

Can monitoring data contribute to the biodiversity-ecosystem function debate? Evaluating data from a highly dynamic ecosystem

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Abstract One of the most controversially discussed topics in current biodiversity-ecosystem function research is the transfer of results from experimental and theoretical studies to natural ecosystems. At the same time, monitoring data on biodiversity are requested as key indicators for the state of an ecosystem in most environmental evaluation frameworks. We analyse two monitoring data sets comprising information on abundance and biomass of macrozoobenthos communities in the German Wadden Sea in order to evaluate how much information monitoring data on biodiversity provide concerning ecosystem functioning and what implications this information (or the lack thereof) has for future monitoring programmes. Our results show a positive correlation between number of species of macrozoobenthos and its standing stock. Despite differences in overall biomass and individual size in different functional groups, this correlation remained consistent for different feeding guilds and therefore is likely to be independent of certain species traits. Moreover, functional turnover analyses indicate that increasing species richness is needed to maintain biomass levels over increasing periods of time. Whereas our data thus corroborate predictions from theory, we could not determine any causal relationships, because monitoring data commonly include only vague proxies for very few functional parameters, in our case standing biomass as a proxy for production. As to the use of diversity as an indicator for ecosystem functioning, we advise that management decisions are to be based on verified

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causal relationships and therefore strongly suggest the general incorporation of unambiguous proxies for functional parameters in the measuring campaigns of monitoring programmes.

Keywords Functional turnover · Ecosystem stability · Tidal flat · Species richness · Evenness · Functional diversity

Introduction

The assessment and evaluation of the state of an ecosystem continues to be one of the most important topics in ecology, as we currently face a new high in species extinction rates and habitat degradation. Most conservation programmes have been developed and implemented with the intention to maintain species richness levels, based on the assumption that high species richness is positively correlated with the functioning of an ecosystem, or more precisely with the rates of ecosystem processes. Therefore, species richness is one of the fundamental parameters to be recorded in almost all monitoring and environmental assessment schemes. It serves as a proxy for biodiversity, which itself is used as an indicator for the ecological status of an ecosystem. As such, it is a requested variable in many international assessment programmes (European Union: Water Framework Directive, Birds Directive, Habitat Directive, UNEP: United Nations Environmental Program). However, the question whether high species numbers are generally related to high process rates is still far from being solved. In fact, the possibility of a link between biodiversity and the rate and stability of ecosystem processes has been a controversially discussed topic in the fields of ecosystem and community ecology for several decades (Loreau 2010). Although it has given rise to well established theoretical constructs like niche theory (Hutchinson 1957, 1961) and concepts such as the complementarity effect (Tilman et al. 2001) and sampling effect (Aarssen 1997; Huston 1997), the biodiversity-ecosystem functioning (BEF) debate has not lost any of its momentum. Mainly experimental studies have been conducted in search of general patterns and the majority of them do indicate a positive effect of increasing biodiversity levels on ecosystem processes and services. Nonetheless, a generalisation across ecosystem types, properties or trophic, functional and organisational levels has been stated as not recommendable according to a number of meta-analyses (Gross and Cardinale 2005; Balvanera et al. 2006; Cardinale et al. 2006). Albeit, the inconsistent outcomes could be the result of limitations of the experimental character of these studies, such as limited duration times, highly controlled and simplified experimental setups or the fact that most studies focus on only one ecosystem function or service (Stachowicz et al. 2008; Duffy 2009). Several recent studies have underlined the importance of high diversity levels for the maintenance of multiple processes (Hector and Bagchi 2007; Gamfeldt and Hillebrand 2008; Zavaleta et al. 2010) and in the presence of temporal and spatial variation (Isbell et al. 2011). Hillebrand and Matthiessen (2009) and Duffy (2009) even suggest that many experiments might in fact underestimate the importance of biodiversity for ecosystem functioning in natural ecosystems.

The detection of causal pathways in natural systems presents a number of challenges due to our limited ability to control for the many interacting components that contribute to the complex pattern of BEF relationships. This is especially true for highly dynamic ecosystems where variable environmental conditions complicate the quantification of the

respective contribution of species diversity, composition and local environmental conditions to ecosystem functioning (O'Connor and Donohue 2013). It is therefore not surprising that only very few studies have extended the inference from experimental to natural systems (Essink et al. 1998; Grace et al. 2007; Tylianakis et al. 2008; Cardinale et al. 2009) and that their results do not yet allow to generalise the validity of a positive link between biodiversity and ecosystem functioning to natural ecosystems.

