

# Benthic trophic networks of the southern North Sea: contrasting soft-sediment communities share high food web similarity

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**ABSTRACT:** We examined whether taxonomically distinct benthic communities from contrasting sediments in the German Bight (southern North Sea) also differ in their trophic structure. As a case study, we compared the *Amphiura filiformis* community (AFC) of silty sands and the *Bathyporeia–Tellina* community (BTC) of fine sands using a combination of stable isotope analysis and data on trophic interactions. Differences between the food webs were evident in the feeding guild composition of important primary consumers: deposit and interface feeders are the most diverse primary consumer guilds in the AFC, whereas suspension and interface feeders play a major role in the BTC, reflecting differences in physical properties and food availability at the sediment–water interface. While all primary consumer guilds had the same trophic level (TL) in the AFC, deposit feeders of the BTC occupied a trophic position intermediate between other primary and higher-order consumer guilds, likely explained by partially incomplete knowledge of their trophic ecology and selective feeding, including the ingestion of meiofauna. Most food web properties, however, were similar between the AFC and BTC: they mainly depend on pelagic primary production, reach TL 4 and are characterized by a prevalence of generalist higher-order consumers. Furthermore, both trophic networks had similar linkage densities and high directed connectance, the latter feature suggesting considerable food web robustness. Our findings suggest that although communities in the German Bight differ in some aspects of their trophic structure, they share a similar food web topology, indicating a comparable degree of resilience towards natural and anthropogenic disturbances.

**KEY WORDS:** Food web structure · Contrasting sediments · *Amphiura filiformis* community · *Bathyporeia–Tellina* community · Stable isotopes · Trophic links

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## 1. INTRODUCTION

Soft-sediment biota encompass the majority of marine biodiversity (Snelgrove 1999) and play an important role in ecosystem processes such as biogeochemical cycling, sediment reworking/stabilization,

benthic–pelagic coupling and the redistribution of pollutants (Snelgrove 1997, Lohrer et al. 2004). Benthic secondary production provides food resources for higher trophic levels (TLs), including commercially exploited fishes and invertebrates (Snelgrove 1997, Frid & Caswell 2015). While the utilization of marine

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living resources is deeply rooted in human history (de Groot 1984, Jackson et al. 2001), the current unprecedented pace and magnitude of anthropogenic impacts can severely affect the provision of ecosystem services (Vitousek et al. 1997, Jackson et al. 2001, Pawar 2016). In this context, the study of trophic interactions can provide valuable insights into pathways of energy and organic matter (OM) flows through biological communities (Odum 1957, Kemp & Boynton 2004), and thereby the functioning of ecosystems, as well as their resilience to natural and human-related disturbances (Dunne et al. 2002a, Renaud et al. 2011, Yen et al. 2016). This is particularly essential in areas subjected to strong anthropogenic pressures, such as many shelf sea and coastal regions (Vitousek et al. 1997, Halpern et al. 2008).

The German Bight (southeastern North Sea) is a highly dynamic shallow-water region and is regarded as one of the most heavily exploited shelf sea ecosystems worldwide (Heath 2005, Emeis et al. 2015). In addition to frequently occurring natural disturbances such as storm-induced sediment reworking (Rachor & Gerlach 1978, Eisma et al. 1987) or exceptionally cold winter temperatures (Kröncke et al. 2013), human activities, particularly decades of intense bottom trawling, have shaped benthic assemblages, resulting in a reduction of large, slow-growing species and a shift towards small, fast-growing opportunists (Kröncke 1992, Thatje & Gerdes 1997, Shojaei et al. 2016), along with increased benthic production (Heath 2005). More recently, local benthic assemblages have also been subjected to warming water temperatures (Wiltshire & Manly 2004), the introduction of non-indigenous species (Reise et al. 1998, Gollasch et al. 2009), eutrophication (Brockmann et al. 2007) and offshore windfarm construction (Krone et al. 2017).

The sublittoral German Bight is characterized by a predominance of soft sediments, ranging from clayey silt to coarse sands (Salzwedel et al. 1985, Eisma et al. 1987). It is inhabited by 4 major biological communities whose core distribution areas are related to sediment type and water depth and have been rather stable over time (e.g. Salzwedel et al. 1985, Fiorentino et al. 2017): the *Amphiura filiformis*, *Bathyporeia-Tellina*, *Goniadella-Spisula* and *Phoronis* communities (Fiorentino et al. 2017). While their taxonomic composition has been the subject of numerous investigations (e.g. Hagmeier 1925, Stripp 1969, Salzwedel et al. 1985, Schroeder 2005), we still lack basic information on their trophic structure (but see Dannheim 2007, Dannheim et al. 2014) and potential differences between the food webs of communities inhabiting contrasting sediment types.

Sediment properties and the availability of food resources, however, exert a strong influence on the functional properties of benthic assemblages (Sanders 1958, Rhoads & Young 1970, Lovell & Trego 2003). Recent studies highlighted substrate-related differences in the role of suspension and deposit feeders for OM flows in the English Channel and southwestern North Sea (Garcia et al. 2011), as well as in the dominance patterns of feeding guilds between macrobenthic assemblages in the German Bight (Shojaei et al. 2015). These findings suggest that benthic food web structure in the southern North Sea may substantially differ between communities from contrasting sediment types, even at small spatial scales.

Naturally dynamic environments, anthropogenic impacts and climate change, on the other hand, are known to favor broadly adapted taxa over specialists (Clavel et al. 2011) and may be reflected in similarly structured but resilient food webs across communities in the German Bight. Indeed, recently, Shojaei et al. (2016) provided evidence for a trend of functional homogenization of the German Bight benthic communities, based on the analysis of species functional traits and benthic time series data.

In this study, we compare the food webs of the 2 most widely distributed benthic communities: the *Amphiura filiformis* community (AFC) inhabiting silty sands and the *Bathyporeia-Tellina* community (BTC) of fine to medium sands (Salzwedel et al. 1985, Fiorentino et al. 2017). We use an integrative approach combining stable isotope analysis and a comprehensive literature search on species-specific trophic interactions. While carbon and nitrogen isotope compositions yield time-averaged information on the origin of assimilated food sources and species' relative trophic positions, respectively (Fry 1988, Post 2002), information on trophic interactions enables the calculation of metrics describing food web topology. Summary metrics derived from species richness and the number of trophic interactions, such as directed connectance, linkage density and the distribution of links among consumers, further provide valuable insights into food web robustness and the degree of species' trophic specialization (Dunne et al. 2002a,b, Link 2002, Yen et al. 2016).

The integration of both approaches enabled us to assess in detail whether taxonomically distinct communities from contrasting sediments also differ in their trophic structure or if food web similarity is high across habitats in the German Bight. Our findings not only provide insights into the trophic functioning of the 2 most widespread benthic communities in this

region but may also serve as a base for future quantitative trophic studies and a modern baseline against which potential future changes in the trophic structure can be gauged.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Benthic food webs were studied at 2 time series stations in the German Bight, southern North Sea, off the island of Helgoland (Fig. 1). The 2 sites represent typical examples of the AFC and BTC (Schroeder 2005), the 2 most widely distributed benthic communities in the sublittoral German Bight (Salzwedel et al. 1985, Fiorentino et al. 2017). The AFC station ( $54^{\circ}00.50'N$ ,  $007^{\circ}49.00'E$ ), hereafter called AF, is located within the submerged Pleistocene Elbe River valley at 36 m water depth. The sediment consists of silty sand with a median grain size (MdGS) of  $\sim 83 \mu m$ , and contains approximately 25% silt and clay (Schroeder 2005). The total OM content (mean  $\pm$

SD) is  $1.6 \pm 0.7\%$  of sediment dry mass ( $n = 4$ , samples taken in spring in 4 different years; J. Dannheim unpubl. data). The BTC station ( $54^{\circ}22.50'N$ ,  $007^{\circ}37.00'E$ ), hereafter called BT, is located northwest of Helgoland at 26 m water depth. The seafloor consists of homogeneous fine sand (MdGS  $\sim 180 \mu m$ ) with less than 1% silt and clay (Schroeder 2005) and some scattered large rocks from the last glacial period. The OM content is  $0.5 \pm 0.1\%$  of sediment dry mass ( $n = 5$ , samples taken in spring in 5 different years; J. Dannheim unpubl. data). Annual quantitative sampling of macrozoobenthos has been conducted at both stations in spring since 1969 in the framework of the Alfred Wegener Institute's (AWI) macrozoobenthos time series (see Schroeder 2005). In addition, larger epifauna and demersal fishes have been sampled in several years with beam and otter trawls, mostly during the same spring cruises. Therefore, detailed long-term data on taxonomic community composition were available prior to this study for selecting species to target for food web analysis (see next paragraph). For a detailed account on the taxonomic structure and the spatial and temporal vari-

