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Subtidal temperate reefs in marginal seas enhance biodiversity, food web complexity, and ecosystem stability

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ABSTRACT: Marine reefs are habitats that underpin key ecosystem services, including supporting diverse faunal communities. However, the ecological functioning of reefs in subtidal temperate waters has remained underexplored. Simultaneously, interest in restoring lost reefs is increasing due to the establishment of marine protected areas and the development of offshore wind farms. To explore the ecological importance of these reefs, we investigated how different subtidal temperate reef types affect faunal communities and their food web structures in the North Sea as an example of a temperate sea. We focused on the shallow nearshore Voordelta and the deeper offshore Borkum Reef Grounds in the Netherlands. Both sites hosted either geogenic (rocks) and/or biogenic (*Lanice conchilega* or bivalve) reefs, which we compared to a sandy non-reef reference. We sampled benthic macrofauna using box corers or grabs and mobile communities with baited traps and reconstructed food webs using stable isotope analysis and the literature. Results showed that reef presence enhanced benthic taxa richness, evenness, and abundance, with biogenic reefs creating intermediate communities between sand and rocks. Certain species of commercial interest (*Cancer pagurus* and *Trisopterus luscus*) were positively associated with the reefs. Reefs were found to increase food web complexity and connectivity, which are linked to the network's stability and resilience to disturbances and influence the proportion of intermediate consumers. We conclude that temperate subtidal reefs enrich ecosystems and stabilise food webs, suggesting that their restoration and conservation could help mitigate anthropogenic impacts and enhance the overall health of marine ecosystems.

KEY WORDS: Temperate subtidal reefs · Marine biodiversity · Food web complexity · North Sea ecosystems · *Lanice conchilega* · Oyster reef · Rocky reef · Ecological restoration

1. INTRODUCTION

Identifying and characterising key habitats that support biodiversity is crucial for addressing the increasing degradation of marine ecosystems and enhancing their resilience (Hitchman et al. 2018). Marine reefs are highly productive habitats, critical for maintaining biodiversity as they provide substrates,

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foraging, shelter, and nursery grounds for a wide range of species (Moberg & Folke 1999, Beck et al. 2001, Spalding et al. 2001). Reefs also underpin key ecosystem services, including food provisioning and support for a diverse array of species, including some of commercial value, while contributing to nutrients, carbon cycling, and carbon burial (Grabowski et al. 2012, Pratchett et al. 2014, zu Ermgassen et al. 2016, Lee et al. 2020).

Reefs are defined as 3-dimensional structures that rise above the seafloor and create distinct habitats from the surroundings (Brown et al. 1997). Geological formations like rocks form geogenic reefs, while biogenic reefs result from the accumulation, entanglements, or growth of external structures produced by organisms defined as ecosystem engineers (Jones et al. 1994, Holt et al. 1998). Coral reefs in tropical and subtropical regions are the most well-known examples of biogenic reefs with disproportionate impacts on biodiversity (Spalding et al. 2001, Messmer et al. 2011). In temperate latitudes, biogenic reefs are built predominantly by ecosystem engineers such as oysters, mussels, and polychaete worms (Holt et al. 1998, Lenihan & Peterson 1998, Hendrick & Foster-Smith 2006, Lindenbaum et al. 2008, Rabaut et al. 2009). Over the past decade, interest in temperate reefs has grown, with increasing research efforts aimed at characterizing and describing their ecological functioning and value (Rabaut et al. 2009, Coolen et al. 2015, Jenkins et al. 2018, Fariñas-Franco et al. 2023).

