study 2

Life under exceptional conditions - Isotopic niches of benthic invertebrates in the estuarine maximum turbidity zone

Abstract

The estuarine maximum turbidity zone (MTZ) can be assumed to be a stressful environment featuring special conditions of great biological importance with an excess of organic matter, high-deposition rates, large variations in salinity, and dredging activities. Under such harsh conditions, populations may remain below the carrying capacity and competition is assumed to be of little importance, as predicted by the stress-gradient hypothesis. Therefore, we hypothesized that invertebrates of similar feeding types may utilize the same resources. To test our hypothesis, we chose the three most abundant taxa classified in literature as deposit feeders (*Bathyporeia pilosa*, *Boccardiella ligerica*, *Marenzelleria* sp.) and two taxa classified as predominately predacious (*Palaemon longirostris*, *Crangon crangon*) and determined their isotopic niches based on a stable isotope analysis for the MTZ of the Elbe Estuary (Germany). We expected the isotopic niches of similar feeding types to show a clear overlap if our hypothesis was true. Our results showed that the isotopic niches of no two taxa overlapped within each feeding group, indicating different resource use and the absence of competition. The sediment analysis revealed that two of the deposit feeders inhabited significantly different mean grain sizes. The lack of overlap of isotopic niches within each feeding group may be due to differences in habitat and feeding behavior in the case of the deposit feeders and due to different migration behavior in the case of the predominately predacious species. However, competition may have occurred in the past, resulting in a divergence of feeding niches during evolution.

Keywords: Elbe Estuary, estuarine maximum turbidity zone, benthos, stable isotope analysis, isotopic niche, trophic position

Due to copyright issues, the text of this chapter was replaced by the reference information. The interested reader is kindly asked to read the published paper via the following reference:

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7 Study 3

Functionally similar but taxonomically different: benthic communities in 1889 and 2006 in an industrialized estuary

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Functionally similar but taxonomically different: benthic communities in 1889 and 2006 in an industrialized estuary

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Abstract

Understanding shifts in benthic communities along gradients over time is of crucial importance in estuarine ecology and for conservation. Yet studies considering historical data and both taxonomic and functional aspects are rare. We analysed data of macrobenthic invertebrates of the highly modified Elbe Estuary (Germany) from 1889, 1985, 1986 and 2006 to assess community shifts and considered both taxonomic and functional aspects. The number of species, functional richness (FRic) and functional redundancy (FR) reached minimum values in 1985 and 1986 and were highest and similar in 1889 and 2006. However, beta-diversity analysis showed that species assemblages in 1889 and 2006 greatly differed, almost exclusively owing to species replacement. Most striking was the decline in gastropods after 1889 to levels approaching extinction in the estuary in the other sampling years, most likely due to elevated concentrations of chemical substances, such as tributyl tin. Functional beta diversity was mainly a result of functional nestedness and was exceptionally low in a comparison of data from 1889 and 2006, which indicated nearly complete functional recovery. Null models revealed that function loss in 1985 and 1986 was non-random, consistent with habitat filtering. All functional groups were present on all sampling dates, which suggested that FR might have provided protection from significant ecosystem function loss. Our results indicate that FRic and FR in 1889 could have promoted ecosystem resilience and stability.

Keywords: Benthic invertebrates; functional redundancy; functional richness; nestedness; species turnover; Elbe Estuary

1. Introduction

Estuaries are among the most threatened aquatic systems (Blaber et al., 2000) due to a variety of human-caused alterations in the last centuries that have resulted in the destruction of habitats and depletion of species (Lotze et al., 2006). Consequently, studies in European estuaries have been conducted since the late 19th century to understand changes in species assemblages in relation to both natural gradients and pollution (e.g. Dahl, 1891; Remane, 1934; Alexander et al., 1936). Benthic invertebrates are especially suitable organisms for studying such changes because they are structured along natural gradients, e.g. salinity gradient (Taupp and Wetzel, 2014), and are sensitive to several anthropogenic disturbances (e.g. Diaz and Rosenberg, 1995; Taupp and Wetzel, 2013; Wetzel et al., 2013a).

Alterations in estuarine communities have traditionally been analysed in terms of taxonomic differences using number of species, abundances, taxonomic composition and beta diversity (e.g. McErlean et al., 1973; Claridge et al., 1986; Ysebaert et al., 2003). A consideration of beta diversity as the dissimilarity in species composition between two assemblages (hereafter referred to as taxonomic beta diversity) enables the assessment of the extent to which the structure of a community changes along a gradient (Whittaker, 1960) and reflects two different aspects, namely nestedness, as a result of species loss, and species turnover, as a result of species replacement (Baselga, 2010). However, focusing solely on taxonomy could neglect important information on ecosystem function (Walker, 1992), and consequently, it has been suggested that approaches should also incorporate species traits (Villéger et al., 2010). Functional beta diversity is based on traits and is an important aspect of biodiversity. Analogous to taxonomic beta diversity, it also reflects nestedness and turnover. Disentangling these two components is of crucial importance for a better understanding of the processes structuring communities along gradients. For instance, high functional turnover can indicate niche differentiation between communities and low functional turnover can show different niche filtering intensity between assemblages (Villéger et al., 2013).

The space filled by species traits (i.e. the functional richness, FRic) is an important feature of assemblages and represents one fundamental aspect of functional diversity

(Villéger et al., 2008). Diversity can act as insurance for the provision of ecosystem processes (‘insurance hypothesis’) if perturbations cause species extinctions, which could be compensated by species that are functionally similar but differ in their responses to environmental changes or disturbances (Walker, 1992; Naeem, 1998; Yachi and Loreau, 1999). FRic is assumed to be a sensitive predictor of disturbances because it decreases at high disturbance levels when species are filtered out due to trait filtering, whereas it is believed that numbers of species peak at intermediate disturbance levels (Cornwell et al., 2006; Mouillot et al., 2013). The habitat-filtering concept (‘habitat filtering’, hereafter used synonymously with ‘environmental filtering’) suggests that the functional traits of a species determine whether it persists or fails in a certain environment (Cornwell and Ackerly, 2009; Katabuchi et al., 2012). Consequently, the range of successful strategies within an assemblage is reduced due to habitat filtering (Cornwell et al., 2006). It is assumed that species with similar traits contribute similarly to an ecosystem function, i.e. they perform similar roles for, e.g. productivity or nutrient cycling (Walker, 1992; Loreau, 2004). These species are consequently considered to be functionally redundant, and one or more of these species can be replaced by others that perform similar functions with little or no impact on ecosystem functioning (Lawton and Brown, 1993). Functional redundancy (FR) can enhance resilience (Pillar et al., 2013), i.e. the ability of an ecosystem to return to its previous state after changing because of a disturbance, and thus promotes long-term ecosystem stability (‘redundancy hypothesis’) (Walker, 1992; Kang et al., 2015).

Long-term ecosystem research is important because it could provide insights into ecosystem changes caused by disturbances, help to assess the success of conservation measures and provide baselines (Lindenmayer and Likens, 2009). Thus, it supports management decisions and helps to avoid misjudgements that can occur when long-term data analyses remain unconsidered, for instance when environmental changes remain hidden because they occur slowly over many decades or when effects lag years behind causes (Magnuson, 1990). In the Elbe Estuary (Germany), human impacts with high potential to change the relatively pristine state began in 1840 (e.g. port, fairway and levee construction; wastewater discharge) (Riedel-Lorjé and Gaumert, 1982; Li et al., 2014) and were exceptionally high in the 1980s before the German reunification (e.g. intensified expansion, chemical loads) (ARGE ELBE, 1997, 2007). Today, the estuary is highly modified and still under severe anthropogenic pressure (e.g. dredging, dumping, chemicals) (Wetzel et al., 2012; Taupp and Wetzel, 2013; Wetzel et al., 2013a). To assess changes in functional and taxonomic aspects in the Elbe Estuary, we determined (1) changes in the number of species and taxonomic composition, (2) the two components of taxonomic and functional beta diversity (i.e. turnover and nestedness), and (3) changes in FRic and FR of the benthic community at three points in time within a period of 117 years, which included a historical, most natural state (in 1889), a highly disturbed state (in 1985 and 1986) and a relatively recent state (in 2006). Based on our findings, we evaluated how well the combined taxonomic and functional approach revealed changes between the three points in time and whether FR had been able to buffer the community against function loss.

2. Material and methods

2.1 Study site

The Elbe Estuary (Germany) discharges the River Elbe into the North Sea (Fig. 1). Today, its landward boundary is located at river kilometre 585 at the weir Geesthacht. The seaward margin of the estuary is located approximately at river kilometre 730 at the city of Cuxhaven (Boehlich and Strotmann, 2008). Prevailing salinity conditions at the end of the 19th century are unknown, but today the estuary is characterized by poikilohaline conditions and a mean salinity (PSU) of approximately 0.3 at river kilometre 630, which increases continuously to a maximum of around 21 at river kilometre 730 (Taupp and Wetzel, 2014). Sampling sites for this study are located between river kilometres 630 and 730.

2.2 Benthos data

We used benthos data from four studies of the Elbe Estuary. The earliest study was carried out in 1889 (Dahl, 1891) and reflects the most natural conditions. Studies from 1985 and 1986 (Fiedler, 1991), before the German reunification, reflect the estuarine state with probably the highest pollution levels. The most recent study was conducted in 2006 (Wetzel et al., 2013a). The number of samples and the distribution of the sampling sites within the estuary differed between the four sampling years (1889: n = 68; 1985: n = 41; 1986: n = 44; 2006: n = 52). Thus, for better comparability, we randomly chose samples that matched the following criteria: (1) the number of samples should be equal for the four sampling years, (2) samples should cover the entire longitudinal gradient from river kilometre 630 to 730 and (3) samples should be similarly distributed within the estuary. This procedure resulted in n = 31 samples for each of the four sampling years for subsequent analyses (Fig. 1). In 1985, 1986 and 2006, benthic invertebrates were collected with Van Veen grab samplers (0.1 m² surface) and subsequently sieved (0.5 mm mesh size). In 1889, dredges that catch epifaunal and endofaunal taxa from the upper few centimetres of the sediment were used; consequently, taxa inhabiting deeper sediment horizons are lacking in the 19th century samples. To account for this methodological difference, we excluded polychaetes and oligochaetes , which were underrepresented in the 1889 samples. We considered Malacostraca, Gastropoda, Bivalvia, Sessilia, Hydrozoa, Cirripedia, Insecta, Nemertea and Gymnolaemata in our study. For all analyses, we used presence/absence data because abundance data were not provided in the 1889 data set.