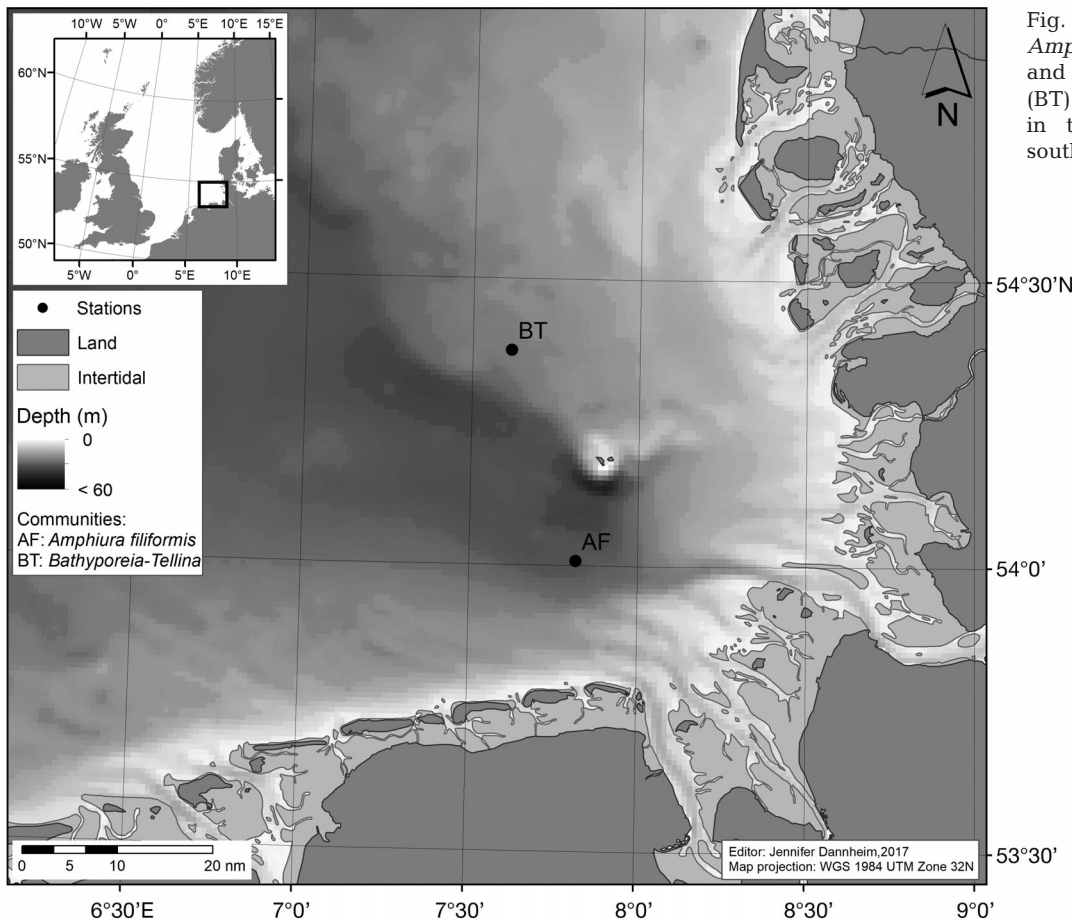


Fig. 1. Location of the *Amphiura filiformis* (AF) and *Bathyporeia-Tellina* (BT) community stations in the German Bight, southeastern North Sea

ability of the AFC and BTC at the long-term stations analyzed in this study, see Schroeder (2005).

## 2.2. Selection of taxa for food web analysis

Primary food sources, benthic invertebrates and demersal fishes were analyzed in this study. For the taxonomically diverse group of macrobenthic invertebrates, a focus was put on the trophically most important taxa of the AFC and BTC (hereafter called target species), using body mass-scaled abundance as a proxy of species' relative contributions to total community energy flow (see Dannheim et al. 2014). The energy flow (EF) parameter of Dannheim et al. (2014) is a measure for the relative magnitude of energy flow through populations, as population metabolism is related to both species abundance and average individual body mass (metabolic rate generally scales with body mass by an exponent of 0.75, see review by West & Brown 2005). The EF parameter for any species  $i$  is given by:

$$EF_i = N_i \cdot M_i^{0.75} [\text{J m}^{-2}] \quad (1)$$

where  $N_i$  is the abundance ( $\text{m}^{-2}$ ) and  $M_i$  is the average individual body mass of species  $i$ , converted to energy units (J) (Dannheim et al. 2014). Consequently, community EF ( $EF_{\text{com}}$ ) is given by:

$$EF_{\text{com}} = \sum_{i=1}^n (N_i \cdot M_i^{0.75}) [\text{J m}^{-2}] \quad (2)$$

where  $n$  represents the number of species in the community (Dannheim et al. 2014). In contrast to abundance or biomass as the selection criterion, EF has the advantage of better balancing the relative importance of more abundant, small taxa vs. less common, large species in the food web.

To consider a diverse spectrum of benthic invertebrates and level out interannual population fluctuations, target species identification was based on separate analyses of available community data from van Veen grab and beam trawl samples collected within a 10 yr period (2002–2011). While grab data provide a good coverage of small invertebrates, beam trawl data were analyzed to account for the underrepresentation of larger epifauna in grab samples. In total, 50 grab samples per station (5 replicates per year) as well as 10 (AF) and 9 (BT) beam trawl samples were available for the analysis. No beam trawl data were available for 2011 (for both stations), and 2004 (for BT), whereas a spring and autumn sample was available for 2007 for both stations.

For EF calculations, mean individual wet mass of taxa (g) for each sample was converted into energy

units (J) using conversion factors provided by Brey (2001) and Brey et al. (2010). If no factor was available at the species level, factors for the closest higher-ranking taxa were used. Per-sample taxon-specific EF values were summed over all years, yielding cumulative taxon EF values. The latter were ranked from highest to lowest, and corresponding percentages of cumulative  $EF_{\text{com}}$  at each station were calculated. The highest-ranking taxa cumulatively contributing  $\geq 90\%$  to  $EF_{\text{com}}$  at each station were defined as target species. Brittle stars (*Ophiura* spp., mostly *Ophiura albida*) were only considered in the grab dataset, as the shallow in- and epifaunal *O. albida* alone accounted for ca. 84% of cumulative  $EF_{\text{com}}$  in beam trawl samples from AF, and would have strongly limited the spectrum of larger epifaunal target species in this study. Besides the selected invertebrates, all species of demersal fish caught during the field sampling campaign were considered as target species, as the comparatively low species diversity in the study area would allow the analysis of all sampled taxa.

In very few cases, a particular target species was not collected during the field campaign for this study, likely reflecting the pronounced population dynamics well known for several benthic invertebrate taxa in the German Bight (e.g. Kröncke et al. 2013); these non-available target species were replaced by the next ranking taxon.

## 2.3. Stable isotope-based food web analysis

### 2.3.1. Field sampling

Sources of OM as the base of the food web and consumers were sampled during cruise HE 460 aboard the RV 'Heincke' in April 2016. Suspended particulate organic matter (POM) was collected from 3 (at AF) to 5 (at BT) replicate water samples taken 2 to 2.5 m above the seafloor with a Niskin bottle. Aliquots of 500 to 850 ml were filtered over precombusted (12 h at 500°C) Whatman GF/F glass fiber filters (25 mm diameter, 0.7  $\mu\text{m}$  pore size). Any larger zooplankton trapped on the filters were immediately removed under a dissecting microscope. Sediment samples were collected from the top 5 to 6 cm of van Veen grab samples (0.1  $\text{m}^2$  sampling area, approx. 70 kg, 3 replicates at both stations) by push coring (surface area: 13.85  $\text{cm}^2$ ). Filters and sediment samples were immediately frozen at  $-20^\circ\text{C}$  until further processing in the lab.

Infauna was collected from 13 (AFC) to 15 (BTC) replicate van Veen grabs sieved through a 1 mm

mesh. The retained material was cooled, and organisms were sorted alive on board and frozen at  $-20^{\circ}\text{C}$  until further processing. As many infaunal invertebrates became moribund within a short time after extraction from the sediments, starvation was unfortunately not possible. To avoid potential biases of stable isotope values from gut contents, other tissues were used if possible. Epifauna and demersal fishes were sampled by 1 to 3 replicate hauls with a 3 m beam trawl (1 cm stretched cod-end mesh size, towed at 2–3 knots for 10–20 min) and a demersal otter trawl (ca. 15 m opening width, 1 cm stretched cod-end mesh size, trawled for 20 min at 6 knots). Fish were sacrificed, and white muscle tissue was sampled in large species. Smaller fish species and invertebrate epifauna were frozen *in toto* for dissection in the lab. All samples were stored at  $-20^{\circ}\text{C}$  until further treatment.

Target species were prioritized, but some non-target species available were also analyzed for a more complete taxonomic coverage of the studied communities. These data, however, were excluded from between-site comparisons depending on species numbers (e.g. descriptive food web metrics) to maintain comparability of the results between communities. It is explicitly stated for each analysis whether non-target taxa were included.

### 2.3.2. Sample preparation and analysis

Animal samples were freeze-dried and ground into powder using a mortar and pestle or a mixer mill. Muscle tissue was used whenever possible; however, other tissues (limbs of crustaceans, tails of small fish, sections of polychaetes and nemerteans, arms of asteroids/ophiuroids or body wall of echinoids and anthozoans) were also used in smaller species. For the smallest species, 1 or several whole individuals were pooled in a sample.

As carbonates are enriched in  $^{13}\text{C}$  compared to soft tissues (Haines & Montague 1979), sample aliquots were decalcified by addition of  $1\text{ mol l}^{-1}\text{ HCl}$  (Jacob et al. 2005) in taxa where carbonate-free tissue could not be obtained (e.g. echinoderms and small crustaceans). HCl was added until cessation of  $\text{CO}_2$  formation, and samples were subsequently dried at 50 to  $55^{\circ}\text{C}$  and ground into powder again. Hygroscopic samples were resuspended with ultrapure water and freeze-dried before grinding. As acidification can affect nitrogen isotope composition (Mateo et al. 2008), measurements of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were performed separately on decalcified and untreated ali-

quots, respectively, to ensure quality and comparability of the results. Lipid removal was not performed, as benthic organisms generally contain low amounts of lipids (Clarke & Peck 1991) and because low-lipid muscle tissue was analyzed whenever possible.

POM filters were freeze-dried for 24 h. Filters were bisected, and one-half of each filter was exposed to HCl fumes for 16 h followed by air-drying, as suspended POM may contain significant amounts of carbonates (Søreide et al. 2006). Acidified and untreated halves were used for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  value determination, respectively.

Sediments were freeze-dried and ground into powder. A subsample of each replicate was decalcified as described for animal tissues, and separate analyses were carried out for the determination of  $\delta^{13}\text{C}$  (decalcified samples) and  $\delta^{15}\text{N}$  (raw samples) values.

Stable isotope analyses and determination of percentages of C and N were performed at the Littoral, Environment and Societies stable isotope facility of the University of La Rochelle, France, using a Flash 2000 elemental analyzer (Thermo Scientific) coupled to a Delta V Plus isotope ratio mass spectrometer via a ConFlo IV interface (Thermo Scientific). Acetanilide (Thermo Scientific) and peptone (Sigma-Aldrich) were used as internal standards (2-point calibration). IAEA standards used for calibration were USGS-24, IAEA-CH6 and IAEA-600 for  $\delta^{13}\text{C}$  values and IAEA-N2, IAEA-NO-3 and IAEA-600 for  $\delta^{15}\text{N}$  values. Analytical precision was  $<0.15\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values.

Stable isotope compositions are expressed in the conventional  $\delta$ -notation relative to international standards (Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$ , atmospheric  $\text{N}_2$  for  $\delta^{15}\text{N}$ ) after:

$$\delta X = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \cdot 1000 \text{ [‰]} \quad (3)$$

where  $X$  is the isotope under consideration ( $^{13}\text{C}$  or  $^{15}\text{N}$ ), and  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the ratios of heavy to light isotopes ( $^{13}\text{C}:^{12}\text{C}$  or  $^{15}\text{N}:^{14}\text{N}$ ) in sample and standard, respectively (Peterson & Fry 1987, Fry 1988). Values are reported as mean  $\pm$  SD.