Investigating temperate reefs presents numerous challenges, particularly in subtidal areas, where highly energetic environmental conditions require complex and costly logistics, including the use of specialised research vessels and expensive instruments to access these habitats (Støttrup et al. 2014). Moreover, the transient nature of some polychaetae reefs, such as those formed by sabellarids (*Sabellaria spinulosa* or *S. alveolata*) or *Lanice conchilega*, complicates long-term monitoring efforts (Zühlke 2001, Callaway et al. 2010, Polgar et al. 2015). Another major obstacle in studying temperate reefs is their substantial degradation over centuries due to human activities, including intense bottom disturbances like trawling, dredging, mineral and boulder extractions, and overharvesting of oysters or mussels (Beck et al. 2001, Airoldi et al. 2008, Cook et al. 2013, Støttrup et al. 2017). These activities have led to a dramatic global decline in reef extent, particularly oyster reefs, which have reduced by 85% since the 1700s (Beck et al. 2011, zu Ermgassen et al. 2012). This has resulted in the functional extinction of the European oyster *Ostrea edulis* (Thurstan et al. 2024, zu Ermgassen et al. 2024) and in significant losses of other species like the Atlantic oyster *Crassostrea virginica*, which has halved in Chesapeake Bay and other coastal areas (Rothschild et al. 1994, zu Ermgassen et al. 2012, Gillies et al. 2020). Moreover, there is a lack of comprehensive historical data on the presence and extent of other temperate reefs, posing challenges in assessing the degrees of habitat loss quantitively and qualitatively, including gaps in knowledge regarding pristine temperate reefs (Fariñas-Franco et al. 2023).

Recognizing their importance, international agreements (e.g. Ramsar Convention, EU Habitat Directive, OSPAR Commission, Fisheries Act) now classify temperate reefs as needing special conservation efforts. Within European waters, marine protected areas (MPAs) and special conservation areas are being implemented by local legislations to maintain and protect existing reef habitats. Restoration projects for oyster reefs are gaining momentum in Europe, Australia, and other regions (zu Ermgassen et al. 2020, Howie & Bishop 2021), although in many places, including Europe, oyster restoration is still in its infancy. Restoration projects targeting sabellarids are still in the early stages and face limitations due to the lack of an established method for transporting transplants (Franzitta et al. 2022). Some debates still exist on whether *L. conchilega* qualifies as a reef-building species (Rabaut et al. 2009), and as such, no indications of active restoration projects for this species have been found. More published work exists on oysters, although it is still mostly focused on the Atlantic oyster *C. virginica*, which may offer some transferability to reefs of other species but also lead to erroneous assumptions and compromise restoration success (Fitzsimons et al. 2020, Gillies et al. 2020, zu Ermgassen et al. 2020). Understanding the specific needs of ecosystem engineers that build reef ecosystems and of reefs in a healthy state is essential for designing effective metrics for successful interventions (Howie & Bishop 2021).

Despite the growing body of knowledge surrounding temperate reefs, gaps remain, as many studies have been performed on restored habitats (Green & Crowe 2013, Støttrup et al. 2014), intertidal habitats (Rabaut et al. 2009, Callaway et al. 2010, De Smet et al. 2015a,b), or recovering ones (Christianen et al. 2017, Fariñas-Franco et al. 2023), leaving a lack of understanding of habitats in their optimal conditions. Moreover, incorporating food web analysis into ecological studies has proven more beneficial in deepen-

ing the understanding of ecosystem functioning compared to classical biodiversity metrics (Christianen et al. 2017). Currently, most literature on temperate reefs that incorporates the analysis of food webs has focussed on intertidal or sheltered ecosystems (Christianen et al. 2017, Nauta et al. 2023a, Witte et al. 2024) or solely on larger fauna (Kent et al. 2017).

This work aims to contribute to the foundational knowledge of natural temperate reefs and explore their community structure and food web dynamics. Specifically, we aim to test the hypothesis that temperate subtidal reefs enhance biodiversity and the complexity of the food webs, thereby contributing to their overall stability (Dunne et al. 2004), comparably to what was found in other studies on temperate reefs (Christianen et al. 2017, Borst et al. 2018, Nauta et al. 2023a, Witte et al. 2024). The North Sea was selected as a suitable model system for temperate seas for 3 reasons. Firstly, it is home to several geogenic and biogenic reefs, such as bivalve reefs (*Modiolus modiolus*, *Mytilus edulis*, *O. edulis*, and *Magallana gigas*), but also polychaetes reefs (*S. spinulosa*, *L. conchilega*). Secondly, recent evidence suggests temperate reef recovery in the North Sea, either through natural occurrence (*O. edulis*, Christianen et al. 2018; *L. conchilega*, Coolen et al. 2015) or as a result of restoration efforts (geogenic reef; Støttrup et al. 2017). Thirdly, one of the selected locations (Voordelta) presented a unique reef built by a mix of different bivalve species like *M. edulis* and *O. edulis* but also the invasive species *M. gigas*. The combination of existing geogenic reefs and biogenic reefs presents an exclusive opportunity to investigate temperate subtidal reef systems.