2.3 Comparing data of invertebrates collected with different types of sampling gear

A possible interference in comparisons of data from studies obtained at different points in time is the application of different types of sampling gear. Marine biology sampling gear has evolved over time so that direct comparisons are not always possible without prior testing. Dahl (1891) did not define the type of dredge that he used; however, it is likely that he used the so-called ‘Kieler Kinderwagen’ (mesh size: 0.5 cm, approximately 1 m² opening), which was used in German marine surveys as a standard tool for at least a century. This dredge has a tendency to penetrate into the upper sediment (Rees, 2009) and becomes easily clogged, then acting like a soft-sediment sampler. It catches both epibenthic and endobenthic fauna, including small species such as *Bathyporeia* spp. and *Pisidium* spp., which were common in the benthos samples of Dahl (1891). The ‘Kieler Kinderwagen’ is still used in German marine biological studies.

To test whether samples collected by the ‘Kieler Kinderwagen’ are comparable to those collected with the Van Veen grab, we used benthos data obtained with these sampling gears in 2002, 2006, 2008 and 2009 at four sites in the Elbe estuary at river kilometre 655, 674, 690 and 716, respectively. At every site and in every year, six Van Veen grabs (0.1 m² surface) and one dredge haul with the ‘Kieler Kinderwagen’ were collected. The grab samples were subsequently sieved (0.5 mm mesh size).

We used presence/absence data of nine taxonomic groups that we also used in our main analysis (Malacostraca, Gastropoda, Bivalvia, Sessilia, Hydrozoa, Cirripedia, Insecta, Nemertea and Gymnolaemata) to test for significant differences in community composition using a permutational (i.e. non-parametric) MANOVA (Anderson, 2001; McArdle and Anderson, 2001). Community differences were compared between sampling years (pairwise comparisons) and sampling gear (Van Veen grab vs. ‘Kieler Kinderwagen’). The results from these tests showed no significant differences for years ($df = 1$, $R^2 = 0.21$, $p = 0.16$) or for sampling gear ($df = 1$, $R^2 = 0.16$, $p = 0.31$). Consequently, we assume that a comparison of the qualitative data for the nine chosen taxonomic groups from different years collected with the two different sampling gears is justified.

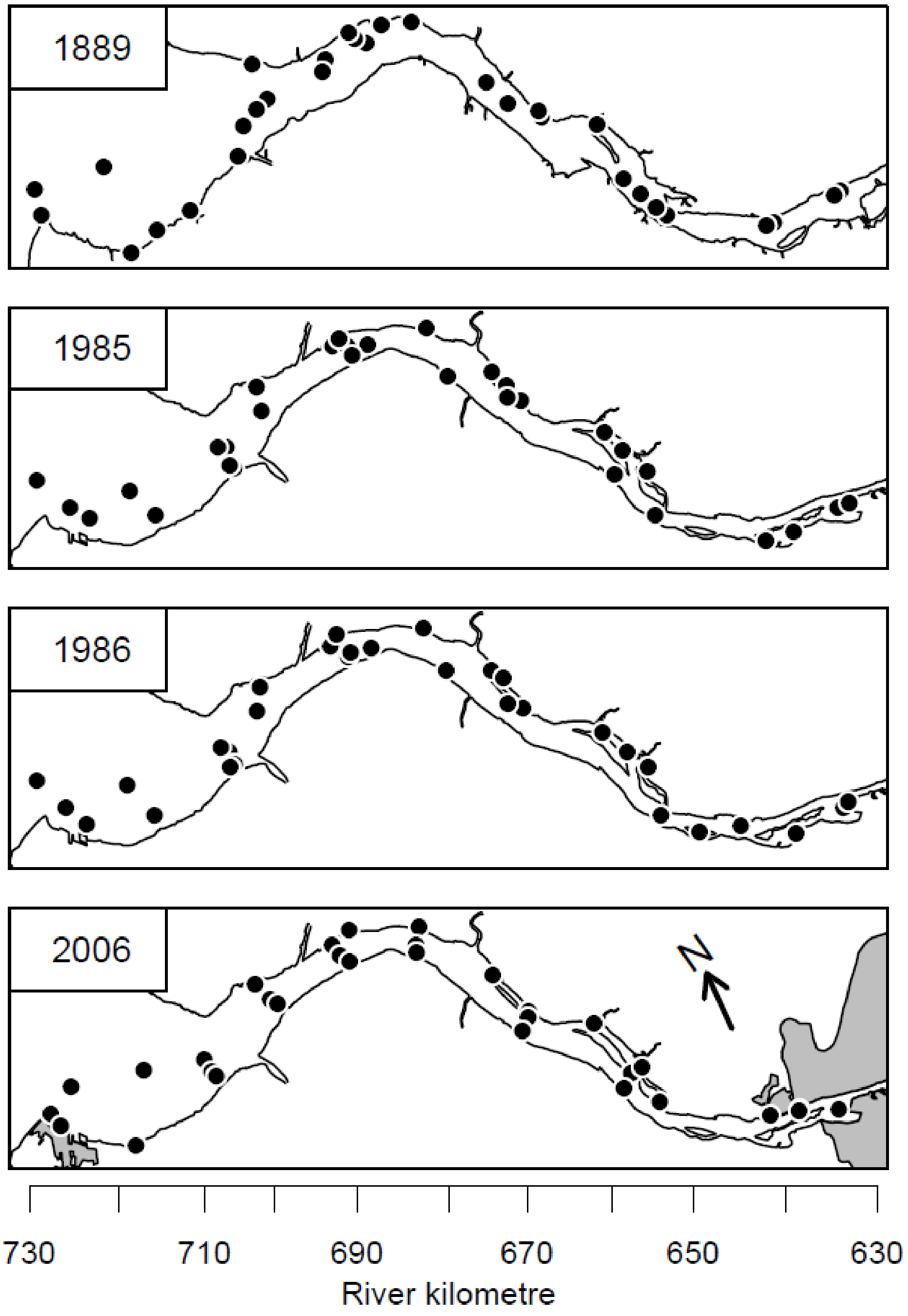

Fig. 1 The Elbe Estuary with benthos sampling sites (black dots) in 1889, 1985, 1986 and 2006 (n = 31 samples in each sampling year). The city limits of Cuxhaven (left) and Hamburg (right) in 2006 are shaded grey.

2.4 Comparison of the benthic communities of the different time points

To minimize the risk of confounding differences among single years with those related to different environmental conditions, ideally data of more than one year around a time point should be used. This is the case for data collected from the entire estuary in 1985 and 1986. We compared the data of these two consecutive years in our main analysis (subsection 3.1 and Table 1). For the other two time points, we had to use a different approach. Dahl (1889) collected his main dataset in 1889, but he also sampled in 1888 with less effort; therefore, we were able to compare the results of sites that he sampled in 1888 and again in 1889. We considered 11 sites ranging from river kilometre 700 to 730 (Fig. S1) that were sampled with the same method in the two years. Likewise, for the most recent time point, we were able to compare results of sites sampled in a less-detailed survey in 2005 with the results from the same sites in the detailed survey of 2006. We considered 8 sites between river kilometre 650 and 720 (Fig. S2) that were sampled with the same method in the two years.

If the benthic assemblages of each set of consecutive years did not differ significantly, we assumed that any taxonomic and functional differences between the three time points in the main analysis (1889, 1985/1986, 2006) were likely a result of different environmental conditions. The species assemblages of each set of consecutive years (1888 vs. 1889, 2005 vs. 2006) did not significantly differ ($p > 0.05$, MANOVA) (Tables S1 and S2).

2.5 Trait data

We chose eight biological traits (Table 2) that show both a close linkage to important ecosystem functions (e.g. energy and element cycling, productivity, bioturbation, physical processes) and sensitivity to environmental or disturbance gradients (Table S3) (Bremner et al., 2006b). These traits cover morphology, reproduction, development, feeding and habitat characteristics of the benthic invertebrate fauna and have been used in various combinations in other studies (e.g. Charvet et al., 2000; Usseglio-Polatera et al., 2000; Bremner et al., 2003; Frid et al., 2008). Traits were sub-divided into categories (i.e. modalities; 27 in total) and subsequently fuzzy coded (Chevenet et al., 1994).

Table 1 Results of the permutational MANOVA test for the comparison of the benthic communities between the sampling years (n = 31 samples each year). Significance ($p < 0.05$) is indicated by an asterisk; n.s. = not significant.

	df	R^2	p
1889 vs. 1985	1	0.23	<0.01 *
Residuals	60	0.78	
1889 vs. 1986	1	0.28	<0.01 *
Residuals	60	0.72	
1889 vs. 2006	1	0.45	<0.01 *
Residuals	60	0.85	
1985 vs. 1986	1	0.03	0.17, n.s.
Residuals	60	0.97	
1985 vs. 2006	1	0.15	<0.01 *
Residuals	60	0.85	
1986 vs. 2006	1	0.20	<0.01 *
Residuals	60	0.80	

In the course of the fuzzy-coding procedure, each modality was given a value from 0 to 3 to reflect the degree of affinity of the species with the modality as follows: 0 = no affinity, 1 = weak affinity, 2 = moderate affinity and 3 = strong affinity (Bremner et al., 2006a). After assigning the modalities, the scores were standardized to 1 within a trait. Trait data originated from numerous journal publications, books and internet sources of scientific institutions or online databases. Missing data were substituted using expert judgement or trait data of the nearest phylogenetic neighbour (in 9.8% of the cases) (cf. Tillin et al., 2006; Cooper et al., 2008; Dimitriadis et al., 2012). For the complete list of species traits, see Table S4.