### 2.3.3. Stable isotope data analysis

All species were assigned *a priori* to one of 5 different feeding guilds based on the literature (see Table S1 in Supplement 1 at [www.int-res.com/articles/suppl/m628p017\\_supp1.pdf](http://www.int-res.com/articles/suppl/m628p017_supp1.pdf) for a list of references): suspension feeders, deposit feeders, interface feeders (species capable of feeding on



suspended particles and bottom detritus), omnivores/scavengers (defined here as species feeding on POM/sediments as well as on other macrofaunal animals) and predators/scavengers (Tables S2 & S3 in Supplement 1). As the guild concept implies that individuals have a similar feeding ecology, isotope-based statistics for guilds (see below) were calculated based on individual replicate isotope measurements.

TLs of consumers were calculated, as they enable a direct comparison of consumers' trophic positions across sites, considering that TL estimates take into account the  $\delta^{15}\text{N}$  values of the local food web baseline. TLs were estimated according to (Post 2002),

$$\text{TL}_i = \frac{(\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{baseline}})}{\Delta^{15}\text{N}} + \text{TL}_{\text{baseline}} \quad (4)$$

where  $\text{TL}_i$  is the (continuous) TL estimate of species  $i$ ;  $\delta^{15}\text{N}_i$  and  $\delta^{15}\text{N}_{\text{baseline}}$  are the  $\delta^{15}\text{N}$  values of species  $i$  and the food web baseline, respectively;  $\Delta^{15}\text{N}$  is the trophic fractionation factor for  $\delta^{15}\text{N}$ ; and  $\text{TL}_{\text{baseline}}$  is the pre-defined TL of the food web baseline (e.g. 1 for primary producers). Mean  $\delta^{15}\text{N}$  values of all POM and sediment samples per station (AF:  $6.6 \pm 0.8\text{‰}$ , BT:  $6.2 \pm 0.5\text{‰}$ ) were used to compute  $\delta^{15}\text{N}_{\text{baseline}}$  values to avoid potential biases of primary consumer baselines due to selective feeding (e.g. Nadon & Himmelman 2006). We used the widely accepted trophic fractionation factor of  $3.4\text{‰}$  for  $\delta^{15}\text{N}$  per TL (Minagawa & Wada 1984).

Isotopic niche widths of feeding guilds were quantified by calculating their Bayesian standard ellipse area ( $\text{SEA}_B$  [ $\text{‰}^2$ ]) (Jackson et al. 2011). Standard ellipses are the bivariate analogues to SDs of univariate data and, in contrast to convex hull statistics, rather insensitive to sample size differences, as they generally contain approximately 40% of the data (Batschelet 1981). In addition to  $\text{SEA}_B$ , we calculated the standard ellipse area corrected for small sample size ( $\text{SEA}_C$ ), which is particularly robust for sample sizes  $<30$  (Jackson et al. 2011).

The community-scale trophic structure of the AFC and BTC, based on consumer guilds' centroids in  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  space, was analyzed by calculating the 6 descriptive metrics first proposed by Layman et al. (2007) and later implemented in a Bayesian framework by Jackson et al. (2011). These metrics provide a useful means for comparing the trophic structure of the AFC and BTC, as there are only 2 sources of OM in both food webs, which are further characterized by a similar magnitude of differences in their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (see Section 3). The first 4 Layman metrics describe the

trophic diversity within a community, and correspond to the spacing of food web components (species or functional groups—here, feeding guilds) within  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  space:  $\delta^{15}\text{N}$  range (NR) provides information on the trophic length of the community, while  $\delta^{13}\text{C}$  range (CR) reflects the diversity of food resources; total convex hull area (TA) is a proxy of the isotopic niche space occupied by a community, and the mean distance to centroid (CD) informs about the average trophic diversity. The other 2 metrics inform about trophic redundancy: mean nearest neighbor distance (MNND) describes the density of spatial packing of the food web components, while the standard deviation of nearest neighbor distance (SDNND) is a measure of the evenness of packing (i.e. lower SDNND values correspond to higher trophic redundancy). The Bayesian approach of calculating these metrics yields improved estimates and enables a quantification of their uncertainties. Because of its sensitivity to sample size and extreme values, however, TA was not used in this study. The Bayesian Layman metrics and all ellipse statistics were calculated using the SIBER package (Jackson et al. 2011) in the statistical programming environment R (R Development Core Team 2008).

Univariate statistical tests were used to test for differences in stable isotope compositions, C:N ratios of food resources and the TLs of feeding guilds. Data were checked for normality (Kolmogorov-Smirnov test) and homogeneity of variances ( $F$ - and Bartlett tests) before running parametric tests ( $t$ -test, ANOVA). If assumptions were not met, tests with fewer assumptions (Welch's  $t$ -test, Kruskal-Wallis test) were used. Normality was assumed for groups with very small sample sizes ( $n < 5$ ), but any significant results were interpreted with caution. Pairwise Tukey's and Dunn's post hoc tests were run to identify significantly different groups following ANOVA and Kruskal-Wallis tests, respectively. Differences in  $\text{SEA}_B$  of guilds were assessed by checking for overlap in their 95% credible intervals and by calculating the probability that the  $\text{SEA}_B$  of any one guild was smaller than that of another guild, based on 4000 posterior estimates of the standard ellipse areas.

## 2.4. Literature-based food web analysis

### 2.4.1. Trophic link matrix construction

Qualitative information on species-specific trophic interactions was gathered through an extensive liter-

ature search (see Table S1 for a list of references). A trophic link between species was assigned if taxon A fed on taxon B (see Martinez 1991), i.e. focusing on the consumer role of taxa (so-called incoming trophic links). Trophic link data were assembled in a binary matrix of sampled target species and sources of OM (in this context also referred to as species) from the AFC and BTC. Data were mostly collected at the consumer species level; however, in a few cases, data for consumer genera or families (e.g. *Ophiura* spp., Pleuronectidae) were included.

In many cases, prey items had not been identified to species level in the literature. To account for such information at supraspecific taxonomic resolution, potential prey among target species were inferred from estimates of predators' maximum prey size (in terms of prey body mass), themselves based on the average predator–prey body mass ratios in our study communities. This approach is based on body size as an important constraint of feeding interactions, i.e. in most cases, larger predators consume smaller prey (Cohen et al. 1993). As average predator–prey body mass ratios are greater for vertebrate than invertebrate predators (Brose et al. 2006), separate calculations were performed for these predator types. Average predator–prey body mass ratios were calculated from trophic interactions between target species reported in the literature at the species level: first, predator–prey body mass ratios were determined for each species-specific interaction, using average individual body masses of species (2002–2011 AWI time series data; for the anemones *Metridium dianthus* and a species of Sagartiidae, mean individual body mass was estimated from specimens collected for isotope analysis). Subsequently, average predator–prey body mass ratios for vertebrate and invertebrate predators were calculated as geometric means (see Brose et al. 2006) of all interactions involving the respective predator type. Deposit- and suspension-feeding links were not considered in the calculations, as a value for body mass was not assignable to the food sources. Finally, average predator–prey body mass ratios were used to estimate the maximum prey size for each consumer species. All target species representatives of a higher-level prey taxon mentioned in the literature and on average smaller than the maximum prey size of a given consumer were regarded as potential prey items of that consumer.

After completion of the matrix, it was split into community-specific matrices containing only target species and sources of OM of either community and their trophic interactions.

#### 2.4.2. Descriptive food web metrics and prey-averaged TLs

Commonly used descriptive food web metrics were computed for each community, including the number of species ( $S$ ) and trophic links ( $L$ ), linkage density (the average number of trophic links per species,  $L/S$ ) and directed connectance  $C$  ( $L/S^2$ ). The latter is a measure of the proportion of directed trophic links realized within a food web, including mutual predation and cannibalism (Martinez 1991), and is positively correlated with the robustness of food webs against secondary species extinctions (Dunne et al. 2002a).

Prey-averaged TLs, defined as 1 plus the mean TL of all diet items of a consumer (Williams & Martinez 2004), were calculated from trophic link data in the statistical programming environment R (R Development Core Team 2008) using the Cheddar package (Hudson et al. 2013, 2015). The relationship between prey-averaged TLs and stable isotope-based TLs was modelled by standardized major axis regressions, and tested using the R package smatr 3 (Warton et al. 2012). The robust option for line fitting and testing of regression parameters was used, as it is insensitive to potential outliers in the data (Taskinen & Warton 2011, Warton et al. 2012).

The potential effects of the inclusion of all fish species on food web metrics were evaluated by calculating the same descriptors considering only fishes fulfilling the selection criteria applied to invertebrates (assessed using beam and otter trawl data for AF and BT from 2002 to 2011). We compared our results with other food web studies of various regions, including the northern Baltic Sea (Nordström et al. 2015), the northeastern US shelf (Link 2002), a Caribbean coral reef ecosystem (Opitz 1996, analyzed by Dunne et al. 2004) and the Arctic and Antarctic (Bodini et al. 2009, Raymond et al. 2011, de Santana et al. 2013) to put our results into a broader context.