In marine systems the almost complete lack of functional parameters as part of common monitoring campaigns is one of the most profound reasons for the small number of studies dealing with BEF relationships in natural systems. Hence, there is a need to evaluate the information content of currently collected monitoring data.

Here, we present a first step to assess whether monitoring data can contribute to the discussion concerning the effect of biodiversity on ecosystem functioning and if the entailed information is sufficient to justify the use of biodiversity as an indicator for highly variable ecosystems like tidal flats. In a case study, we employ two typical monitoring data sets from the German Wadden Sea and test for existing relationships between measures of structure (biodiversity) and function (biomass). Further, we discuss which efforts are needed to successfully incorporate findings from experimental and theoretical BEF research into ecosystem monitoring programmes.

Materials and methods

Data

We analysed two data sets from the German Wadden Sea. Both were provided by the Lower Saxony Water Management, Coastal Defence and Nature Conservation Agency and the National Park “Niedersächsisches Wattenmeer”. The first data set was collected as part of several measuring campaigns (German Marine Monitoring Program (BLMP), Trilateral Monitoring and Assessment Program (TMAP), Joint Assessment and Monitoring Program (JAMP)) and is in its temporal extent unique for the German part of the Wadden Sea. Samples were taken at eight permanent sampling stations (MZB1–MZB8, Fig. 1a) along a north–south oriented transect between the Frisian island of Norderney and the German mainland. All sampling stations are located in the eulittoral zone. Station MZB4 and MZB5 are separated by one of the three big tidal drainage channels. The four stations on the island side of the channel are located higher (MZB1: 0.407 m, MZB2: 0.271 m, MZB3: 0.025 m, MZB4: –0.182 m) than the stations south of the channel (MZB5: –1.018 m, MZB6: –0.749 m, MZB7: –0.552 m, MZB8: –0.147 m). Height above sea level increases from the channel towards the island/mainland. Station MZB6 and MZB7 differ from the other stations in that they are located in a mussel bed area, where samples of MZB6 are always taken from within the mussel patches and samples for MZB7 are taken from the sediment between patches. Therefore they represent two different community assemblages despite their proximity. The data set comprises abundance and biomass values of macrozoobenthos communities over a 14 year time series between 1999 and 2012. Out of the eight stations, the four closest to Norderney were sampled four times a year (usually in January, March/April, June/July and September/October) from 1999 to 2006. Station MZB4 was not visited again after 2006. For the other years and stations sampling was carried out twice (usually in March/April and September/October) a year, resulting in a total of 268 unique samples. For each sampling occasion 10 sampling cylinders with an area of 181.46 cm² each (sampled area in total 0.181 m²) and length of 30 cm were

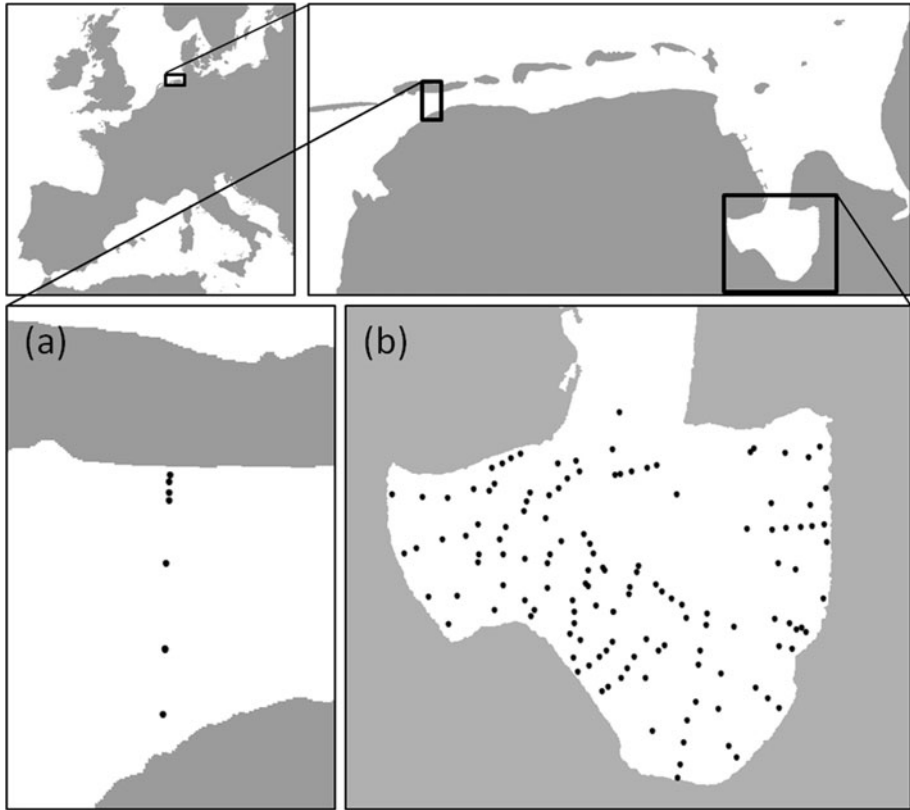


Fig. 1 Map of the two sampling areas Norderney (a) and Jade Bay (b) in northwest Germany