Table 2 Biological traits of benthic invertebrates used in this study, respective trait modalities (categories) and explanations. Superordinate trait groups are shown in bold.

Biological trait	Trait modality	Abbreviation, explanation
Morphology		
Potential size	<5 mm	S1, small
	5–10 mm	S2, small to medium
	10–20 mm	S3, medium
	20–40 mm	S4, medium to large
	40–80 mm	S5, large
	> 80 mm	S6, very large
Protection	No protection	P0, without protection
	Low protection	P1, tube or burrow
	Soft shell	P2, exoskeleton or hard cuticula
	Hard shell	P3, hard shell, e.g. mussels
Reproduction		
Sexual differentiation	Hermaphrodite	BH, exhibiting both sexes
	Gonochoristic	BG, exhibiting separate sexes
Reproductive technique	Asexual	RA, fragmentation or budding
	Ovi/ovoviviparous	RO, laying eggs/hatching from eggs inside maternal body
Larval type	No larvae	L0, direct development without larvae
	Planktotrophic	LP, larvae feeding on plankton
	Lecitotrophic	LL, larvae feeding on yolk
Development		
Adult longevity	<1 year	A1, short
	1–2 years	A2, medium
	2–5 years	A3, long
	>5 years	A4, very long
Feeding		
Feeding habits	Predator	FP, carnivore; captures animals
	Filter/suspension feeder	FS, feeding on suspended material
	Deposit/sediment/periphyton feeder	FD, food collected from the surface or within the sediment
Habitat		
Local habitat	Pelagic	HP, living in the water column
	Epi/hyperbenthic	HE, living on the sediment surface/in nearby water layer
	Endo/infauna	HI, living within the substrate

2.6 Index calculation

To assess taxonomic changes between two benthic communities, we calculated numbers of species *S* for each sampling year. Of the 31 samples in each sampling year, we derived species lists that we used to calculate total taxonomic beta diversity (Sørensen pairwise dissimilarity) between the sampling years. We also calculated the two components of taxonomic beta diversity, namely taxonomic turnover (Simpson-based pairwise dissimilarity) and nestedness (Baselga, 2010; Villéger et al., 2013).

For determining temporal functional shifts, we applied a fuzzy correspondence analysis (FCA) of species traits (all four sampling years together) to obtain a representation of species functional distances (Chevenet et al., 1994). FCA is a linear ordination that uses Eigen analysis to investigate differences between samples based on species traits and has been shown to be an appropriate approach for biological trait analysis (Bremner et al., 2006b). We used the FCA results to determine functional richness (FRic) and shifts in FRic (FShift) (Villéger et al., 2008; Mouillot et al., 2013). FRic is defined as the amount of functional space occupied by a species assemblage (Villéger et al., 2008) and is calculated as the surface of the convex hull encompassing species in the two-dimensional species-trait space obtained by the FCA. Consequently, FRic is higher if the range of the traits within a community is high, and lower if the range is low (Villéger et al., 2011). FRic for each study is given as the percentage of the convex hull surface of the entire species pool of the four studies. FShift was calculated as the percentage of the sum of the non-overlapping functional space of two convex hulls in relation to the combined functional space of the two hulls (Mouillot et al., 2013). We used the FCA results and the species list of each year to calculate total functional beta diversity and its two components functional nestedness and turnover (Villéger et al., 2013).

FR was determined by calculating the species richness within functional groups (i.e. aggregations of species with similar traits; cf. Blondel 2003; Dumay et al. 2004) following the method proposed by Laliberté et al. (2010) with modifications: to define functional groups, a distance matrix (Euclidean distance) was created with the species coordinates obtained by the FCA. The distance matrix was subsequently used for hierarchical clustering (Ward, 1963). We used the method proposed by Scott and Symons (1971) to find the best partition of the clustering results, i.e. the best number of functional groups in the species-trait space. For each study, the number of species in each functional group was determined. Subsequently, the number of species within each functional group was ranked to account for differences in species numbers between the functional groups, thus representing FR.

2.7 Statistical analysis

We used a null model approach to test whether FRic in the respective sampling years was significantly less than expected by chance, i.e. we tested whether the reduced functional space is due to habitat filtering (cf. Cornwell et al., 2006) if FRic values within a certain sampling year showed a clearly reduced functional space. We define sampling years with clearly reduced functional space as years with FRic values less than 75%. For each sampling year with FRic < 75%, we randomly drew the number of species found in the respective sampling year from the species pool without replacement and calculated FRic. This procedure was repeated 1000 times. Subsequently, we tested for significant differences between the real FRic value in the respective sampling year and the 1000 FRic values obtained from the random drawing using the non-parametric Wilcoxon test (e.g. Sokal and Rohlf, 1995).

To test for temporal trends in FR, we determined potential breakpoints in linear regression relationships of the FR ranks following an algorithm for simultaneous estimation of multiple breakpoints (Bai and Perron, 2003). Within this procedure, a breakpoint is defined as a point where the linear regression coefficients shift from one stable regression relationship to a different one (‘broken-stick regression’). For each segment defined by a breakpoint, a linear model was fitted and tested for significance, and Pearson’s product moment correlation coefficient was calculated.

All analyses were done in the R environment (R Core Team, 2013) using the packages vegan (Oksanen et al., 2013), ade4 (Dray and Dufour, 2007), geometry (Barber et al., 2013), strucchange (Zeileis et al., 2002, 2003) and betapart (Baselga et al., 2013).

3. Results

3.1 Comparison of the benthic communities

Pairwise comparisons of the benthic communities of the four sampling years (1889, 1985, 1986 and 2006) showed significant differences in all cases ($p < 0.01$, MANOVA) except for the comparison of 1985 and 1986, which was not significant ($p = 0.17$, MANOVA) (Table 1).

3.2 Temporal changes in taxonomy

The total number of species in the entire estuary was higher in 1889 (26 species) than in 1985 (16 species) and 1986 (11 species); the total number of species was highest in 2006 (27 species) (Table 3). The most marked decline in the number of species was that of gastropods, with 7 species in 1889 and 1 species in each of the other years. The number of species within the Bivalvia was lowest in 1986 (2 species) and highest in 1889 (9 species). Within the Malacostraca, the number of species was lowest in 1889 (6 species) and highest in 2006 (16 species). For the complete list of species, see Table S5.

Total taxonomic beta-diversity values indicated that the pairwise dissimilarities between the communities of the four sampling years were relatively high and constant, with values ranging from 0.57 to 0.66, except for 1985 vs. 1986, where total taxonomic beta diversity was 0.3 (Fig. 2). With the exception of 1889 vs. 1986, the turnover component (indicating species replacement) of beta diversity was always higher than the nestedness component (indicating species loss). The turnover component was exceptionally high (0.65) in the comparison of 1889 and 2006, which indicates that the relatively high total beta diversity (0.66) was predominantly due to species replacement.

Table 3 Number of species within each functional group (A, B, C), total number of species, and number of species within the most important taxonomic groups (i.e. groups with at least five taxa within at least one sampling year).

	Number of species			
	1889	1985	1986	2006
Group A	9	8	4	12
Group B	5	6	6	12
Group C	12	2	1	3
Total	26	16	11	27
Bivalvia	9	5	2	5
Gastropoda	7	1	1	1
Malacostraca	6	8	7	16

Within the most important (i.e. the most species-rich) taxonomic groups Bivalvia, Gastropoda and Malacostraca, the most striking results were observed for (1) Bivalvia in a comparison of data from 1889 and 2006, where the total taxonomic beta diversity of 0.80 was only due to species turnover without a nestedness component, and in a comparison of 1889 and 1986, where the total taxonomic beta diversity of 0.64 was only due to nestedness without a turnover component, (2) Gastropoda in a comparison of all four sampling years, where the turnover component was 0 and (3) Malacostraca in a comparison of 1889 with 1985 and with 1986, where the total beta diversity was mainly due to species turnover.

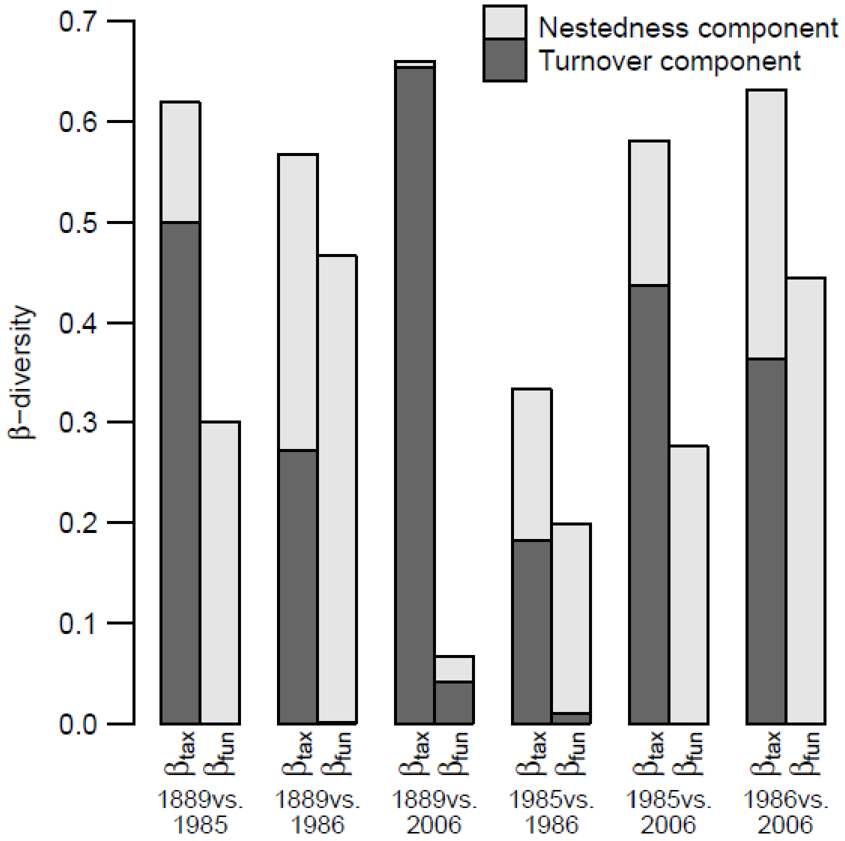

Fig. 2 Pairwise comparison of beta diversity in the four sampling years in the Elbe Estuary. Total height of stacked bars refers to total beta diversity. The two components of beta diversity (nestedness and turnover) are shown for taxonomic (tax) and functional (fun) beta diversity.