### 3. RESULTS

#### 3.1. Feeding guild and taxonomic composition of target species

The AFC and BTC had a similar proportion of primary consumers among target species (36 vs. 33 % of the 33 target species of each community, respectively), but primary consumer feeding guild composition was markedly different (Fig. 2, left panel). In the

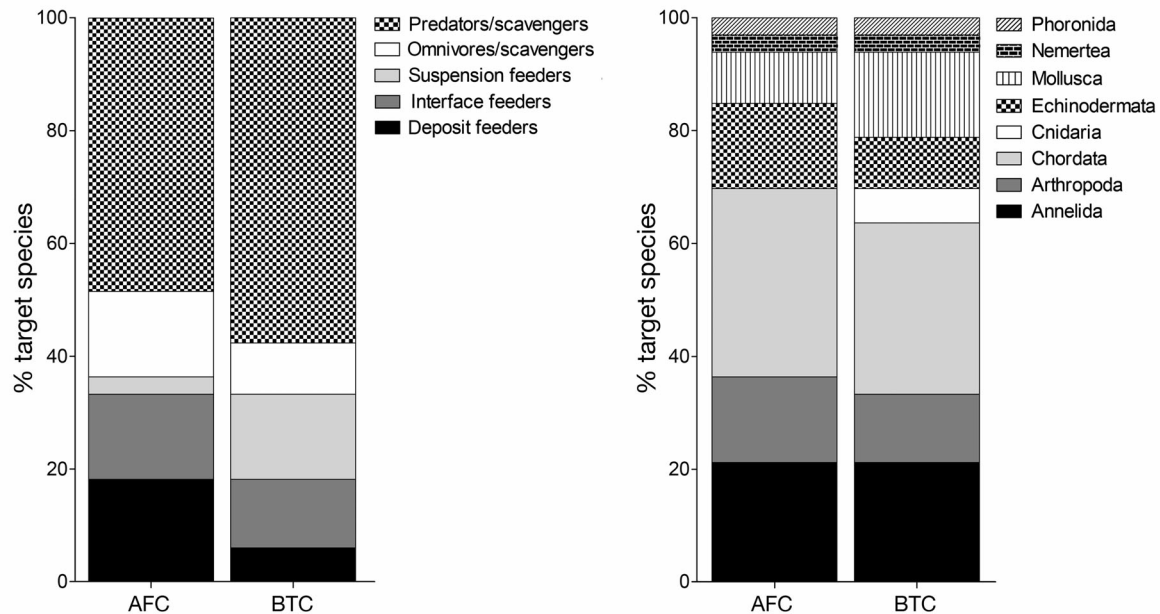


Fig. 2. Feeding guild (left panel) and taxonomic composition (right panel, phylum level) of target species of the *Amphiura filiformis* community (AFC) and *Bathyporeia-Tellina* community (BTC), displayed as percentages of total target species number ( $n = 33$  for each community)

AFC, deposit and interface feeders were the most species-rich primary consumer guilds, accounting for 18 and 15% of target species, respectively; suspension feeders were represented by only 1 species (3%, Fig. 2). In contrast, suspension (15%) and interface (12%) feeders were the most diverse primary consumer guilds in the BTC, whereas only 2 species (6%) were deposit feeders (Fig. 2). In both communities, predators/scavengers represented the most diverse trophic group (48 and 58% of AFC and BTC target species, respectively). Omnivores/scavengers were more diverse in the AFC (15%) compared to the BTC (9%, Fig. 2).

In contrast to feeding guilds, phylum-level taxonomic composition of target species was rather similar in both communities (Fig. 2, right panel). The AFC had a slightly higher share of echinoderm species (15%, represented by Asteroidea, Echinoidea and Ophiuroidea) compared to the BTC (9%, represented by Asteroidea and Echinoidea), whereas mollusks (bivalves only) were better represented among the target species of the BTC (15 vs. 9% in the AFC). Cnidaria (represented by Anthozoa) were only present among the target species of the BTC.

### 3.2. Stable isotope-based food web analysis

Stable isotope compositions of 2 basal food resources (sediment OM and suspended POM) and 52 con-

sumers from a wide taxonomic background were determined in this study. Compilations of species-specific mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, TL estimates, sample sizes and feeding guild affinity for each taxon are provided in Tables S2 & S3 in Supplement 1.

#### 3.2.1. Sources of OM

At both stations, the 2 sources of OM were clearly separated by their carbon isotopic compositions (Fig. 3):  $\delta^{13}\text{C}$  values of sediment OM (AF:  $-22.9 \pm 0.2\text{‰}$ , BT:  $-21.7 \pm 0.2\text{‰}$ ) were significantly lower than those of suspended POM (AF:  $-21.0 \pm 0.3\text{‰}$ , BT:  $-19.3 \pm 0.7\text{‰}$ ): AF:  $t(4) = 9.83$ ,  $p < 0.001$ ; BT:  $t(6) = 5.69$ ,  $p < 0.01$ .  $\delta^{15}\text{N}$  values of sediment OM (AF:  $6.8 \pm 1.0\text{‰}$ , BT:  $5.8 \pm 0.6\text{‰}$ ) and suspended POM (AF:  $6.3 \pm 0.5\text{‰}$ , BT:  $6.4 \pm 0.1\text{‰}$ ) were, however, comparable within stations (AF:  $t(4) = 0.66$ ,  $p = 0.54$ ; BT: Welch  $t(2) = 1.70$ ,  $p = 0.23$ ).

Basal food resources at AF had significantly lower  $\delta^{13}\text{C}$  values than at BT (sediment OM:  $t(4) = 9.90$ ,  $p < 0.001$ ; suspended POM:  $t(6) = 4.05$ ,  $p < 0.01$ ), while their  $\delta^{15}\text{N}$  values were not significantly different (sediment OM:  $t(4) = 1.36$ ,  $p = 0.24$ ; suspended POM: Welch  $t(2) = 0.36$ ,  $p = 0.76$ ). The C:N ratio of sediment OM was significantly higher at AF ( $8.3 \pm 0.3$ ) than at BT ( $6.8 \pm 0.3$ ;  $t(4) = 6.22$ ,  $p < 0.01$ ), while that of suspended POM was similar ( $5.6 \pm 0.4$  at AF vs.  $5.4 \pm 0.5$  at BT;  $t(6) = 0.43$ ,  $p = 0.68$ ).



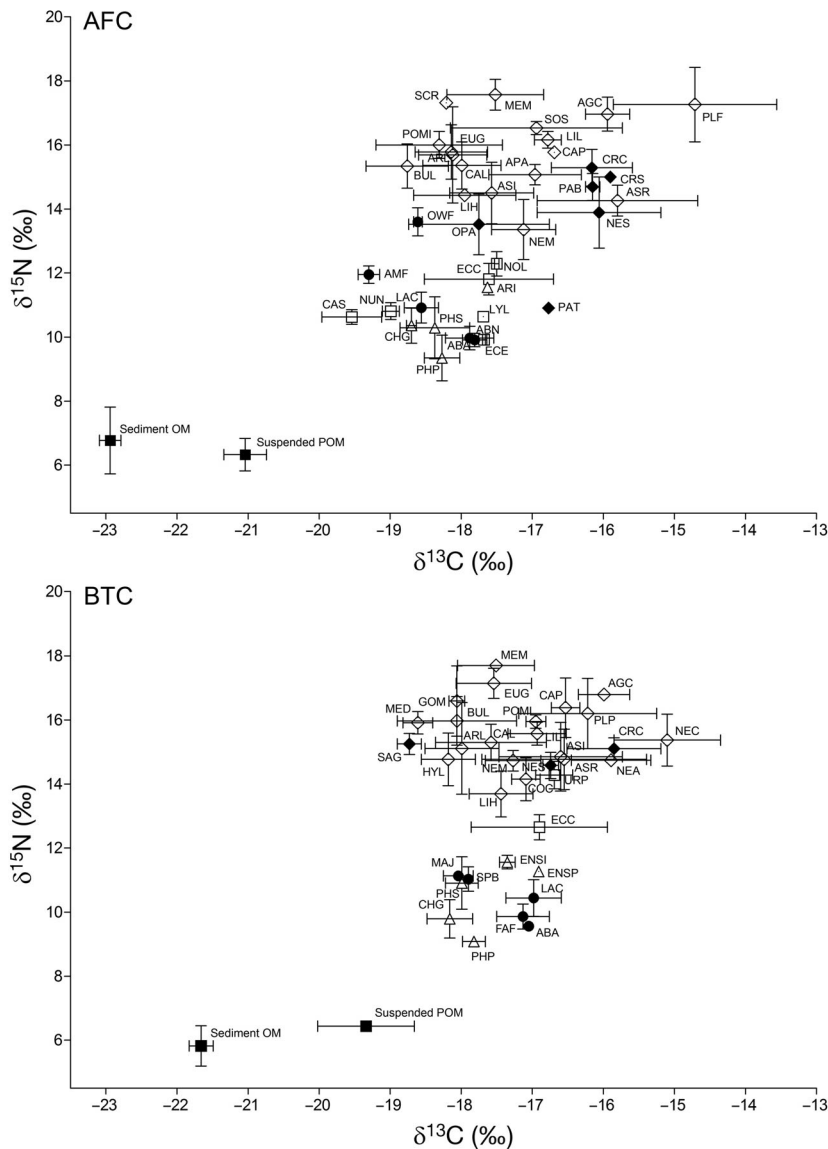


Fig. 3. Stable isotope compositions ( $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$  in ‰, mean  $\pm$  SD) of sources of organic matter (OM) and consumers (target species and additional taxa) of the *Amphiura filiformis* community (AFC, top panel) and *Bathyporeia-Tellina* community (BTC, bottom panel). Filled squares: OM sources; open squares: deposit feeders; filled circles: interface feeders; open triangles: suspension feeders; filled diamonds: omnivores/scavengers; open diamonds: predators/scavengers. POM: particulate organic matter. For a key to individual species codes, see Table S1 in Supplement 1 at [www.int-res.com/articles/suppl/m628p017\\_suppl1.pdf](http://www.int-res.com/articles/suppl/m628p017_suppl1.pdf)

### 3.2.2. Consumers

Of the 38 (AFC) and 35 (BTC) consumer taxa analyzed for isotope compositions, 33 were target species in each community, and 17 target species (8 fishes and 9 invertebrates) were shared by the AFC and BTC (Tables S2 & S3). Ranges of  $\delta^{13}\text{C}$  values of consumers were wider in the AFC than in the BTC:

$\delta^{13}\text{C}$  values spanned 4.8‰ in the AFC (from  $-19.5 \pm 0.4$ ‰ in *Callianassa subterranea* to  $-14.7 \pm 1.2$ ‰ in *Platichthys flesus*; Table S2, Fig. 3) compared to 3.6‰ in the BTC (from  $-18.7 \pm 0.2$ ‰ in Sagartiidae to  $-15.1 \pm 0.8$ ‰ in *Nephtys caeca*; Table S3, Fig. 3). In contrast, ranges of  $\delta^{15}\text{N}$  values were similar between communities, spanning 8.2‰ in the AFC (from  $9.4 \pm 0.7$ ‰ in *Phaxas pellucidus* to  $17.6 \pm 0.5$ ‰ in *Merlangius merlangus*; Table S2, Fig. 3) and 8.6‰ in the BTC (from  $9.1 \pm 0.2$ ‰ in *P. pellucidus* to  $17.7 \pm 0.1$ ‰ in *M. merlangus*; Table S3, Fig. 3).