To test our hypothesis, we studied 2 areas with subtidal temperate reefs: the Borkum Reef Grounds and the Voordelta in the southern North Sea. Both sites hosted either geogenic (rocks) and/or biogenic (*L. conchilega* or bivalve) reefs, which we compared to a sandy non-reef reference. The objectives of the study were to gather insight into (1) the effect of different reef habitats on faunal community composition, diversity, evenness, and abundance and (2) whether such effect varies between biogenic and geogenic reefs. We then reconstructed the food webs for each community using stable isotopes and calculated basic metrics to (3) characterize and compare food webs for each habitat. The faunal communities targeted within this study were macrobenthic (invertebrate epifaunal and infaunal species of >1 mm) and mobile communities (mobile species of >1 cm), including species of commercial interest for fishery such as crabs, lobsters, and fish.

2. MATERIALS AND METHODS

2.1. Study areas: the Borkum Reef Grounds and the Voordelta

To investigate the biodiversity and complexity of temperate subtidal reefs, we selected 2 areas in the Dutch North Sea: the Borkum Reef Grounds and the Voordelta (Fig. 1A). These areas each feature 2 different types of reefs and a sandy reference area at a comparable distance from each other (range area of 2–2.5 km^2), allowing for a comparative analysis of reef effects on communities and bare areas without reefs (Fig. 1B,C). The Borkum Reef Grounds, selected as the deeper offshore site, is located approximately 20 km off the island of Borkum (Fig. 1). This area includes a rocky reef (estimated area: 9.8 km^2; Coolen et al. 2015) (Fig. 1D) and a *Lanice conchilega* reef with patches reaching densities of over 1500 ind. m^{-2} (estimated area: 74 km^2; Coolen et al. 2015) (Fig. 1E) at depths of 24–26 m (Fig. 1B). The Voordelta, selected as a shallower nearshore area, is located near the coast of Zeeland at depths of 2–6 m (Fig. 1C) and supports 2 types of biogenic reefs. These include a mixed bivalve reef (estimated area: 0.54 km^2; Kamermans et al. 2024, Christianen et al. 2018) (Fig. 1F) composed of *Ostrea edulis*, *Magallana gigas*, and *Mytilus edulis*, with reported densities of around 7, 19, and 9 ind. m^{-2}, respectively (Christianen et al. 2018). Additionally, the Voordelta hosts an *L. conchilega* reef with patches exceeding 2000 ind. m^{-2} (van der Have et al. 2019) (Fig. 1G). Both areas were surveyed in 2020 during 2 distinct research cruises; respectively, between 31 August and 12 October 2020 and between 14 and 17 October 2020. At the Voordelta, additional faunal samples for stable isotope analysis were taken on 29 October and 6 November 2020.

2.2. Sampling design

To locate the actual position of the reefs and define the sampling stations, ground-truthing of the seabed was performed at the Borkum Reef Grounds using an HD-towed underwater camera. The video was live-streamed onboard to be scrutinized in real time for the presence and approximate percentage cover of the targeted features (*L. conchilega*, rocks, sand). The seafloor assessment was logged and linked to the vessel position. A sampling grid was then projected on the convex hulls around the logged positions with the highest density of *L. conchilega* or rocks. Sampling stations were randomly selected along the grids