3.3 Functional changes over time

Total functional beta diversity was in all cases lower than total taxonomic beta diversity and was exceptionally low in a comparison of data from 1889 and 2006 (0.07), which indicated almost functional similarity and nearly complete functional recovery (Fig. 2). Between the latter two years, the turnover component of functional beta diversity was higher than the nestedness component. In all other cases, total functional beta diversity was almost exclusively due to functional nestedness.

FRic had the highest value in the 1889 samples (94.9%) and the lowest values in the 1985 (51.1%) and 1986 samples (34.6%) (Fig. 3a–d). In 2006, FRic was again higher (89.9%), which indicated a functional diversity similar to that in 1889. The null models revealed that (1) FRic in 1985 was significantly less than expected by chance (V = 477,930, $p < 0.01$; Wilcoxon test) and (2) FRic in 1986 was significantly less than expected by chance ($V = 495,390$, $p < 0.01$; Wilcoxon test), which indicated habitat filtering. The functional shift (FShift) was lowest in a comparison of 1889 with 2006 (12.7%) and highest in a comparison of 1889 with 1986 (63.6%). FShift was relatively low in a comparison of 1985 with 1986 (33.3%) and ranged from 43.3% to 61.5% in all other cases. Trait modalities that were especially affected by a decline or loss in 1985 and 1986 were species without protection (P0), predators (FP), species with lecitotrophic larvae (LL), very large species (S6) and species that reproduce asexually (RA) (Fig. 3e).

Three different functional groups (A, B, C) were identified (Fig. 4a). The number of species was lowest in groups A and C in 1986 and in group B in 1889 (Table 3). The number of species was highest in groups A and B in 2006 and in group C in 1889. A breakpoint in linear regression of FR was detected in 1986 (Fig. 4b). FR was higher in 1889 than at the breakpoint in 1986 ($r = -0.49$, $t = -1.5$, $p = 0.18$, linear regression), and significantly higher in 2006 than at the breakpoint in 1986 ($r = 0.87$, $t = 3.6$, $p = 0.02$, linear regression). FR was higher in 1985 than in 1986 but lower than in the other two years.

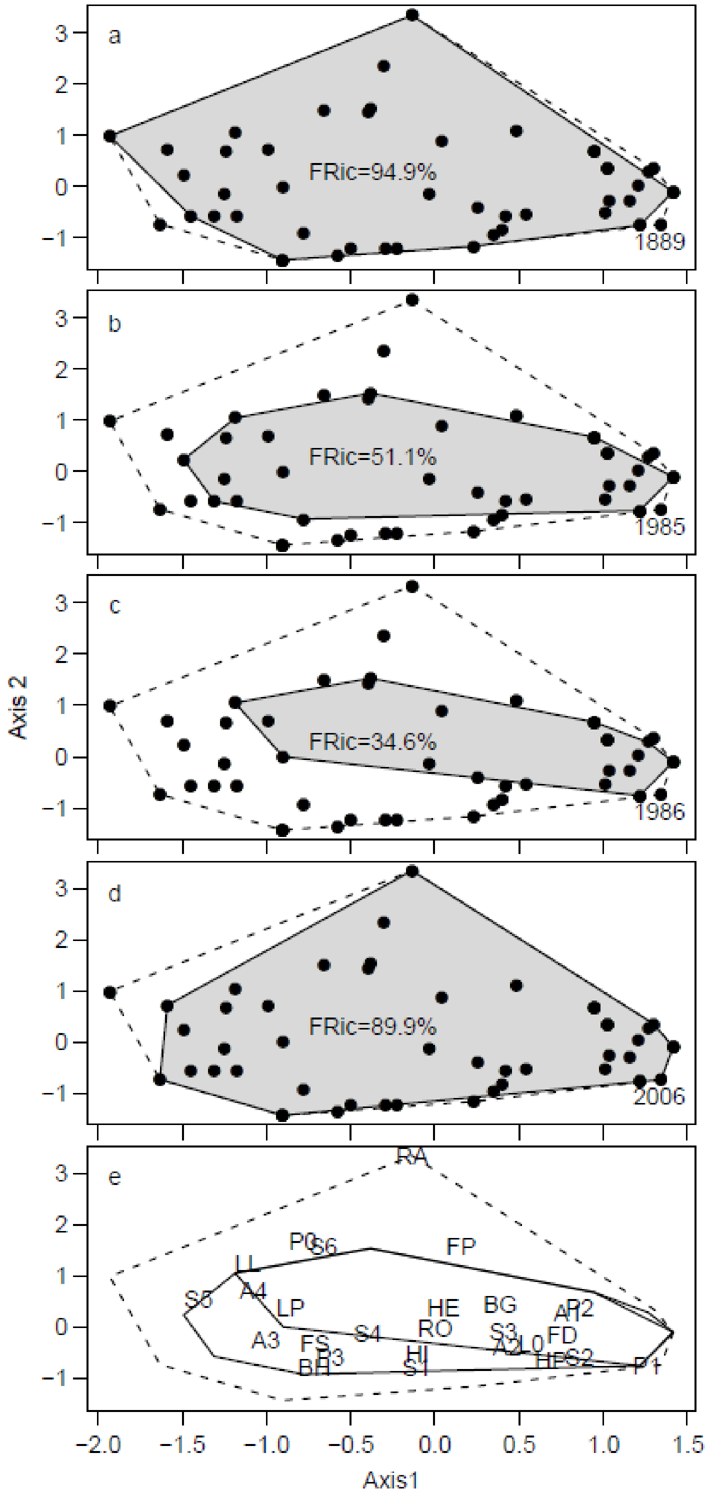

Fig. 3 (a–d) Comparison of convex hulls representing functional richness (FRic) of benthic invertebrate assemblages in the Elbe Estuary for the four sampling years, where each point represents the position of a species in functional space (FCA ordination). (e) Position of traits (see Table 2 for definition of abbreviations) within the functional space. The dashed line encompasses the entire functional space of all assemblages of the four sampling years.

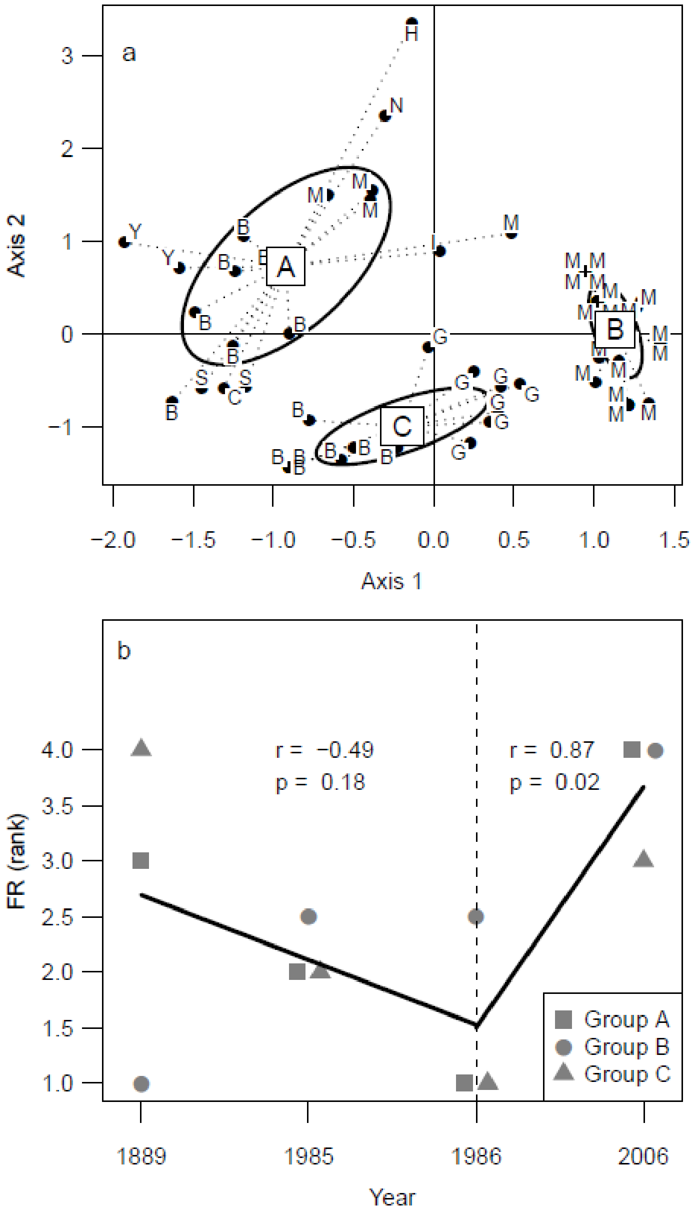

Fig. 4 (a) Functional groups (A, B, C) of benthic invertebrates in the Elbe Estuary, including samples from the four sampling years. Each point represents the position of a species in functional space (FCA ordination). Instead of species names, the higher taxon for each species is given (B = Bivalvia, C = Cirripedia, G = Gastropoda, H = Hydrozoa, I = Insecta, M = Malacostraca, N = Nemertea, S = Sessilia, Y = Gymnolaemata). Ellipse sizes are based on the standard deviation of point scores; dotted lines connect points with the group centroid. (b) Temporal changes in FR in the Elbe Estuary. The dotted vertical line indicates the breakpoint in linear regression. Significance and Pearson’s product moment correlation coefficient (r) are given for each linear regression.