extracted from the upper sediment layer. Former studies indicate that 10 cylinders with a total area of 0.177 m^2 and a respective volume of 0.0531 m^3 are sufficient for obtaining a representative sample of the local species community (Hanslik 2002). For *Arenicola marina* a technique of throwing a sieve in a random direction and counting the number of faeces underneath the sieve was used for the derivation of the number of present specimens. *A. marina* burrows down to 45 cm which is out of the scope of the sampling cylinders and would therefore lead to an underrepresentation of this species. Two more species with similar burrowing depth, *Mya arenaria* and *Ensis dirctus*, do not have big enough siphon openings for this method to be feasible.

All species were counted and identified to species level if possible. For the determination of ash free dry weight (AFDW) the biomass of each species was first dried at $70 \text{ }^\circ\text{C}$ for 48 h and then reduced to ashes at $485 \text{ }^\circ\text{C}$ for 4 h. Species belonging to crustaceans, gastropoda and polyplacophora were reduced to ashes at $385 \text{ }^\circ\text{C}$.

In addition to the species data, up to ten environmental parameters were recorded for each sample (water content, loss on ignition, carbon content, total organic matter, water temperature, air and sediment temperature, pore water salinity and pH and sediment grain size distribution, see Online Resource 1 for further information).

The second data set consists of 135 samples from the intertidal flats of the Jade Bay inlet (Michaelis 1987). The measurements were taken in 1976 and 1977. This data set comprises

samples from eulittoral as well as sublittoral areas. Depending on biotope and sediment type and the according organism densities the sampling area was adjusted varying between 0.011 and 0.768 m² across samples. Mesh sizes of 1 or 0.6 mm were used for mixed sediment samples, respectively samples with high mud contents. Each sampling site was only visited once. Like the first data set this one includes abundance data for each species, but no information on species specific biomass or additional ecosystem functions (which is common practice for benthos monitoring programmes). Therefore, we calculated individual biomass values by dividing the species-specific biomass by the number of individuals for each species and sampling occasion in the Norderney data. The median of these values was then taken as average individual biomass of a specimen of the according Jade Bay species (Online Resource 2). Given the close spatial proximity, this transfer of information is valid. For species that were only present in the Jade Bay data we used conversion factors from other monitoring studies (I. Kröncke, pers. Comm.).

We defined local diversity to be represented by the species community composition at each individual site. We consider the distance between sampling stations to be large enough (100 m or more) in order to interpret each station as a separate location. Only the mussel bed stations MZB6 and MZB7 of the Norderney data set are located relatively close to each other, but represent two distinct communities on and between the mussel patches.

Data analysis

All data analysis steps were performed in the statistics environment R 2.11.1 (R Development Core Team 2010), applying functions from the packages *vegan*, *MASS* and *mgcv*. In order to ensure that the collected samples did in fact represent the local species diversity we evaluated species accumulation and rarefaction curves for the three sampling stations closest to Norderney. For the remaining stations we only had measurements that had been aggregated over the ten sampling cylinders impeding this kind of analysis. However, all obtained curves showed the anticipated convex shape and clearly leveled off with increasing number of samples supporting former studies (Hanslik 2002) in that 10 sampling cylinders of this size represent a sufficient sampling effort for assessing local species diversity in this tidal flat ecosystem.

Neither of the data sets included direct measurements on secondary production. Therefore, we used standing stock (measured as ash free dry weight) as proxy for community productivity. We also converted these biomass values into secondary production estimates applying an empirically derived estimation method (Schwinghamer et al. 1986). We performed all data analysis steps on the converted data, but none of the results changed to a noteworthy degree, which is why we present the results based on the original data.

For the statistical analysis of the relationship between diversity, represented by the number of species, and the total standing stock at a site we applied Spearman's rank correlation coefficient. Due to the long intervals between sampling occasions compared to the rather short generation times of most benthic invertebrates, which together with the system-inherent variability results in highly fluctuating biomass and abundance values, autocorrelation was unlikely. Time series and lagged scatterplots showed no signs of correlation within the time series of each station, so we did not account for autocorrelation in the following data analysis.