Following the pattern observed for sources of OM between sites,  $\delta^{13}\text{C}$  values of primary consumer feeding guilds were lower in the AFC than in the BTC (Fig. S1 in Supplement 1, indicated by a lack of overlap of the 95% confidence ellipses of the bivariate means along the  $\delta^{13}\text{C}$  values axis). In contrast, the confidence ellipses around the isotopic means of higher-order consumer guilds overlapped along the  $\delta^{13}\text{C}$  values axis. The absolute differences in  $\delta^{13}\text{C}$  values between guilds decreased from primary consumers (deposit feeders: 1.6‰, interface feeders: 1.0‰, suspension feeders: 0.5‰) towards higher-order consumers (omnivores/scavengers: 0.6‰, predators/scavengers: 0.1‰; Fig. S1). The standard ellipse areas ( $\text{SEA}_C$ ) of all 3 primary consumer guilds partially overlapped in the AFC, whereas the 2 deposit feeders of the BTC (*Echinocardium cordatum* [ $\delta^{13}\text{C}$ :  $-16.9 \pm 1.0$ ‰,  $\delta^{15}\text{N}$ :  $12.7 \pm 0.4$ ‰] and *Urothoe poseidonis* [ $\delta^{13}\text{C}$ :  $-16.7 \pm 0.3$ ‰,  $\delta^{15}\text{N}$ :  $14.3 \pm 0.4$ ‰]) occupied a distinct isotopic niche located between other primary

and higher-order consumer guilds along the  $\delta^{15}\text{N}$  axis (Fig. 4). In the AFC,  $\text{SEA}_C$  overlap between suspension and deposit feeders was 12.2% of the total non-overlapping ellipse area, while the overlap of interface feeders with suspension and deposit feeders was 24.0 and 36.6%, respectively (Table 1). A similar proportional overlap between interface and suspension feeders (20.1%) was found for the BTC.

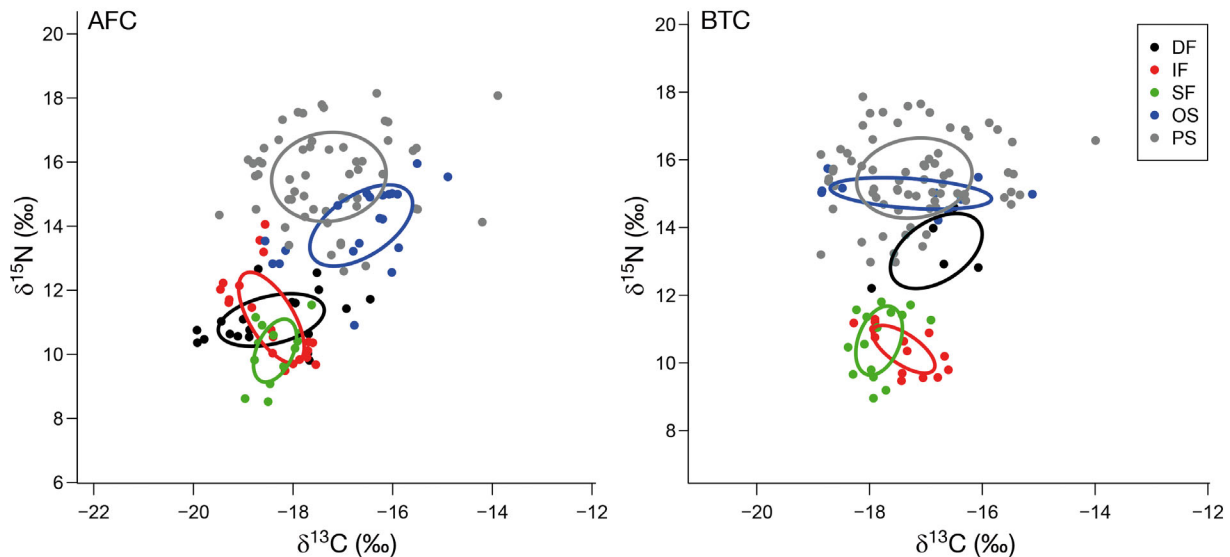


Fig. 4.  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  isotopic niches of consumer feeding guilds (target species and additional taxa) of the *Amphiura filiformis* community (AFC, left panel) and *Bathyporeia*–*Tellina* community (BTC, right panel) as represented by the small sample size-corrected standard ellipse area ( $\text{SEA}_C$ ). Solid lines enclose the  $\text{SEA}_C$  of each guild, while dots represent the isotope compositions of consumer individuals. DF: deposit feeders; IF: interface feeders; SF: suspension feeders; OS: omnivores/scavengers; PS: predators/scavengers

Higher-order consumer isotopic niches did not overlap with those of primary consumer guilds in any community (Fig. 4, Table 1). Among higher-order consumers, the overlap of  $\text{SEA}_C$  between omnivores/scavengers and predators/scavengers was 7.5% in the AFC but 34.1% in the BTC (Table 1, Fig. 4). Suspension feeders in the AFC had a smaller isotopic niche size than deposit and interface feeders (Fig. 5),

with a probability of  $\geq 96\%$  for  $\text{SEA}_B$  being smaller (Table 1). Interface feeders in the BTC had a smaller  $\text{SEA}_B$  than deposit feeders (probability = 95.1%). The probability that the  $\text{SEA}_B$  of any primary consumer guild is smaller than that of higher-order consumers was  $\geq 85\%$  for all comparisons, except for deposit feeders vs. omnivores/scavengers in the BTC, where it was only 40.1% (Table 1, Fig. 5).

Table 1. Small sample size-corrected standard ellipse area ( $\text{SEA}_C$ ) of the 5 feeding guilds of the *Amphiura filiformis* community (AFC) and *Bathyporeia*–*Tellina* community (BTC) food webs (target species and additional taxa), overlap in  $\text{SEA}_C$  (upper, light grey triangular matrices; shown as absolute overlap [%<sup>2</sup>; left number in the table cells] and proportional overlap relative to the total non-overlapping ellipse area [%; right number in the table cells]), and the probability that the Bayesian standard ellipse area ( $\text{SEA}_B$ ) of any guild (in rows) is smaller than that of another guild (in columns), based on the comparison of 4000 posterior draws (lower, dark grey triangular matrices). DF: deposit feeders; IF: interface feeders; SF: suspension feeders; OS: omnivores/scavengers; PS: predators/scavengers

Commu- nity	Guild	$\text{SEA}_C$ (‰ <sup>2</sup> )	DF	IF	SF	OS	PS
AFC	DF	2.54		1.28/36.60	0.41/12.23	0/0	0/0
	IF	2.24	0.608		0.67/24.03	0/0	0/0
	SF	1.20	0.978	0.964		0/0	0/0
	OS	3.48	0.148	0.087	0.002		0.59/7.45
	PS	5.02	0.006	0.002	0	0.085	
BTC	DF	2.54		0/0	0/0	0/0	0/0
	IF	0.90	0.951		0.36/20.05	0/0	0/0
	SF	1.23	0.870	0.241		0/0	0/0
	OS	1.97	0.599	0.043	0.142		1.46/34.14
	PS	3.79	0.132	0	0	0.026	

Based on stable isotope data, the food webs of the AFC and BTC reach TL 4 (Fig. 6, Tables S2 & S3). Within communities, TLs differed significantly between guilds (AFC: ANOVA,  $F_{4,124} = 98.35$ ,  $p < 0.0001$ ; BTC: Kruskal-Wallis test,  $H(4, n = 118) = 73.79$ ,  $p < 0.0001$ ; Fig. 6). In the AFC, TLs of the 3 guilds of primary consumers, i.e. suspension, deposit and interface feeders (range: 2.1–2.4), were similar and significantly lower than those of omnivores/scavengers ( $3.2 \pm 0.4$ ) and predators/scavengers ( $3.6 \pm 0.4$ ) (Tukey's post hoc test,  $p \leq 0.001$ ). Omnivores/scavengers had a lower TL than predators/scavengers ( $p \leq 0.001$ ) (Fig. 6). In the BTC, TLs of interface (2.2  $\pm$  0.2) and suspension feeders (2.3  $\pm$  0.3) were similar and significantly lower than those of omnivores/scavengers ( $3.6 \pm 0.1$ ) and predators/scavengers ( $3.7 \pm 0.3$ )

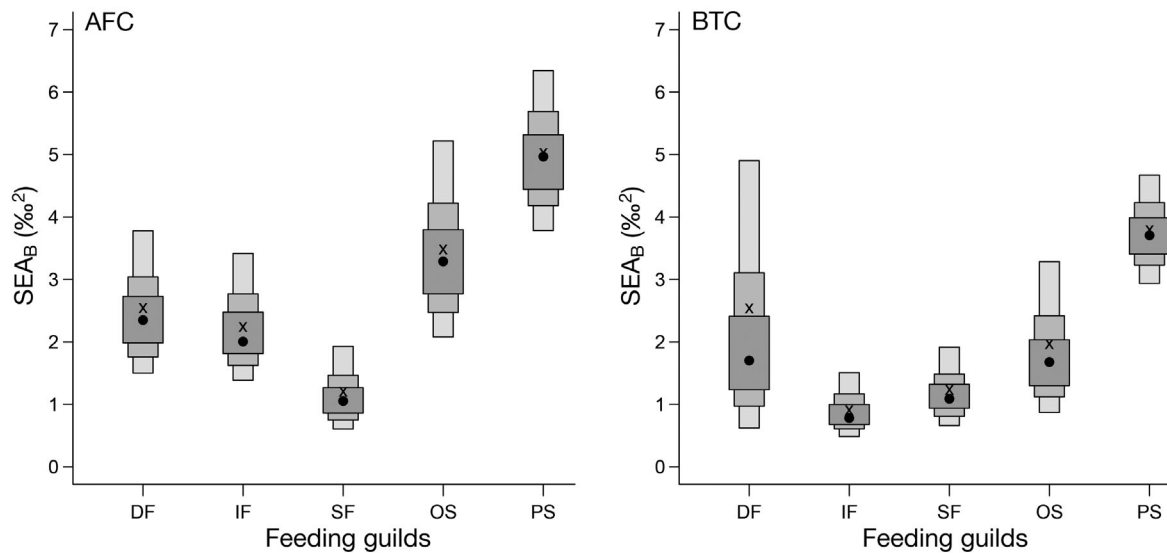


Fig. 5. Density plots of the Bayesian standard ellipse area ( $SEA_B$ , ‰<sup>2</sup>) of the feeding guilds (target species and additional taxa) of the *Amphiura filiformis* community (AFC, left panel) and *Bathyporeia-Tellina* community (BTC, right panel). Light, medium and dark grey boxes represent the 50, 75 and 95 % credible intervals, respectively. Black dots: modes; crosses: standard ellipse area corrected for small sample size ( $SEA_C$ ), shown for comparison. DF: deposit feeders; IF: interface feeders; SF: suspension feeders; OS: omnivores/scavengers; PS: predators/scavengers