4. Discussion

4.1 Environmental changes over time

The number of species, FRic and FR reached minimum values in 1985 and 1986 and were highest and similar in 1889 and 2006. These results could indicate that the environmental conditions in 1889 and 2006 influenced species number at a similar scale, even though species composition changed, and that the conditions were worse in 1985 and 1986. In 1889, the Elbe Estuary had already been subjected to a variety of anthropogenic impacts. It had been in a relatively pristine state up to 1840; after that time, the Port of Hamburg was extended, levees were constructed, and the fairway was maintained by straightening and dredging (5.3 m in 1863) (Riedel-Lorjé and Gaumert, 1982; ARGE ELBE, 2007; Li et al., 2014). In the 19th century in Hamburg, cesspits were increasingly abandoned and increasing numbers of water closets were used, which led to the release of considerable amounts of untreated sewage into the Elbe (Riedel-Lorjé and Gaumert, 1982). In 1895, the Kiel Canal linking the North Sea via the Elbe Estuary and the Baltic Sea was opened and enabled species exchange (Gocke et al., 2008). In 1960, the weir Geesthacht was brought into service at river kilometre 585, which created a clearly defined boundary of the estuary and thereby drastically limited the landward extent of the tide (ARGE ELBE, 2008a). From 1974 to 1978, the estuarine fairway was deepened to 13.5 m (ARGE ELBE, 2007), and consequently flow velocity, tidal range, and dredging and dumping amounts increased (Bergemann, 1995). In addition to these marked physical alterations and organic discharges with a high potential to alter benthic communities, chemical loads increased markedly in the 20th century. These comprised heavy metals, polychlorinated biphenyls, polycyclic aromatic hydrocarbons, pesticides, insecticides, and organo-tin compounds (ARGE ELBE, 1997, 2007). In the 1970s and 1980s, anoxia occurred often in the Elbe Estuary and regularly led to mass death of fish (ARGE ELBE, 1997). Reduction of chemical loads and amelioration of oxygen conditions began in 1990 after the German reunification owing to the decommissioning of industrial plants, changing of production processes and construction of waste-water treatment plants (ARGE ELBE, 1997, 2007). As a consequence, concentrations of most chemical substances declined significantly from 1986 to 2006 (ARGE ELBE, 2008b). From 1998 to 2000, the fairway was deepened to

14.5 m (ARGE ELBE, 2007) to support shipping, mostly to the Port of Hamburg (Boehlich and Strotmann, 2008). Along with rising environmental awareness and establishment of the European Water Framework Directive (European Parliament, 2000) in the 21st century, continued renaturation measures successfully enhanced the ecological quality of the estuary, but further actions are still urgently needed (Schuchardt et al., 2007) because the estuary is still under pressure due to sediment dredging and dumping associated with the maintenance of the navigation channel (Taupp and Wetzel, 2013), flood defence and chemical pollution (ARGE ELBE, 2008b). The historical development of human impacts may explain why biological parameters, such as species richness, FRic and FR, were lowest in 1985 and 1986 when anthropogenic pressure was exceptionally high compared to the other sampling years. The aforementioned biological values were similar in 1889 and 2006, which indicated that benthic communities were similarly influenced. However, as stressors differed between the two time points, functional spaces differed slightly, presumably owing to different environmental filters.

4.2 Decline in gastropods over time

The group with the strongest decline in number of species in the comparison of samples from 1889 with each of the other sampling dates was the gastropods, and this decline was probably a result of the significantly elevated chemical loads in the Elbe Estuary in 1985 and 1986 (ARGE ELBE, 2008b), especially that of the endocrine-disrupting anti-fouling organo-tin compound tributyl tin (TBT). TBT causes gastropod imposex (masculinization of females) and has led to reproductive failure and local extinctions worldwide (Tyler et al., 1998). TBT was used as a biocidal component in paints from the 1960s (Duft et al., 2005) until its worldwide ban in 2008 (Gipperth, 2009). It is likely to be the most toxic substance ever introduced to aquatic systems (Goldberg and Bertine, 2000). TBT concentrations were still elevated within the Elbe Estuary in 2006, most likely due to anthropogenic transport processes (Wetzel et al., 2013a, 2013b).

4.3 Functional changes over time

FRic values were higher in 1889 and 2006 than in 1985 and 1986. This decrease in functional space in the 1985 and 1986 samples indicated the loss of certain functional aspects within the benthic community, as also supported by the results that indicated that functional beta diversity was mainly due to nestedness without a replacement component. A null model revealed that this loss was non-random and hence due to trait filtering (Cornwell et al., 2006), a process by which environmental factors determine whether a species has the required traits to live in a given habitat (Mouillot et al., 2013). Maintaining FRic in ecosystems is important because reduced functional space occupied by a community could, for instance, favour non-indigenous species that can use free niche space formerly occupied by non-invasive taxa (Dukes, 2001). These alien species are a major threat for biodiversity in estuaries worldwide (Ruiz et al., 1997; Dafforn et al., 2009), and today, about 20% of the macrobenthic species in German estuaries are non-indigenous (Nehring et al., 2005). International shipping is assumed to be the most important introduction vector for alien species in Germany (Nehring et al., 2005). This is particularly relevant for the Elbe Estuary because it is the intensively used waterway to the Port of Hamburg, which is the most important transshipment port for Central and Eastern Europe and the Baltic States in Northern Europe (Boehlich and Strotmann, 2008). For instance, *Schistomysis ornata* (Malcostraca) was found in 1888 and 1889 but did not appear in the Elbe Estuary either in 1985/1986 or in later studies. The free niche space formerly occupied by this species could have been filled by alien species, such as the Chinese mitten grab *Eriocheir sinensis* and the decapod *Rhithropanopeus harrisii*. Both species have traits similar to those of *S. ornata,* were introduced in the estuary in the first half of the 20th century (Nehring and Leuchs, 1999), were found in 1985, 1986 and/or 2006, and are still regularly found in samples of other surveys in the Elbe Estuary. This could explain why the functional space in 2006 was similar to that in 1889 and functional beta diversity between these two sampling years was exceptionally low, which suggests similar functional diversity and nearly complete recovery of functions provided by the benthic invertebrates in 1889. Similar FRic values before and after the disturbances in the 20th century support the ‘insurance hypothesis’ and consequently, high FRic values in 1889 could also have promoted ecosystem resilience and stability.

4.4 Functional redundancy

FR was higher in 1889 and 2006 than in 1985 and 1986. Since in 1985 and 1986, each of the three functional groups had at least one member (i.e. species), the remaining species could have taken on the functional role of the extinct taxa. This suggests that FR might have provided protection from significant ecosystem function loss. According to the ‘redundancy hypothesis’, higher values of FR can be interpreted as a higher level of community stability (Walker, 1992; Kang et al., 2015). With this consideration, our results indicated that stability levels in the benthos community of the Elbe Estuary dropped from 1889 to 1985/1986 and increased again in 2006, reaching the same extent found in 1889. However, it is generally not to be taken for granted that FR is an insurance against function loss. If species that perform similar roles in the ecosystem also respond similarly to a certain disturbance, FR could be meaningless, if, for instance, all species with similar traits become extinct because of a specific pollutant (Ramsay et al., 1998). In our study, gastropod species that were taxonomically closely related and responded similarly to a specific disturbance were assigned to one functional group. However, in this case, the loss of gastropods could be functionally compensated by, e.g. mussels with similar traits. On the other hand, it has been argued that generally no two species can be functionally exactly the same and thus cannot replace each other completely, but certain species are undoubtedly more similar than others (Rosenfeld, 2002).

Estuaries are generally species-poor environments (McLusky et al., 1993), even in a pristine state, and the number of species within a functional group may be low, which would result in low FR. It has been assumed that FR is generally lower in species-poor communities than in species-rich communities (Fonseca and Ganade, 2001), but studies have also shown that FR might be low even in highly diverse species-rich systems (Micheli and Halpern, 2005; Guillemot et al., 2011; Mouillot et al., 2014) and high even in species-poor environments (Casatti et al., 2015). Nevertheless, a comparison of the results of different studies that assessed FR is hampered by variation in the FR obtained with the variety of methods used (e.g. de Bello et al., 2007; Villéger et al., 2011; Schmera et al., 2012; van der Linden et al., 2012; Johansson et al., 2013; Gerisch, 2014; Mouillot et al., 2014). Thus, FR determination remains elusive and is an important and challenging task for the future.

5. Conclusions

Although numbers of species, functional beta diversity, FRic and FR suggested that the original state of the Elbe Estuary in 1889 was almost re-established in 2006, taxonomic beta diversity analysis clearly showed that significant community changes occurred from 1889 to 2006. These changes were almost exclusively due to species replacement. Consequently, we suggest that both taxonomic and functional approaches be applied for management and conservation because these two means of community analysis are complementary. A taxonomic approach enables a focus on the protection of specific endangered species (e.g. the IUCN Red List; IUCN, 2016), sensitive species (e.g. AMBI; Borja et al., 2000), or habitat protection or reconstruction. A functional approach might provide additional decision guidance by ranking or choosing measures that also maintain or recover ecosystem functions. Preventing a decline in FRic and FR in estuarine ecosystems remains crucial for future planning and conservation measures in order to promote ecosystem services, resilience and stability.

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The following supporting information accompanies the article

Functionally similar but taxonomically different: benthic communities in 1889 and 2006 in an industrialized estuary

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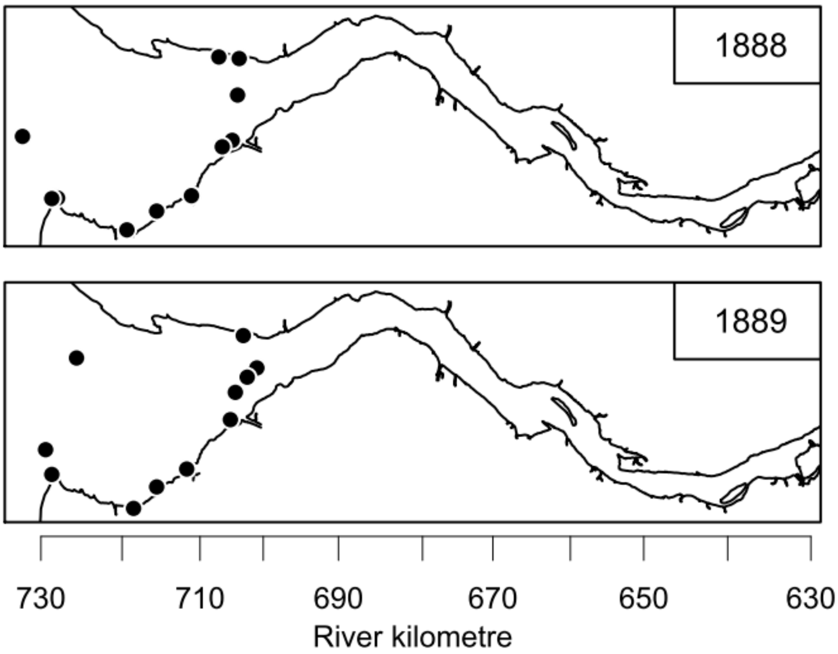

Fig. S1 Sampling sites (n = 11) in the Elbe Estuary used to compare the macrobenthic invertebrate communities of 1888 and 1889 (see also Table S1).