As the stations of the Jade Bay data set were only sampled once, we only used these data for the correlation and regression analyses assessing the relationship between species richness (and evenness), respectively species richness of each functional group, and

biomass production. All other analyses requiring environmental parameters or time series data were applied to the Norderney data only.

We used linear regression for an analysis of variance assessing the effects of three categorical variables year, season (calendric) and sampling station and four continuous variables species richness, <63 μm grain size fraction, total organic carbon (TOC) and sediment temperature on standing stock levels. As the ash free dry weight measurements spanned several orders of magnitude we log-transformed the data for it to meet the homoscedasticity assumptions of the linear regression model. For model comparison and selection we used Akaike's information criterion [AIC (Johnson and Omland 2004)] which is implemented in the `step()` command in R. For this analysis, the data set was reduced to a sample size of 138, due to the necessary exclusion of samples with missing values.

Correlation and regression analyses were also performed when assessing the relationship between diversity indices (Simpson Index, Shannon Index) or evenness measures (Pielou's Evenness Index) and the standing stock values.

For functional classification each species was assigned to one of three functional groups according to their preferred feeding type since this is meant to be the most meaningful way of distinguishing functional traits in macrozoobenthos (Bonsdorff and Pearson 1999). We mainly used the online data base WoRMS (World Register of Marine Species, <http://www.marinespecies.org/>) as a reference for the classification. The three functional groups were (i) deposit feeders and grazers, (ii) predators and (iii) suspension or filter feeders. Out of the total 127 species found at the Norderney stations we assigned 55 species to deposit feeders and grazers, 40 species were assigned to the group of predatory species and 19 species were classified as suspension feeders. For 13 species we did not find any information in the available literature to assign them to one of the groups. In the Jade Bay data set 28 species were classified as deposit feeders, 18 species as predators and eight species were assigned to the group of suspension feeders. For this data set 18 species could not be classified due to missing information concerning their feeding behaviour (For information on individual species please see Online Resource 2). The unclassified species were excluded from the analysis relating functional diversity to biomass production in each functional group, but included in all other analyses.

In order to test relationships between biodiversity and the stability of standing stock levels, we used the temporal coefficient of variance, dividing the standard deviation by the mean of standing stock measures over time:

$$CV = \frac{\text{std}}{\text{mean}}.$$

The coefficient of variance is only one of a multitude of community stability aspects (Donohue et al. 2013), but is a simple metric which could be derived in many monitoring programmes.

Based on functional turnover analyses in previous studies (Isbell et al. 2011; Allan et al. 2011) we calculated S_{min} as the minimum number of species necessary to sustain a level of 50 % of the ecosystem function of interest, in this case standing stock. We used this analysis to answer the question whether the same dominant species are able to sustain local standing stock levels over time or whether the identity of the contributing species changes.

To further evaluate the extent of species turnover in the data set, we used Jaccard's similarity index, which measures the proportion of species that are common between sampling sites or sampling occasions (Jaccard 1912; Koleff et al. 2003). We applied its complement (Jaccard distance) as a measure of dissimilarity between species composition over time, thus comparing samples from one site but different time points. Increasing the

time intervals between the two sampling occasions we obtained temporal species turnover rates (STR).

$$\text{STR} = 1 - \frac{a}{\alpha_1 + \alpha_2 + a},$$

where a is the number of species present at both sampling occasions, α_1 is the number of species only present at the first sampling occasion and α_2 is the number of species only present at the second sampling occasion (Jaccard 1912). Jaccard's distance can take values from zero to one. One represents complete dissimilarity of the two samples, zero signifies that both samples contain the same species. The median values of the species turnover rates for all possible time intervals of a given length between 1 and 10 years were then analysed in an ANOVA including interval length and sampling station as predicting variables.

Results

In total there were 127 species distinguished and identified in the Norderney data set, although five could only be identified to genus level. The Jade bay data set comprised 72 species. This rather big difference in species richness possibly results from the smaller sampled area in Jade Bay, as the probability of finding rare species increases with the number of samples (sampled area) at a station. Thirty-four species were recorded at both locations. This rather low congruence is likely to be a consequence of different sampling procedures (mesh size) and the higher number of habitats sampled in the Jade bay. The large time period between the two surveys will also play a role as Michaelis (1987) mentions significant compositional differences between these Jade Bay samples and others taken 30 years earlier.

The majority of the benthic invertebrate organisms found in the German Wadden Sea belong to the three phyla Annelida, Arthropoda and Mollusca. Species abundances and total biomass values per station fluctuate considerably within as well as between years and stations. The sampling station MZB6 is located on a mussel bed with therefore high population densities of mollusk as well as other species that settle on the structure provided by the mussels. Accordingly, biomass values at MZB6 were on average between 4 and 40 times higher than at the remaining stations. However, the results presented below remain qualitatively unchanged when MZB6 is not considered.