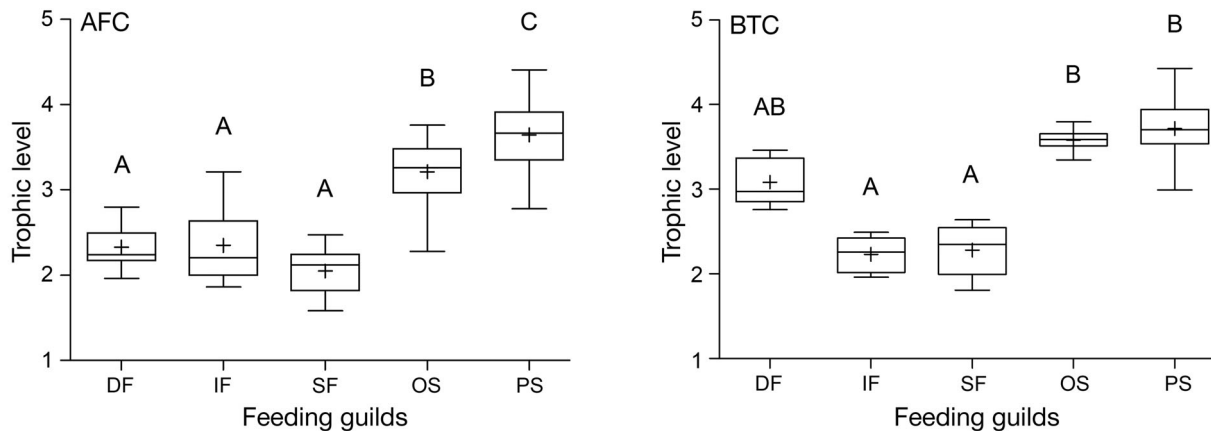


Fig. 6. Isotope-based trophic levels of feeding guilds (target species and additional taxa) of the *Amphiura filiformis* community (AFC, left panel, ANOVA,  $p < 0.0001$ ) and *Bathyporeia-Tellina* community (BTC, right panel, Kruskal-Wallis test,  $p < 0.0001$ ). Boxes: interquartile ranges; horizontal bars: medians; +: means; whiskers: minimum to maximum. Different letters denote significantly different groups (Tukey's and Dunn's post hoc tests for AFC and BTC, respectively). DF: deposit feeders; IF: interface feeders; SF: suspension feeders; OS: omnivores/scavengers; PS: predators/scavengers

(Dunn's test,  $p \leq 0.01$ ). Deposit feeders, however, occupied an intermediate TL ( $3.1 \pm 0.3$ ) and did not significantly differ from any other guild. Omnivores/scavengers and predators/scavengers had similar TLs in the BTC (Fig. 6). The species with the lowest TLs were the suspension feeder *P. pellucidus* (AFC:  $1.8 \pm 0.2$ , BTC:  $1.8 \pm 0.1$ ), the interface feeders *Abra alba* and *A. nitida* (AFC: *A. alba*:  $2.0 \pm 0.1$ , *A. nitida*:  $2.0 \pm 0.1$ ; BTC: *A. alba*:  $2.0$ ) and the deposit feeder *Echiurus echiurus* (AFC:  $2.0 \pm 0.1$ ) (Tables S2 & S3). Fishes of

the orders Scorpaeniformes (AFC and BTC), Gadiformes (AFC and BTC) and Pleuronectiformes (AFC) and the polychaete *Goniada maculata* (BTC) had the highest TLs (TL > 4; Tables S2 & S3). For most taxa, mean TLs  $\pm$  SD overlapped between stations (Fig. 7). The only exceptions were *Echinocardium cordatum* (AFC:  $2.6 \pm 0.1$ , BTC:  $2.9 \pm 0.1$ ), *Eutrigla gurnardus* (AFC:  $3.7 \pm 0.3$ , BTC:  $4.2 \pm 0.1$ ) and *Nemertea* (AFC:  $3.0 \pm 0.3$ , BTC:  $3.5 \pm 0.1$ ), which all had slightly higher mean TLs in the BTC (Fig. 7).

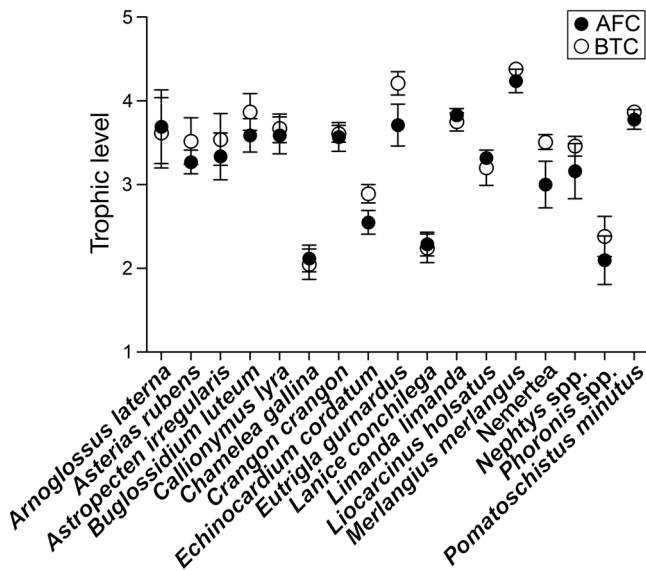


Fig. 7. Comparison of isotope-based trophic levels (mean  $\pm$  SD) of target species and additional taxa ( $n \geq 3$ ) between the *Amphiura filiformis* community (AFC) and *Bathyporeia-Tellina* community (BTC)

The distributions of the 5 community-scale Bayesian Layman metrics were overall very similar for the AFC and BTC, and their 50 % credible intervals mostly overlapped (Fig. 8). The only exception was  $\delta^{13}\text{C}$  range (CR), which had lower values in the BTC and non-overlapping 75 % credible intervals between communities (Fig. 8); however, the difference was not statistically significant (probability that  $\text{CR}_{\text{BTC}} > \text{CR}_{\text{AFC}} = 8.8\%$ ).

### 3.3. Trophic link-based food web analysis

The global trophic link matrix for target species contained 324 species-specific links extracted from the literature (see Table S1 for references) and 351 potential links inferred from average predator-prey body mass ratios (geometric means 27.89 and 4.60 for vertebrate and invertebrate consumers, respectively), yielding 675 links. Community-specific matrices for the AFC and BTC (see Supplement 2 at [www.int-res.com/articles/suppl/m628p017\\_supp2.xlsx](http://www.int-res.com/articles/suppl/m628p017_supp2.xlsx) for matrices and Supplement 1, Section 3 for graphical illustrations of the

food webs) in total contained 355 and 310 links, respectively (Table 2).

Directed connectance (0.29 and 0.25 for AFC and BTC, respectively) and linkage density (10.14 and 8.86 for AFC and BTC, respectively) were similar for both food webs (Table 2). Connectance was marginally lower (0.27 and 0.24 for AFC and BTC, respectively) if only those fishes were considered that met the selection criteria applied to invertebrates (Table 2). Roughly one-third (AFC: 34 %, BTC: 29 %) of the 35 species in each food web (33 consumers, 2 sources of OM) were cannibals (Table 2, see also Figs. S2 & S3 in Supplement 1).

In the AFC and BTC, species most commonly had 0 (sediment OM and suspended POM) to 4 different trophic resources (15 and 14 of 35 species each in the AFC and BTC, respectively; Fig. 9, Figs. S2 & S3), whereas only a few taxa had 20 to 29 prey species (AFC: 5 species, BTC: 4 species). Both food webs shared a well-represented class of consumers with an intermediate range of prey taxa: 9 species had 15 to 19 trophic links per species in the AFC, and 9 species had 10 to 14 links per species in the BTC (Fig. 9). Species linked to only a few trophic resources were either sources of OM or primary consumers (Fig. 9, Figs. S2 & S3). The only exception was the predatory polychaete *G. maculata* in the BTC, which preys on infaunal sedentary polychaetes (Mattson 1981) and only had 1 trophic link in the constructed food web (Fig. S3).

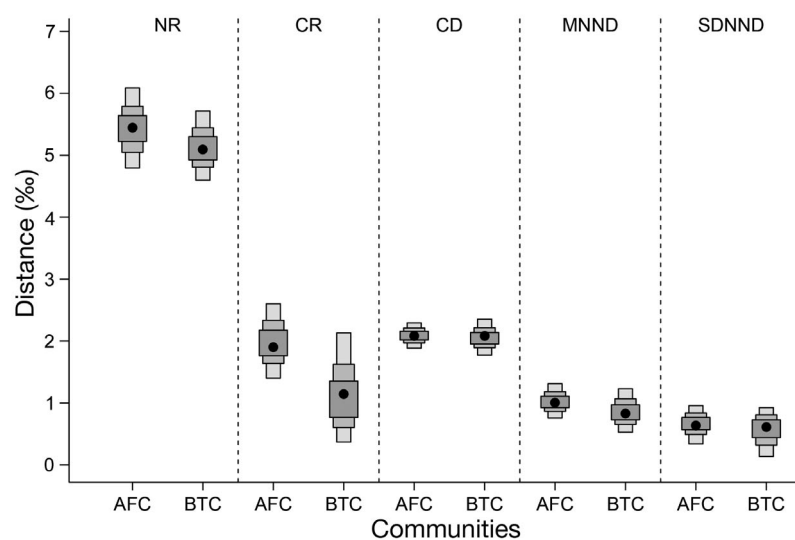


Fig. 8. Density plots of the 5 Bayesian Layman metrics for the *Amphiura filiformis* community (AFC) and *Bathyporeia-Tellina* community (BTC), based on their feeding guild centroids (target species and additional taxa). Light, medium and dark grey boxes, respectively, represent the 50, 75 and 95 % credible intervals. Black dots: modes; NR:  $\delta^{15}\text{N}$  range; CR:  $\delta^{13}\text{C}$  range; CD: distance to centroid; MNND: mean nearest neighbor distance; SDNND: standard deviation of nearest neighbor distance