Table S1 Results of the permutational MANOVA test for the comparison of the macrobenthic invertebrate communities of 1888 and 1889 (see also Fig. S1); n.s. = not significant.

	df	R^2	p
1888 vs. 1889	1	0.09	0.08, n.s.
Residuals	20	0.90	

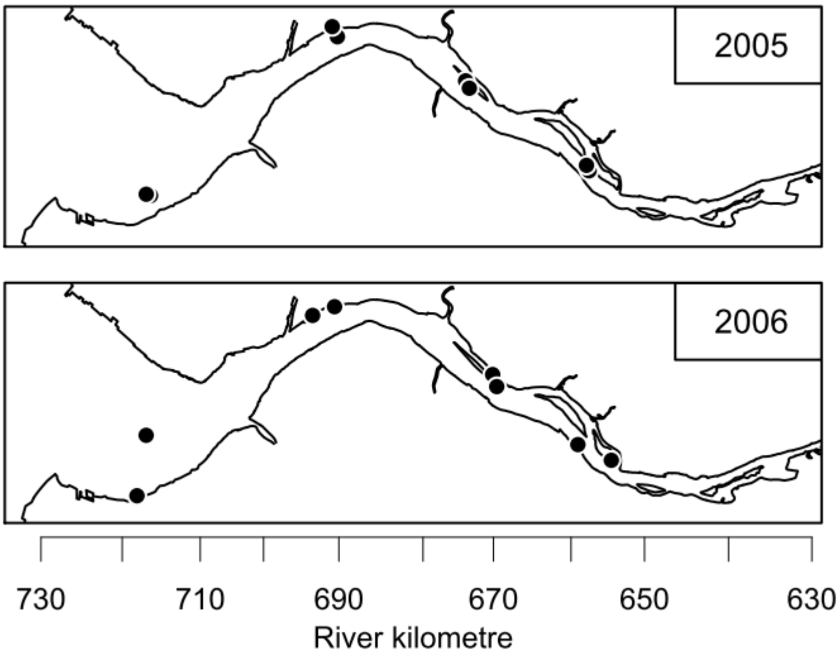

Fig. S2 Sampling sites (n = 8) in the Elbe Estuary used to compare the macrobenthic invertebrate communities of 2005 and 2006 (see also Table S2).

Table S2 Results of the permutational MANOVA test for the comparison of the macrobenthic invertebrate communities of 2005 and 2006 (see also Fig. S2); n.s. = not significant.

	df	R^2	p
1888 vs. 1889	1	0.07	0.45, n.s.
Residuals	14	0.93	

Table S3 Biological traits of benthic invertebrates used in this study and examples of respective links to ecosystem processes and sensitivities to anthropogenic impacts.

Biological trait	Link to ecosystem process	Sensitivity to anthropogenic impact
Potential size	Affects the amount of materials/energy fixed and the amounts of material respired (Bremner et al., 2006)	The number of smaller-sized individuals increases after disturbance (Townsend and Hildrew, 1994)
Protection	Affects the likelihood of consumption and transfer of productivity; affects $CaCO_3$ cycling by shell/exoskeleton production (Bremner et al., 2006)	Mortality risk due to disturbance (e.g. dredging) decreases with increased protection (e.g. for mussels; Kotta et al. 2009)
Sexual differentiation	Gonochorism might be associated with higher fitness (Prevedelli et al., 2006) and might consequently affect the amount of materials/energy fixed. Sexual differentiation is a proxy for turnover (Törnroos and Bonsdorff, 2012)	Hermaphroditism benefits from disturbance (Dolédec and Statzner, 2008)
Reproductive technique	Sexual reproduction is associated with increased niche width and thus with an increased resource base (Case and Taper, 1986)	Eggs are susceptible to damage due to disturbance (Bolam et al., 2016)
Larval type	Planktonic larval phase affects supply of production; moves carbon to the pelagos (Bremner et al., 2006)	Larval type is closely related to dispersal potential (planktotrophic = high, lecitotrophic = medium, direct = no dispersal potential); thus, the proportion of species with planktotrophic larvae increases after disturbance owing to a higher extinction risk of species with medium or no dispersal potential (McHugh and Fong, 2002)
Adult longevity	Affects the amount of materials/energy fixed and the amounts of material respired (Bremner et al., 2006)	The proportion of species with a short life span increases after disturbance (Pearson and Rosenberg, 1978)
Feeding habits	Deposit feeders disrupt sediments, resulting in increased oxygen concentrations; suspension feeding improves water clarity (Snelgrove, 1998 and references therein)	Organic enrichment supports deposit feeders and causes a decrease in suspension feeders (Pearson and Rosenberg, 1978)
Local habitat	Susceptibility to predators depends on local habitat (Törnroos and Bonsdorff, 2012)	The proportion of infaunal species increases after disturbance because their tubes/burrows provide shelter (Statzner and Bêche, 2010; van der Linden et al., 2016)

References associated with Table S3

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Table S4 Biological traits of benthic invertebrates used in this study and the respective fuzzy-coded trait modalities. Sex. diff. = sexual differentiation; Rep. tech. = reproductive technique. See Table 1 in the main article for modality codes.

	Morphology										**Reproduction**						
	Potential size						**Protection**				**Sex. diff.**		**Rep. tech.**		**Larval type**		
Species/Taxon	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**P0**	**P1**	**P2**	**P3**	**BH**	**BG**	**RA**	**RO**	**L0**	**LP**	**LL**
Amphibalanus improvisus	0	0	3	0	0	0	0	0	0	3	3	0	0	3	0	3	0
Apocorophium lacustre	0	3	0	0	0	0	0	3	3	0	0	3	0	3	3	0	0
Asellus (Asellus) aquaticus	0	0	3	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Balanus crenatus	0	0	0	3	0	0	0	0	0	3	3	0	0	3	0	3	0
Bathyporeia pilosa	0	3	0	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Bathyporeia sarsi	0	3	0	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Bithynia leachii	0	3	0	0	0	0	0	0	0	3	0	3	0	3	3	0	0
Bithynia tentaculata	0	0	3	0	0	0	0	0	0	3	0	3	0	3	3	0	0
Carcinus maenas	0	0	0	0	3	0	0	0	3	0	0	3	0	3	0	3	0
Cerastoderma edule	0	0	0	0	3	0	0	0	0	3	0	3	0	3	0	3	0
Chironomidae	3	3	3	1	0	0	3	0	0	0	0	3	0	3	0	3	0
Cirripedia	0	0	3	3	0	0	0	0	0	3	3	0	0	3	0	3	0
Corbicula fluminea	0	0	0	1	3	0	0	0	0	3	3	0	0	3	0	3	0
Cordylophora caspia	0	0	0	0	0	3	3	0	0	0	0	3	3	3	3	0	3
Corophium arenarium	0	3	0	0	0	0	0	3	3	0	0	3	0	3	3	0	0
Corophium volutator	0	3	0	0	0	0	0	3	3	0	0	3	0	3	3	0	0
Crangon crangon	0	0	0	0	0	3	0	0	3	0	0	3	0	3	0	3	0
Diastylis rathkei	0	3	0	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Dreissena polymorpha	0	0	0	3	1	0	0	0	0	3	1	3	0	3	0	3	0
Einhornia crustulenta	0	0	0	3	0	0	3	0	0	0	3	0	0	3	0	0	3
Electra pilosa	0	0	0	0	3	0	3	0	0	0	3	0	0	3	0	0	3
Ensis ensis	0	0	0	0	0	3	0	0	0	3	0	3	0	3	0	3	0
Eriocheir sinensis	0	0	0	0	0	3	0	0	3	0	0	3	0	3	0	3	0
Euglesa casertana	3	0	0	0	0	0	0	0	0	3	3	0	0	3	3	0	0
Gammarus locusta	0	0	0	3	0	0	0	0	3	0	0	3	0	3	3	0	0
Gammarus salinus	0	0	0	3	0	0	0	0	3	0	0	3	0	3	3	0	0

Table S4 (continued)

	Development				**Feeding**			**Habitat**		
	Adult longevity				**Feeding habits**			**Living location**		
Species/Taxon	**A1**	**A2**	**A3**	**A4**	**FP**	**FS**	**FD**	**HP**	**HE**	**HI**
Amphibalanus improvisus	0	0	3	0	0	3	0	0	3	0
Apocorophium lacustre	0	3	0	0	0	0	3	0	0	3
Asellus (Asellus) aquaticus	3	1	0	0	0	0	3	0	3	0
Balanus crenatus	0	0	3	0	0	3	0	0	3	0
Bathyporeia pilosa	3	0	0	0	0	0	3	0	1	2
Bathyporeia sarsi	3	0	0	0	0	0	3	0	1	2
Bithynia leachii	2	2	0	0	0	2	1	0	3	1
Bithynia tentaculata	1	3	1	0	0	2	1	0	3	1
Carcinus maenas	0	0	0	3	3	1	1	0	3	0
Cerastoderma edule	0	0	0	3	0	3	0	0	0	3
Chironomidae	3	0	0	0	1	1	3	0	1	3
Cirripedia	0	0	3	0	0	3	0	0	3	0
Corbicula fluminea	0	0	3	0	0	3	1	0	0	3
Cordylophora caspia	3	0	0	0	3	0	0	0	3	0
Corophium arenarium	0	3	0	0	0	1	3	0	0	3
Corophium volutator	0	3	0	0	0	1	3	0	0	3
Crangon crangon	0	0	3	0	3	1	1	0	3	0
Diastylis rathkei	3	0	3	0	0	0	3	1	1	3
Dreissena polymorpha	0	0	3	0	0	3	0	0	3	0
Einhornia crustulenta	0	0	3	0	0	3	0	0	3	0
Electra pilosa	0	0	3	0	0	3	0	0	3	0
Ensis ensis	0	0	0	3	0	3	0	0	0	3
Eriocheir sinensis	0	0	3	0	3	1	1	0	3	1
Euglesa casertana	0	0	3	0	0	3	0	0	1	3
Gammarus locusta	3	0	0	0	0	0	3	0	3	0
Gammarus salinus	3	0	0	0	0	0	3	0	3	0