We found a positive correlation between the number of species at a site and standing stock levels for both data sets (Fig. 2a, b). Spearman's rank correlation coefficient for the Norderney data was 0.557, for the Jade Bay data set 0.528. When aggregating the data to annual means and mean values per station the positive correlation was still detectable despite only eight remaining data points.

The application of a stepwise selection procedure to the Norderney data set (species number, season, <63 μm grain size fraction, TOC, sediment temperature and sampling station) resulted in a final model with only three variables (sampling station, year and number of species). Any further reduction of the model resulted in increases of the AIC values >27 (Table 1). An analysis of variance confirmed that the three variables all contributed significantly ($p < 0.001$) to explaining the variation in the standing stock data ($\text{adj.}R^2 = 0.781$).

The data showed no correlation between the values of Simpson's Diversity and Shannon Index and standing stock. However, the Spearman correlation coefficients for evenness and standing stock values implied a weak negative relationship between increasingly even species

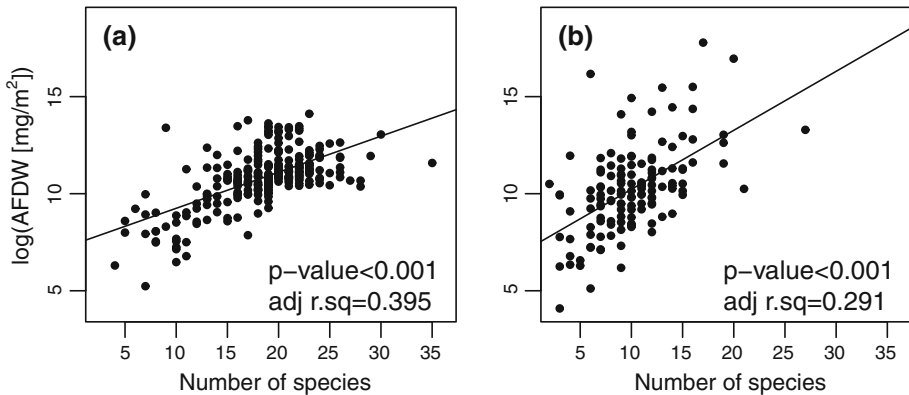


Fig. 2 Correlation of the local number of species **a, b** with the log-transformed biomass (ash free dry weight [AFDW]) for macrozoobenthos communities from Norderney and the Jade Bay

Table 1 ANOVA results of the final model

Dependent	Explanatory	df	Mean Sq	F	<i>p</i>	AIC	ΔAIC
Total biomass	Sampling station	7	28.9	57.5	<2.2e-16		
	Year	13	3.1	6.2	9.9e-09		
	Number of species	1	13.4	26.7	9.9e-07		
	Final model (all three variables)					-74.7	
	Variable species eliminated					-47.6	27.1
	Variable year eliminated					-45.2	29.5
	Variable sampling stations eliminated					38.0	112.7

Standing stock levels (measured as total biomass) are modelled as a function of the explanatory variables sampling station, year and species richness (number of species). ΔAIC is the difference in values of the Akaike Information Criterion (AIC) between the constrained models when eliminating one of the explanatory variables and the AIC of the final model

distributions (abundance as well as biomass) and total biomass at the sampling sites ($p = -0.23$, Norderney; $p = -0.38$, Jade bay). For the Norderney data, linear regression models showed a significant negative effect of evenness on standing stock values ($p = 0.0017$).

In accordance with these results, the allocation of all species to one of three functional groups (deposit feeder and grazer, predator, suspension feeder) revealed that individual biomass differed between the functional groups. Mean individual biomass and standard deviation were 0.014 ± 0.04 g for deposit feeders and grazers and very similar 0.011 ± 0.33 g for predators, whereas suspension feeders had a considerably higher mean individual biomass of 0.073 ± 0.12 g. Deposit feeders and grazers accounted on average for 28 % of total standing stock, predatory species only 4 % and suspensions feeders made up the main part of 68 % of the total standing stock. Nonetheless, with exception for predatory species in the Jade Bay, the same significantly positive relationship between increasing numbers of species and standing stock values is evident in each of the three functional groups as for the whole community (Fig. 3).