Table 2. Comparison of descriptive metrics for the food webs of the *Amphiura filiformis* community (AFC) and *Bathyporeia–Tellina* community (BTC) based on target species, as well as for selected food webs from other geographical regions. For the AFC and BTC, the total number of trophic links ( $L$ ) and links extracted at the species level from the literature (in parentheses) are given. All metrics were calculated (1) considering all sampled target species (upper rows; all target spp.) and (2) considering only fishes which met the selection criteria applied to invertebrates (lower rows; selected fishes, see Section 2 for further details).  $S$ : number of species;  $C$ : directed connectance;  $L/S$ : linkage density; Can: number of cannibalistic species; Can (%): percentage of cannibals; NA: not available

Food web	Reference	$L$	$S$	$C$	$L/S$	Can	Can (%)
AFC (all target spp.)	This study	355 (211)	35	0.29	10.14	12	34.3
AFC (selected fishes)	This study	257 (154)	31	0.27	8.29	10	32.3
BTC (all target spp.)	This study	310 (158)	35	0.25	8.86	10	28.6
BTC (selected fishes)	This study	218 (114)	30	0.24	7.27	7	23.3
NE US shelf	Link (2002)	1562	81	0.24	19.28	25	31
Small Caribbean reef	Opitz (1996), Dunne et al. (2004)	556	50	0.22	11.12	21	42
N Baltic Sea	Nordström et al. (2015)	168	36	0.13	4.67	4	11
Arctic	Bodini et al. (2009)	1035	151	0.05	6.85	NA	NA
Antarctic	Raymond et al. (2011), de Santana et al. (2013)	3990	586	0.01	6.81	NA	NA

### 3.4. Method validation: stable isotope-based vs. prey-averaged TLs

Prey-averaged and stable isotope-based estimates of TL were very similar for most species analyzed, and accordingly, the slopes of the standardized major axis regressions (0.92 and 0.90 for AFC and BTC, respectively; Fig. 10) did not significantly differ from unity (AFC:  $r = -0.26$ ,  $p = 0.15$ ; BTC:  $r = -0.28$ ,  $p = 0.13$ , 33 df each). The most notable deviations between the 2 approaches were observed for primary consumers, for which the continuum of TLs revealed by stable isotope analysis could not be captured using binary link data—in the prey-averaged TL approach, all primary consumers are assigned a TL of 2 by definition (Fig. 10, Figs. S2 & S3). These mismatches were also reflected by intercepts signifi-

cantly greater than 0 for both communities (AFC:  $t = 2.07$ ,  $p = 0.05$ ; BTC:  $t = 2.36$ ,  $p = 0.02$ ). Differences from 0, however, became non-significant when primary consumers were excluded from the analyses (AFC:  $t = -0.77$ , 21 df,  $p = 0.45$ ; BTC:  $t = -0.13$ , 22 df,  $p = 0.90$ ).

## 4. DISCUSSION

We examined whether taxonomically distinct benthic communities from contrasting sediments in the German Bight also differ in their trophic structure. The in-depth comparison of the AFC and BTC revealed that although the 2 food webs differ in some features, most notably the feeding guild composition of important primary consumers, most other proper-

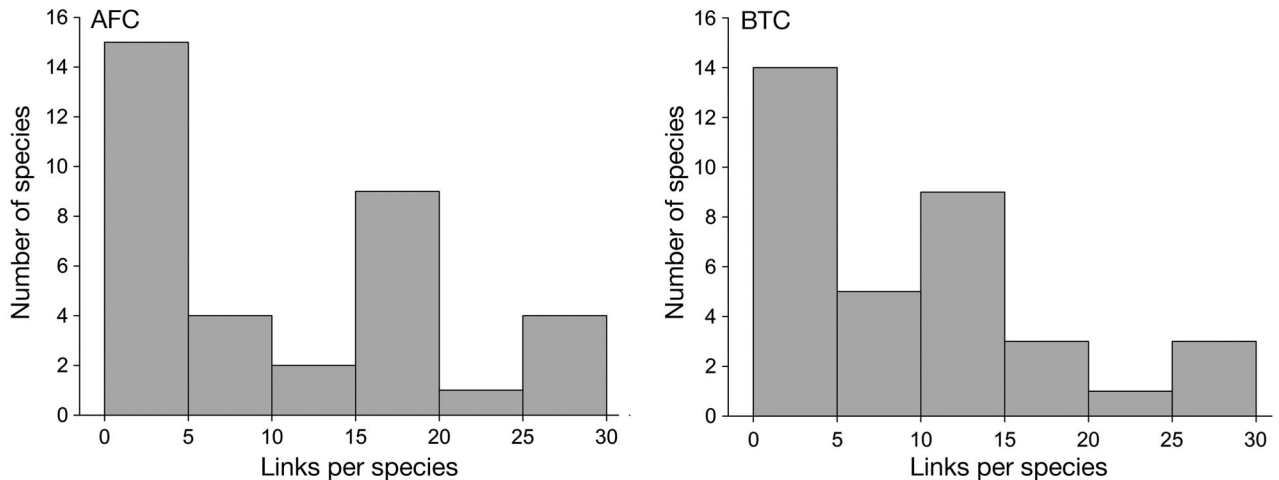


Fig. 9. Distribution of incoming trophic links among target species, including sources of organic matter, of the *Amphiura filiformis* community (AFC, left panel) and *Bathyporeia–Tellina* community (BTC, right panel)



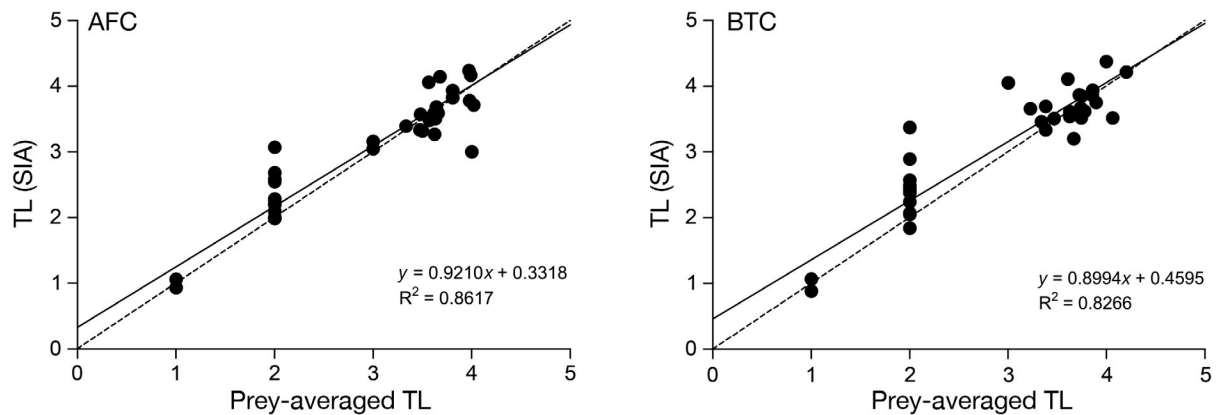


Fig. 10. Prey-averaged trophic levels, TL, calculated from binary trophic link data vs. stable isotope-based trophic levels, TL (SIA), for food resources and target species of the *Amphiura filiformis* community (AFC, left panel) and *Bathyporeia–Tellina* community (BTC, right panel). Dashed lines represent 1:1 relationships; solid lines were fitted using standardized major axis regressions (both  $p < 0.0001$ )

ties were similar. In the following paragraphs, we will (1) revisit the trophic structure of the AFC and BTC, focusing on differences and similarities; and (2) discuss these features in the context of the environmental conditions and the dynamic environment of the southern North Sea.

#### 4.1. Sources of OM for the AFC and BTC

Suspended POM and sediment OM are the 2 basal food resources available for consumers of the AFC and BTC, as the high turbidity in near-coastal areas of the German Bight precludes phyto-benthic growth below 10 to 15 m water depth (Ducrottoy 1999). The  $\delta^{13}\text{C}$  values of suspended POM and sediment OM from AF and BT (ranging from approx.  $-23$  to  $-19\%$ ) suggest that both food sources mostly derive from phytoplankton primary production. However, some input of terrigenous OM likely occurs to the AFC, indicated by the lower  $\delta^{13}\text{C}$  values of suspended POM and sediment OM at AF ( $-1.7$  and  $-1.2\%$ , respectively, compared to BT). Typically,  $\delta^{13}\text{C}$  values of temperate marine phytoplankton range from  $-24$  to  $-18\%$ , whereas more negative ( $-24$  to  $-30\%$ ) values are characteristic of riverine material such as estuarine phytoplankton and river seston (Fry & Sherr 1984 and references therein). Although a differential degree of diagenetic alteration could also underlie or contribute to the observed between-station differences in OM  $\delta^{13}\text{C}$  values (e.g. Freudenthal et al. 2001), rather high concentrations of terrestrial fatty acids in sediments at a nearby location (Station GB in Boon & Duineveld 2012) and the geographic proximity of AF to the Weser and Elbe estu-

aries support our interpretation. Terrestrial OM can be effectively incorporated into coastal marine food webs (e.g. Darnaude et al. 2004a,b), and indeed, primary consumer feeding guilds also had slightly lower mean  $\delta^{13}\text{C}$  values in the AFC than in the BTC. This finding also indicates that differences in  $\delta^{13}\text{C}$  values of food resources are not specific to the particular time of sampling but are more persistent. Although we could not quantify the contribution of fluvial inputs to the AFC food web due to the lack of isotope data for local river POM, absolute  $\delta^{13}\text{C}$  values and rather small differences between stations suggest a minor role compared to suspended POM of marine origin. Furthermore, riverine input is likely limited to near-coastal areas such as AF, and is probably much less important in far-offshore regions also inhabited by an AFC (see community distribution maps in Salzwedel et al. 1985, Fiorentino et al. 2017).