Table S4 (continued)

	Morphology										**Reproduction**						
	Potential size						**Protection**				**Sex. diff.**		**Rep. tech.**		**Larval type**		
Species/Taxon	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**P0**	**P1**	**P2**	**P3**	**BH**	**BG**	**RA**	**RO**	**L0**	**LP**	**LL**
Gammarus tigrinus	0	0	3	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Gammarus zaddachi	0	0	0	3	0	0	0	0	3	0	0	3	0	3	3	0	0
Limecola balthica	0	0	0	3	0	0	0	0	0	3	0	3	0	3	0	3	0
Mesopodopsis slabberi	0	0	3	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Microprotopus maculatus	3	0	0	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Mya arenaria	0	0	0	0	0	3	0	0	0	3	0	3	0	3	0	3	0
Mytilus edulis	0	0	0	0	0	3	0	0	0	3	0	3	0	3	0	3	0
Nemertea	0	0	0	0	0	3	3	0	0	0	0	3	0	3	2	2	2
Neomysis integer	0	0	3	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Parapleustes bicuspis	0	0	3	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Peringia ulvae	3	0	0	0	0	0	0	0	0	3	0	3	0	3	0	3	3
Physa fontinalis	0	0	3	0	0	0	0	0	0	3	3	0	0	3	3	0	0
Pisidium amnicum	0	3	0	0	0	0	0	0	0	3	3	0	0	3	3	0	0
Pisidium moitessierianum	3	0	0	0	0	0	0	0	0	3	3	0	0	3	3	0	0
Pisidium obtusale	3	0	0	0	0	0	0	0	0	3	3	0	0	3	3	0	0
Pseudocuma longicorne	3	0	0	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Radix labiata	0	0	3	0	0	0	0	0	0	3	3	0	0	3	3	0	0
Rhithropanopeus harrisii	0	0	3	0	0	0	0	0	3	0	0	3	0	3	0	3	0
Schistomysis ornata	0	0	3	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Schistomysis spiritus	0	0	3	0	0	0	0	0	3	0	0	3	0	3	3	0	0
Sphaerium corneum	0	0	3	0	0	0	0	0	0	3	3	0	0	3	3	0	0
Sphaerium rivicola	0	0	0	3	0	0	0	0	0	3	3	0	0	3	3	0	0
Sphaerium sp.	0	0	3	1	0	0	0	0	0	3	3	0	0	3	0	3	0
Sphaerium striatinum	0	0	3	1	0	0	0	0	0	3	3	0	0	3	3	0	0
Stagnicola palustris	0	0	3	0	0	0	0	0	0	3	3	0	0	3	3	0	0
Valvata piscinalis	0	3	0	0	0	0	0	0	0	3	3	0	0	3	3	0	0

Table S4 (continued)

	Development				**Feeding**			**Habitat**		
	Adult longevity				**Feeding habits**			**Living location**		
Species/Taxon	**A1**	**A2**	**A3**	**A4**	**FP**	**FS**	**FD**	**HP**	**HE**	**HI**
Gammarus tigrinus	3	0	0	0	0	0	3	0	3	0
Gammarus zaddachi	3	0	0	0	0	0	3	0	3	0
Limecola balthica	0	0	0	3	0	3	3	0	0	3
Mesopodopsis slabberi	3	0	0	0	3	3	0	0	3	0
Microprotopus maculatus	2	2	0	0	0	0	3	0	2	2
Mya arenaria	0	0	0	3	0	3	3	0	0	3
Mytilus edulis	0	0	0	3	0	3	0	0	3	0
Nemertea	0	3	0	0	3	0	0	0	3	0
Neomysis integer	3	0	0	0	3	3	0	0	3	0
Parapleustes bicuspis	2	2	0	0	0	0	3	0	2	2
Peringia ulvae	0	3	0	0	0	0	3	0	3	0
Physa fontinalis	0	3	0	0	0	0	3	1	3	0
Pisidium amnicum	0	0	3	0	0	3	0	0	1	3
Pisidium moitessierianum	0	0	3	0	0	3	0	0	1	3
Pisidium obtusale	0	0	3	0	0	3	0	0	1	3
Pseudocuma longicorne	0	3	0	0	0	0	3	1	1	3
Radix labiata	2	3	0	0	0	0	3	1	3	0
Rhithropanopeus harrisii	0	3	0	0	3	0	0	0	3	0
Schistomysis ornata	3	0	0	0	3	3	0	0	3	0
Schistomysis spiritus	3	0	0	0	3	3	0	0	3	0
Sphaerium corneum	1	3	0	0	0	3	0	0	0	3
Sphaerium rivicola	1	3	0	0	0	3	0	0	0	3
Sphaerium sp.	1	3	0	0	0	3	0	0	0	3
Sphaerium striatinum	1	3	0	0	0	3	0	0	0	3
Stagnicola palustris	3	0	0	0	0	0	3	0	3	0
Valvata piscinalis	2	2	0	0	0	2	2	0	2	3

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Table S5 Species list of benthic invertebrates used in this study.

	1889	1985	1986	2006
BIVALVIA				
Cerastoderma edule		x		
Corbicula fluminea				x
Dreissena polymorpha	x			
Ensis ensis		x		
Euglesa casertana				x
Limecola balthica	x	x	x	
Mya arenaria	x			x
Mytilus edulis	x	x	x	x
Pisidium amnicum	x			
Pisidium moitessierianum				x
Pisidium obtusale	x			
Sphaerium corneum	x			
Sphaerium rivicola	x			
Sphaerium sp.		x		
Sphaerium striatinum	x			
GASTROPODA				
Bithynia leachii	x			
Bithynia tentaculata	x			
Peringia ulvae	x	x	x	x
Physa fontinalis	x			
Radix labiata	x			
Stagnicola palustris	x			
Valvata piscinalis	x			
GYMNOLAEMATA				
Einhornia crustulenta				x
Electra pilosa	x			
HYDROZOA				
Cordylophora caspia	x			x

	1889	1985	1986	2006
MALACOSTRACA				
Apocorophium lacustre				x
Asellus (Asellus) aquaticus			x	
Bathyporeia pilosa	x	x	x	x
Bathyporeia sarsi				x
Carcinus maenas				x
Corophium arenarium				x
Corophium volutator	x	x	x	x
Crangon crangon	x	x	x	x
Diastylis rathkei			x	
Eriocheir sinensis		x		x
Gammarus locusta	x			
Gammarus salinus				x
Gammarus tigrinus				x
Gammarus zaddachi		x	x	
Mesopodopsis slabberi		x		x
Microprotopus maculatus				x
Neomysis integer	x	x	x	x
Parapleustes bicuspis				x
Pseudocuma longicorne				x
Rhithropanopeus harrisii				x
Schistomysis ornata	x			
Schistomysis spiritus		x		
MAXILLOPODA				
Amphibalanus improvisus				x
Balanus crenatus	x			
OTHERS				
Cirripedia		x		
Nemertea				x
Chironomidae	x	x	x	x

8 Discussion and perspectives

In three studies conducted within the Elbe Estuary, I tested whether the Venice System and the zonation method of Bulger et al. (1993) can be applied in this estuary (study 1), investigated the importance of food competition within the benthos of the estuarine MTZ (study 2), and analyzed how taxonomic and functional aspects of the benthic community changed over more than a century (study 3). With these studies, I aimed at improving our understanding of estuarine benthic ecology and to provide support for management and conservation decisions.

The results of study 1 showed that salinity variation rather than mean salinity determined the distribution of benthic invertebrates in the central part of the estuary (and thus also within the MTZ). As the Venice System boundaries were only valid at both ends of the estuary, where salinity variation is low, and the boundaries derived from the method proposed by Bulger et al. (1993) differed greatly from those of cluster analysis, neither the Venice System nor the method proposed by Bulger et al. (1993) are applicable for determining the salinity zones in poikilohaline estuaries. The main reason for this is that these two methods were developed for homoiohaline waters, which have relatively stable isohalines. Moreover, the following methodological constraints make the results of these two methods questionable. In the mixohaline part, the Venice System defines three subzones, namely the oligohaline, mesohaline, and polyhaline zone. This subdivision goes back to Naumann (1921), who proposed to divide aquatic systems into three zones and introduced the terms ‘oligo’, ‘meso’ and ‘poly’ to aquatic science. However, this a priori tripartition is purely arbitrary and has no scientific basis. The system introduced by Bulger et al. (1993) suffers from methodological restrictions. It uses only presence/absence data instead of species abundances and is based on a principal component analysis (PCA), which is a method known to have some important constraints. PCA requires some haphazard decisions, e.g., how many components to keep and the choice of the cut-off for the loadings. Moreover, PCA analyses tend to show an artifact called the ‘horseshoe effect’; if this artifact is present, the PCA results are invalid. Instead, I found that the similarity profile routine (SIMPROF; Clarke et al., 2008), which finds subgroups that differ significantly based on hierarchical cluster analysis, is suitable for defining salinity zones in the poikilohaline Elbe Estuary based on macroinvertebrate occurrences. In contrast to SIMPROF, the Venice System and the method proposed by Bulger et al. (1993) always result in distinct zones along the longitudinal gradient and thus must fail in revealing the recurring communities in the Elbe Estuary. Zones derived with SIMPROF could be implemented in the European Water Framework Directive, but owing to large environmental and biotic differences between estuaries, methods for determining the zones should ideally be derived for each estuary individually. It is important to consider that estuarine systems are also highly variable in space and time, and this variability is reflected in the location of zone boundaries. Hence, distribution patterns of organisms in estuaries can be regarded as a continuum (Elliott and McLusky, 2002), and zone boundaries within estuaries could be viewed as not being very sharp and as expanded regions where changes are accelerated (Boesch, 1977).