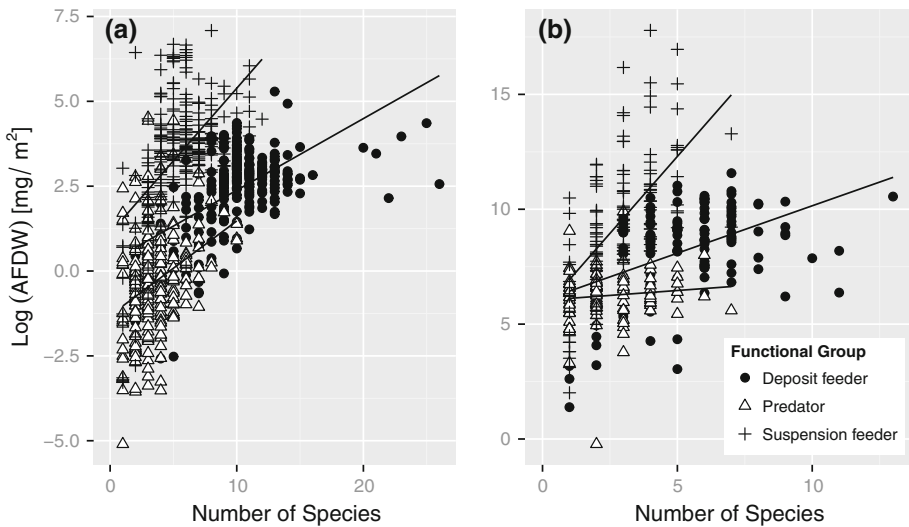


Fig. 3 Correlation of the local number of species within functional groups and the log-transformed biomass (ash free dry weight [AFDW]) for each of the groups. Except for predatory species in the Jade Bay all functional groups show significant positive relationships. **a** Norderney: Deposit feeders: p values <0.001 , adj. $R^2 = 0.321$, Predators: p values <0.001 , adj. $R^2 = 0.102$, Suspension feeders: p values <0.001 , adj. $R^2 = 0.284$; **b** Jade Bay: Deposit feeders: p values <0.001 , adj. $R^2 = 0.205$, Predators: p values = 0.293, adj. $R^2 = 0.001$, Suspension feeders: p values <0.001 , adj. $R^2 = 0.356$

The biomass contribution calculated for each species revealed that the major part of the amount of biomass found at a site depends on the contribution of a rather small group of species. On average the biomass of only one to three species amounted to 50 % of the total biomass measured at a site. A considerable increase in the number of species contributing to standing stock levels only occurred for values above 80 % of the total standing stock. These results were consistent across all stations regardless of species richness levels or total standing stock values. The identity of species contributing dominantly to biomass is available in the Online Resource 3. Apart from mollusk species such as *Cerastoderma edule* and *Macoma balthica*, species like *Hediste diversicolor*, *Heteromastus filiformis*, *Lanice conchilega* and *Arenicola marina* also showed considerable contributions to total standing stock values at different sites.

When analysing the Norderney data set in terms of temporal aspects of the relationship between species richness and standing stock levels we found that the number of species needed to sustain threshold levels of standing stock clearly increases with increasing time intervals from 2 to 14 years (Fig. 4). Across the eight sites, S_{\min} (the minimal number of species contributing 50 % of total standing stock) varied over a period of one year between 2.091 and 3.875. In order to maintain 50 % of the total biomass over the 14 years of the time series minimum numbers of species between 8 and 14 were necessary. The slopes in Fig. 4 suggest that functional turnover is likely to increase further with the length of the time interval.

Likewise, the analysis of species turnover rates calculated with Jaccard's distance revealed a significant increase of changes in the community composition with time. Between two consecutive years, Jaccard's distance on average was 0.465, between 10 years it was 0.602, which represents an increase by 0.137. An ANOVA on Jaccard's

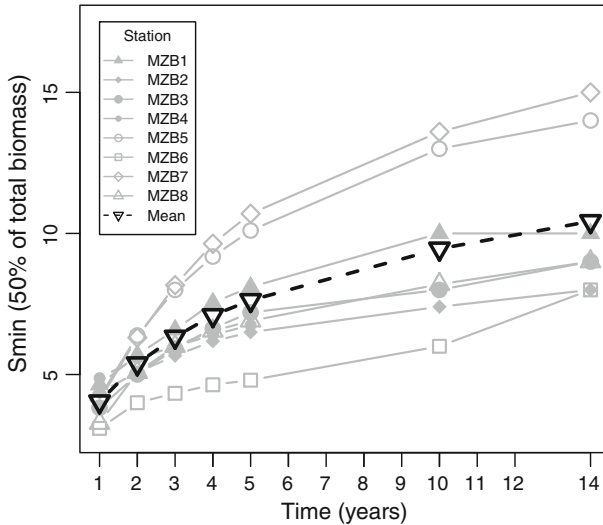


Fig. 4 The minimum number of species (S_{\min}) necessary for maintaining 50 % of the total standing stock levels over periods of time ranging from 1 to 14 years. S_{\min} is shown for each single station and the mean over all stations

distance including sampling station and length of time interval as explanatory variables yielded significant effects ($p < 0.001$) for both factors.