#### 4.2. Differences in the trophic structure of the AFC and BTC

Although several target species were shared by the AFC and BTC, differences between both food webs were apparent in the feeding guild composition of trophically important primary consumers. Deposit and interface feeders dominated among the target primary consumers of the AFC, whereas suspension feeders were the most diverse primary consumer guild in the BTC, followed by interface feeders. This finding reflects the influence of sediment properties on benthic community structure and predominant feeding strategies (e.g. Sanders 1958, Rhoads & Young 1970, Lovell & Trego 2003). Fine-grained

muddy sediments are often dominated by deposit feeders, while suspension feeders are more typical of sandy substrates (Sanders 1958, Rhoads & Young 1970, Snelgrove 1999). The physical instability of muddy sediments, particularly those intensely reworked by deposit feeders, can lead to high loads of suspended material in near-bottom waters, clogging feeding organs of suspension feeders and creating unfavorable conditions for their recruitment (Rhoads & Young 1970). Conversely, the higher contents of OM ( $1.6 \pm 0.7$  vs.  $0.5 \pm 0.1\%$  at AF and BT, respectively) and bacteria in muddy bottoms make them a more suitable habitat for deposit feeders compared to sands (Sanders 1958, Levinton 1972, Lopez & Levinton 2011). The few trophically important deposit feeders in the BTC, such as the urchin *Echinocardium cordatum*, likely depend on suspended POM which transiently settles on the seafloor during slack tide (Jenness & Duineveld 1985) or is injected into the rather organic-poor sandy sediment by advective interfacial water flows caused by ripple-induced horizontal pressure gradients (Huetzel & Rusch 2000).

While the vertical trophic structure was overall similar in both assemblages (see next paragraph), deposit feeders in the BTC occupied an intermediate trophic position between primary and higher-order consumers. In contrast, all 3 primary consumer guilds had a distinctly lower TL than higher-order consumers in the AFC. Target species of the BTC included only 2 species of deposit feeders, *E. cordatum* and *Urothoe poseidonis*, whereas those of the AFC included 6 species. The relatively high TL of *U. poseidonis* in our study indicates that it is probably not only a sand licker or grazer/deposit feeder (e.g. Dannheim 2007, Dubois et al. 2007) but may also selectively feed on a more  $^{15}\text{N}$ -enriched food source, such as sediment meiofauna. Indeed, Lackschewitz & Reise (1998) found remains of diatoms but also nematodes and copepods in the fecal pellets of *U. poseidonis*, supporting this assumption. Incomplete knowledge of the feeding ecology of *U. poseidonis* and a low number of trophically important deposit-feeding taxa in the BTC, which puts a high weight to isotope compositions of individual species, therefore contributed to the intermediate trophic position of this guild. However, *E. cordatum*—the second deposit feeder among target species in the BTC—also had a higher TL in the BTC than in the AFC, suggesting potential habitat-specific differences in its trophic ecology. Growth rates of *E. cordatum* are higher in organic-poor sandy bottoms than in more organic-rich silty sands (Buchanan 1966, Wieking & Kröncke 2003). This apparent contradiction was attributed to

the higher quality of OM generally found in sands (e.g. Jenness & Duineveld 1985, Wieking & Kröncke 2003), combined with the greater ingestion efficiency of *Echinocardium* in loose sediments (Buchanan 1966, Wieking & Kröncke 2003). The greater accessibility of high-quality OM in sandy habitats might not only affect the growth of urchins but could also lead to a more selective feeding behavior, i.e. a preferential ingestion of particular fractions of the sediment OM pool, affecting their TL. Indeed, selective feeding of *E. cordatum* has been confirmed by a greatly enriched organic content in its digestive tract compared to the ambient substrate (De Ridder et al. 1984, Boon & Duineveld 2012) and the observation that starved individuals consume a higher proportion of surface sediment than normally fed ones (De Ridder & Jangoux 1985). Boon & Duineveld (2012) further found a higher selectivity for particular food compounds in *E. cordatum* in habitats with low food concentrations, suggesting that urchins might even be able to adapt their degree of selectivity according to food availability.

#### 4.3. Common features of the AFC and BTC food webs

Despite the differences mentioned in the previous paragraph, we found many similarities between the food webs of the AFC and BTC, including their dependence on phytoplankton primary production. While some of the primary consumers in the AFC and BTC exploit food resources exclusively via suspension or deposit feeding, several of the most abundant macrobenthic taxa, such as the brittle star *Amphiura filiformis* (AFC), the bivalves *Abra* spp. (AFC) and *Fabulina fabula* (BTC) and the polychaete *Magelona johnstoni* (BTC), are interface feeders which can facultatively utilize suspended or deposited OM depending on its availability (Lopez & Levinton 1987). These trophically versatile taxa are well adapted to the environmental conditions in the German Bight, which are characterized by the influence of tidal currents and, consequently, variable near-bottom current velocities (Duineveld & Boon 2002). Indeed, the importance of local hydrodynamics and pelagic-benthic coupling for both food webs was also suggested by the lack of clustering of primary consumer species by guild affinity (stable isotope biplots) and the partial overlap of  $\text{SEA}_C$  between suspension and deposit feeders (except for the BTC, see previous paragraph), which point to an overlapping resource use among primary consumers. According to

model estimates, as much as approximately 24 % of the phytoplankton net primary production can reach the sea floor in the Southern Bight of the North Sea (Lancelot et al. 2005), where it forms the basis for high benthic productivity (Ducrotoy 1999, OSPAR Commission 2000). Deposit feeders in the southern North Sea may therefore frequently ingest freshly settled water column POM, while conversely, suspension feeders in dynamic shallow water settings are often exposed to resuspended bottom deposits (see Grant et al. 1997, Sarà 2007), e.g. during storm events. The longer-term pool of sediment OM with its lower  $\delta^{13}\text{C}$  values, on the other hand, does not seem to be a major food resource for deposit feeders in the German Bight, as the position of their guild  $\text{SEA}_\text{C}$  on the  $\delta^{13}\text{C}$  axis is closer to that of suspended POM. However, this finding cannot be generalized to the species level (see e.g. the rather low  $\delta^{13}\text{C}$  values of some deposit feeders in the AFC and their generally wider guild  $\text{SEA}_\text{C}$  compared to suspension feeders). Furthermore, the relative importance of fresh suspended POM and sediment OM for deposit feeders may vary over the course of the year depending on phytoplankton productivity, although seasonal sampling designs are needed to test this hypothesis.

At the community level, the trophic structure overall was very similar between the AFC and BTC, as indicated by the overlap of the 50 % credible intervals for most Bayesian Layman metrics. This suggests that not only the trophic length of the AFC and BTC (given by NR) but also their average trophic diversity (CD) and redundancy (MNND and SDNND) are similar. Regarding their vertical extension, both food webs reached TL 4, with the highest TLs—according to  $\delta^{15}\text{N}$  values—occupied by fishes (in the AFC and BTC) and the carnivorous polychaete *Goniada maculata* (only in the BTC). Similar results were obtained when constructing the food webs from binary trophic link data between target species, although nemerteans were among the top consumers in the AFC, while *Goniada* was not among those in the BTC. Food webs with 4 TLs are known from various geographic regions, e.g. the temperate Bay of Banyuls-sur-Mer (French Mediterranean coast; Carlier et al. 2007) and northern Bay of Biscay (French Atlantic coast; Le Loc'h et al. 2008), but also from the coastal habitats of Antarctica (Gillies et al. 2013).

The linkage densities observed for the AFC and BTC in this study (10.14 and 8.86, respectively) and the distribution of trophic links among consumers suggest that many higher-order consumers in the German Bight are trophic generalists. We are aware

that the inclusion of trophic links inferred from literature diet data at supraspecific resolution may cause an overestimation of linkage density (and directed connectance) values and their similarity between communities, as (1) not all inferred links might actually be realized, and (2) potential links were inferred using the same constraints (predator–prey body mass ratios) for both communities. However, considering the commonness of unspecialized feeding in the marine realm (Link 2002, Dunne et al. 2004) and that all involved taxa are target species (i.e. likely represent readily available prey at AF and/or BT), we are confident that the obtained values provide a more realistic picture of the actual food webs than would the omission of a large body of diet information, because it was not available at species-level resolution. Species with broad prey spectra play an important role in food webs of spatially expansive (e.g. marine) ecosystems, as they can adapt their diet according to the availability of prey items and dampen oscillations in prey populations (McCann et al. 2005a,b). Trophic generalists thereby exert a stabilizing effect on biological communities (MacArthur 1955).

The directed connectance of the AFC and BTC food webs was high (0.29 and 0.25, respectively), even slightly exceeding that of other highly connected marine food webs (see e.g. Dunne et al. 2004, covering a connectance range of 0.22–0.24). This was not merely an artifact of the unselective inclusion of sampled fishes, as these numbers were only marginally lower (0.27 vs. 0.29 and 0.24 vs. 0.25 for the AFC and BTC, respectively) when selecting fishes based on the criteria applied to invertebrates. Marine food webs with a similarly high connectance have been observed in the heavily anthropogenically impacted northeastern US continental shelf ( $C = 0.24$ , including pelagic and benthic taxa; Link 2002) and the Puerto Rico–Virgin Islands shelf complex (the small Caribbean reef food web,  $C = 0.22$ ; Opitz 1996, Dunne et al. 2004), while lower connectance was reported, for example, for the Baltic Sea ( $C = 0.13$ ; Nordström et al. 2015) as well as the Arctic and Antarctic ( $C = 0.05$  and  $0.01$ , respectively; de Santana et al. 2013). High connectance increases the robustness of food webs against secondary extinctions (Dunne et al. 2002a, 2004) and, together with the prevalence of trophic generalists, suggests a high robustness of the AFC and BTC food webs. Our findings thus corroborate previous studies reporting high trophic redundancy, resistance and resilience of benthic communities in the German Bight (Dannheim 2007, Shojaei 2016).

## 5. CONCLUSIONS

Our results highlight that although the AFC and BTC in the German Bight differ in some aspects of their trophic structure, they share many similarities. Differences were evident in the proportional species richness of primary consumer guilds among target species, highlighting the significance of sediment properties, local hydrodynamics and food availability as determinants of benthic trophic structure. The distinct isotopic niche of deposit feeders vs. other primary consumers in the BTC might reflect a difference in the trophic ecology of deposit feeders in the sandy and rather organic-poor substrates at BT compared to the more muddy site AF, although further studies involving a larger number of deposit-feeding taxa from the BTC are required to test the generality of our findings. Most food web properties, however, are similar between the 2 food webs, including their dependence on pelagic primary production, partially overlapping isotopic niches of primary consumers, top consumers reaching TL 4, a prevalence of generalist consumers and high directed connectance. The latter feature suggests a considerable robustness of the trophic networks against secondary extinctions, consistent with the pronounced population fluctuations characteristic for many benthic taxa in the dynamic shallow-water environment of the German Bight. The robust network properties and generalism of consumers likely play an important role in buffering ecosystem functioning against potential changes in community composition resulting from exceptionally cold winters, climatically induced range shifts, species extirpations and/or biological invasions.

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