Although it is thought that salinity is the main environmental factor responsible for the distribution of biota within estuaries (Basset et al., 2012; Telesh and Khlebovich, 2010), other variables also determine whether a species persists or fails in a given environment. Because of this, future methods for determining zones in lotic waters with longitudinal changing salinity could be improved by incorporating more than a single factor, i.e., not only salinity, as it is usually done. Especially grain size, which differs significantly within the Elbe Estuary (Taupp and Wetzel, 2013), is generally closely related to the occurrence of soft-sediment organisms (Anderson, 2008). I showed this for selected benthic species in the Elbe Estuary in study 2.

The results of the stable isotope analysis in study 2 in the MTZ of the Elbe Estuary showed that the isotopic niches of no two benthic taxa within each of the two feeding groups ‘deposit feeders’ and ‘predators’ overlapped. This indicates that taxa within each feeding group used different resources and that competition for food is negligible in the MTZ. Distinct isotopic niche space might occur for several reasons. First, resource competition might have been stronger in the past, leading to the divergence of feeding niches during evolution. Second, taxa used different habitats (e.g., habitats with different grain sizes) that provide isotopically different food sources. In the case of the highly mobile decapods, distinct niche space is most likely due to their migrating behavior. The results of study 2 also support the validity of the stress gradient hypothesis within the MTZ of the Elbe Estuary assuming that populations are kept below carrying capacity due to stress. The stress gradient hypothesis might also be valid for the entire estuary because the estuary as a whole can be regarded as a stressful environment (Elliott and McLusky, 2002). However, the results of stable isotope analysis of the MTZ cannot simply be transferred to other regions of the estuary because of both the pronounced environmental gradients and the significantly different communities that were identified in study 1. Since the trophic relationships within the rest of the estuary have not yet been studied, the degree of food competition in these reaches is unknown, and thus additional studies are urgently needed to understand how assemblages are structured and how ecosystems function (May, 2006; Polis et al., 1997). These studies should ideally incorporate multiple trophic levels of benthic invertebrates and higher trophic levels, such as fish, birds, and seals, and also consider all relevant resources, such as plankton and sediment organic matter. The results of study 1 indicated that at least four taxonomically significantly different communities exist in the Elbe Estuary, and thus, at least four food webs should be described and analyzed. Although the benthic assemblages in the two stretches upstream and downstream of the MTZ did not significantly differ, as shown in study 1, it seems preferable to investigate whether and how the food webs in these two regions differ. However, stable isotope analysis studies of the entire estuary would be both expensive and time consuming; consequently, alternative approaches should be considered. For instance, Gray et al. (2015) recently proposed a method to generate food webs automatically based on taxonomic lists and data of trophic interactions. An extensive dataset of trophic interactions is provided by the authors, but unfortunately only for freshwater species. However, data for estuarine taxa could be determined by analysis of stable isotopes or gut contents or both (cf. Jardine et al., 2005) and be used as a data pool for further studies.

Study 3 clearly showed that both taxonomic changes and functional changes can occur in benthic assemblages if long time spans are considered. All taxonomical and functional parameters were at their worst in 1985 and 1986. The loss of functions from 1889 to 1985/1986 was non-random and thus due to habitat filtering. The benthic community in 1889 significantly differed from that in 2006 owing to species replacement. Most striking was the decline in gastropods, which were nearly extinct in 2006, most likely due to elevated concentrations of the endocrine-disrupting anti-fouling organo-tin compound tributyl tin (TBT). Despite the significant change in species composition, functional features provided by the benthic invertebrates in 1889 were almost re-established in 2006, which indicated that high functional richness promoted ecosystem stability and resilience.

The necessity and importance of long-term data analyses for providing baselines, evaluating changes in communities, and finding appropriate management measures has long been known (Lindenmayer and Likens, 2009; Magnuson, 1990). However, data older than a few decades are often not available, not easy to access, or suffer from inadequate methods or study designs that did not allow statistical analysis. It is the crux of the matter that anthropogenic impacts climaxed just when sufficient data were lacking. But with increasing environmental awareness and implementation of environmental legislations, such as the European Water Framework Directive (European Parliament, 2000), we need to define reference conditions of waters, which ideally should reflect the most natural state, to assess the ecological quality status (EQS) of the respective waterbody. Today, there is still much debate about how to set up reference conditions since we have no knowledge of the pristine conditions of any lotic water in Europe (Borja et al., 2012; Muxika et al., 2007). Searching, preparing, and using historical data, such as the data from 1889 used in study 3, is a meaningful approach to bring this issue forward (Muxika et al., 2007).

The results of my studies can also support the development of EQS metrics. EQS assessment tools often fail to assess the ecological status in estuaries. This is, among other reasons, because these environments exhibit both pronounced natural environmental gradients and anthropogenic alterations, which make it difficult to distinguish between the two (Elliott and Quintino, 2007; Rakocinski et al., 1997). In the Elbe Estuary, the EQS is currently determined using two different approaches, depending on the water body type. In water body types T1/T2 (transitional waters) and N1 to N4 (marine waters), the M-AMBI (Multivariate Azti Marine Biotic Index; Muxika et al., 2007) is used. It was initially developed for marine waters, and the results obtained with this index in zones with low salinity are usually not reliable because many freshwater species are missing in its species list (Taupp and Wetzel, 2013). In water body types 20 (sand-dominated streams) and 22.3 (marshland streams), where salinity is lower, the AeTI (Aestuar Typie Index) (Krieg, 2005) is usually applied. It has been proposed that AeTI be generally applied in the Elbe Estuary independent of the water body type (Krieg, 2006). The AeTI calculation places great importance on the oligochaete fauna, which is absent in regions with higher salinity, and consequently, the reliability of the results obtained wit this index, at least in the outer regions of estuaries, are questionable. M-AMBI and AeTI use species number, diversity, and a species-specific measure of sensitivity to derive the EQS. In other European countries, other metrics have been developed for estuaries, and many efforts have been made to compare them, to find the best one, and to identify unfit ones (e.g., Borja and Dauer, 2008; Dauvin and Ruellet, 2007; Nebra et al., 2014). The debates about how to assess the EQS in European estuaries could be brought forward if estuaries are no longer considered as entities, as it is done in the European Water Framework Directive (therein referred to as transitional waters). The term ‘transitional’ already implies large differences and variations and contradicts the idea of a unity. Instead, in a first step, significantly differing communities could be identified as in study 1 using taxonomic and/or functional dissimilarity. Subsequently, EQS metrics could be developed, adjusted, and tested within each estuarine zone separately to account for the extremely different assemblages within this highly variable environment (cf. study 1). In the second step, these metrics should include functional aspects, e.g., functional diversity (cf. study 3), instead of (or additionally to) taxonomic diversity. It can be expected that this approach would improve the validity of the EQS results significantly because it considers and represents ecological relationships more accurately. This would possibly require updating the European Water Framework Directive; changes in the directive should not be fundamentally problematic because it has been generally recognized that functional aspects (i.e., the traits of organisms) should be incorporated in ecological analyses (Villéger et al., 2010).

Trait data, which are necessary for every study related to functional aspects, of many estuarine and marine benthic invertebrates are still unknown, incomplete, or simply not published (Tyler et al., 2012). The online database MarLIN (2006) tries to fill this gap, but, although continuously improved (Costello et al., 2015), is much more incomplete than comparable databases of freshwater species (e.g., Schmidt-Kloiber and Hering, 2015; Tachet et al., 1996). In estuaries, species feeding traits can vary spatially depending on the habitat and thus can differ from data provided in the literature or online databases, as for instance shown in study 2. In this case, stable isotope analysis can help to identify feeding-related traits of benthic invertebrates that can subsequently be used in functional ecology studies.

In a rapidly changing world, life in lotic waters also changes quickly, and consequently, the validity of the results of ecological studies, including those of studies 1-3 of this thesis, can be limited in time and has to be checked regularly. This is due to several reasons. For instance, global climate change is linked with increasing temperatures, increasing global mean sea levels, changing precipitation regimes (Domisch et al., 2013; Robins et al., 2016), and an increasing frequency of extreme events, such as floods, droughts, and heat waves (IPCC, 2007). Such events alter estuarine benthic communities (Grilo et al., 2011), food webs and trophic interactions (e.g. Ledger et al., 2012; Woodward et al., 2012), trait composition of assemblages (Poff et al., 2010), and ecosystem functioning (Meyer et al., 1999). Global climate change also supports the introduction of non-indigenous species (Occhipinti-Ambrogi, 2007). In German estuaries, the number of alien macrobenthic species already comprises about 20% of the species, which clearly indicates significant alterations in native assemblages (Nehring et al., 2005). The establishment of non-indigenous species is supported if ecological niches become unoccupied, e.g., owing to species loss as a result of environmental changes (cf. studies 2 and 3). International shipping is assumed to be the most important introduction vector of non-indigenous species in Germany (Nehring et al., 2005), and this is particularly relevant for the Elbe Estuary, which is an intensively used waterway to the Port of Hamburg - the most important transshipment port for Middle and Eastern Europe and the Baltic States in Northern Europe (Boehlich and Strotmann, 2008).

Finally, estuarine ecosystem research is of great importance for our society and offers a large number of exciting possibilities for future studies. Unfortunately, the number of studies of estuarine ecosystems is still lower than those of freshwater and marine ecosystems. Thus, enhancing our understanding of estuarine ecology remains an important, promising, and challenging task for the future. I hope that I, with my dissertation, have made a small but valuable contribution to a better understanding of this fascinating ecosystem.

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