A comparison of the mean CV (coefficient of variance) of biomass measurements for individual species populations and the biomass CV for the whole species community indicated higher biomass fluctuations in single species populations than in the community for all sampling sites (Fig. 5). CV values for the individual species varied between 3.12 and 3.58, CV values for the whole community between 0.48 and 1.23. The difference of the two measures was similar for all sites ranging from 2.32 to 2.90. However, we could not detect any relation between this stability measure and the number of species at a sampling site.

Discussion

Our analysis of two typical monitoring data sets from a highly variable system indicates that the data currently collected in many marine monitoring programmes is not sufficient to contribute much additional information to the discussion on the existence and nature of the relationship between biodiversity and most ecosystem functions and processes. One of the main reasons is the lack of information on functional parameters and ecosystem process rates in most monitoring protocols of marine environments. Standing stock is the only regularly measured variable that vaguely approximates the functional aspect of productivity. It should be noted here that the conversion of abundances into biomass values, which was necessary for the Jade Bay data set due to a lack of direct biomass measurements, certainly adds further uncertainty to our results. Nevertheless we are highly confident that this did not alter the main outcomes of the according analyses. Our results confirm previous experimental results on the positive correlation between species richness and standing stock found in aquatic (Duffy 2003; Stachowicz et al. 2007) and terrestrial

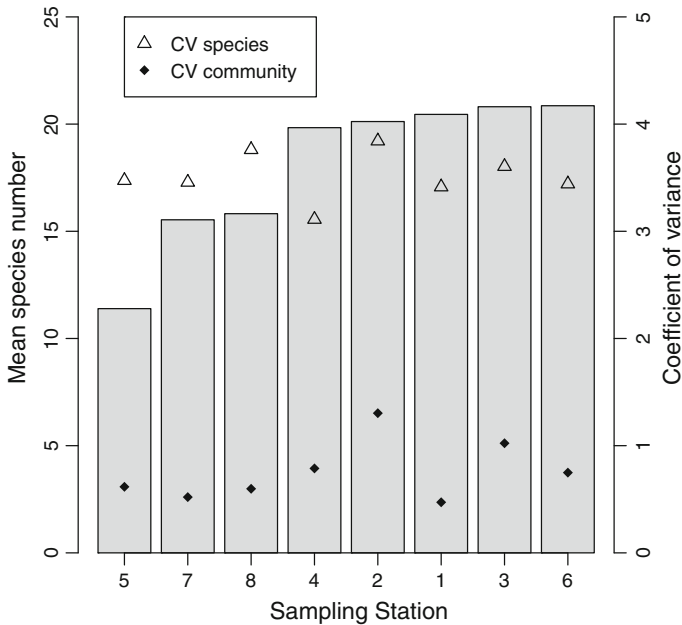


Fig. 5 Coefficient of variance (CV) for single species populations (*triangle*) and the entire species community (*diamond*). The bars represent the local mean number of species at each sampling station

(Tilman et al. 2001; Cardinale et al. 2007) systems. As with observational data in general, our results do not allow conclusions on causal relationships. There are numerous practical and theoretical studies that discuss the possible reasons for the observed positive correlation. Environmental conditions and habitat characteristics (Beukema 1976), disturbances (Cardinale et al. 2000) or species identity effects (Covich et al. 2004; Bruno et al. 2005) are often assumed to be the ultimate determinants of productivity and other ecosystem functions rather than species diversity. However, in the analysis of variance of the Norderney data set the temporal variables (year, season) and number of species remained in the final model after model selection, in contrast to the parameters characterising the habitat or environmental conditions (Table 1).

Especially in marine ecosystems, further aspects complicate the analysis of effects of richness on productivity. Due to lifetime and body weight differences of several orders of magnitude between macrozoobenthos species the measures of ash free dry weight cannot be interpreted as a direct proxy for the community's productivity. A mollusk specimen of a few years of age can contribute considerably to total biomass values of the community whereas its productivity in terms of new biomass production might equal zero. Consequently, standing stock or biomass measurements as commonly collected in most monitoring programmes cannot serve as immediate surrogates for the productivity of a community which is different from terrestrial ecosystems where standing stock is used as a direct measure for productivity in systems dominated by annual species (Tilman et al. 2001). A number of empirically derived approaches for the conversion of abundance and biomass data to secondary production of macrozoobenthos species exist (Banse and Moshier 1980; Schwinghamer et al. 1986; Mistri et al. 2001). As stated in the method section, the application of Schwinghamer's conversion index to our data did not produce

qualitatively different results. Either we accept the need to incorporate more meaningful proxies for productivity such as assimilation efficiency or resource use efficiency in our monitoring schemes, or we accept this limitation and thus the use of standing stock values as a sufficiently accurate proxy for productivity in macrozoobenthos communities. The concern that presence or absence of single species or a functional group dominate and bias the relationship between species richness and standing stock values can be mitigated, however: The same positive correlations between biomass and species richness prevailed in each of the three functional groups (Fig. 3), such that traits of a single functional group (e.g. high individual biomass values of some mollusk species) are not driving the correlation between richness and biomass in the whole data set.

In our analysis, monitoring data carry important information on other aspects of the biodiversity ecosystem functioning relationship. When comparing the number of species required to maintain 50 % of total standing stock levels over time intervals of increasing length, this measure (S_{min}) increased with time, a trend consistent over the 14-year period. Thus, for each station, the identity of species mainly contributing to total biomass values changes significantly with time (functional turnover sensu Hillebrand and Matthiessen 2009). In this analysis the mussel bed station MZB6 showed the lowest rate of increase as at this site clearly the few big mollusk species dominate standing stock values even over longer periods of time. Whereas in general it can be concluded that although only very few species were necessary to secure biomass levels at a time, low levels of biodiversity increase the risk of reduced functions over extended time periods (Isbell et al. 2011; Allan et al. 2011). It is noteworthy that the analysis of species turnover revealed that the species mainly contributing to biomass are different to the ones joining or leaving the community, indicating that these two processes are not directly related. Maintenance of productivity over time can require higher contributions of previously subdominant species, which in our case was more important than immigration by new species. Previously, Hillebrand et al. (2012) experimentally showed that compositional and functional turnover were highly correlated in micro-algal communities subjected to changing environmental conditions.

The temporal variability in environmental conditions and the according changes in community composition over time characterise many marine habitats. This and the absence of functional parameters from survey programmes are important aspects of currently practiced monitoring efforts. By implication, these need to be considered for a more effective monitoring and gain of possibly higher information content with regard to the BEF debate in highly dynamic marine environments. Apart from underlining the importance of long-term monitoring data sets as mentioned in former studies (Wiltshire et al. 2008), we additionally want to emphasise caution in the choice of sampling locations. Tidal flats like in the German Wadden Sea comprise a multitude of continuously changing habitats which need to be accounted for in the interpretation of changes in community structure and composition at one site. Community composition is an equally important aspect as the number of species and changes in species communities therefore need to be studied as thoroughly. Marine monitoring programmes will also have to start focusing on the inclusion of functional parameters like it is being practised in terrestrial studies (Fischer et al. 2010). For tidal flats these could be for instance the measures of biogeochemical fluxes at the sediment water interface using benthic chambers (Berelson et al. 1998; Hughes et al. 2000) or the evaluation of nutrient ratios in organism tissue and sediment samples allowing conclusions on resource use efficiencies as practiced in a number of studies on plankton communities (Ptacnik et al. 2008).

In summary, our analyses suggests that monitoring data focusing on biodiversity can inform us about ecosystem processes, but can only indirectly contribute to the biodiversity

ecosystem functioning debate. If this gap is to be closed, monitoring efforts need to be redirected or complemented by additionally collected data. One might argue that diversity in itself presents a way better indicator for the state of an ecosystem than biomass production or other process rates. We would note though that this is a common assumption that has not actually been proven for natural systems yet. Undoubtedly, diversity of life is highly valuable and high proportions of species loss can have profoundly negative effects on the functioning of entire ecosystems and ecosystem services derived thereof (Tilman et al. 1996; Duffy 2003; Cardinale et al. 2012). Yet, diversity is a term comprising many different aspects and scales and we are far from being able to identify what aspects of diversity are playing the key roles or whether this is the case for all processes and functions in an ecosystem. The question of how and to what extent the number of species (which is the common measure of biodiversity) represents the key factor driving process rates in an ecosystem or whether this depends on a number of factors such as the type of ecosystem or process, species identity and specific species interactions is in need of further investigation. Although one might argue that the preservation and protection of biodiversity is the main aim of conservation regardless of how individual species are functionally linked to the important processes in an ecosystem, we believe that in the awareness of financial and administrative constraints, which most conservation efforts are facing, the knowledge of functional dependencies can help decision makers in conservation management to prioritise their efforts more effectively.

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