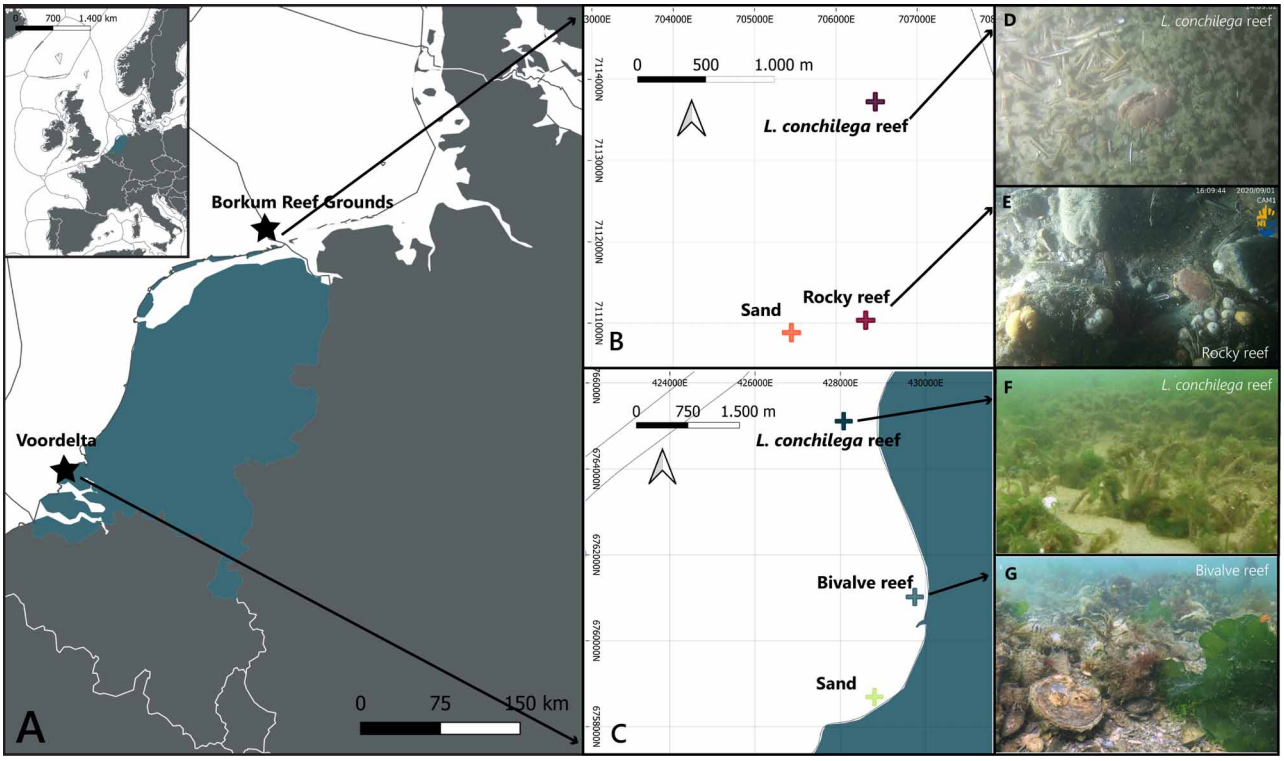

Fig. 1. (A) Location of the 2 study areas: the deeper offshore site, Borkum Reef Grounds, and the shallower nearshore site, Voordelta, in the Dutch North Sea. (B) Close-up view of the position of the 3 sampled habitats at the Borkum Reef Grounds (*Lanice conchilega* reef, rocky reef, sand) and the Voordelta (*L. conchilega* reef, bivalve reef, sand), indicated by the plus signs. Seafloor picture of (D) the *L. conchilega* and (E) rocky reef at the Borkum Reef Grounds, obtained with an HD towed camera during the survey. Seafloor picture of (F) the *L. conchilega* and (G) bivalve reef at the Voordelta, from van der Have et al. (2019)

in reef habitats and the sandy reference area. Moreover, to target high-density patches of *L. conchilega* reef, a drop camera was mounted on the box corer. Selected stations are indicated in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m764p015_supp.pdf.

At the Voordelta, ground-truthing of the seafloor was not possible prior to designing the sampling stations. Hence, the sampling stations were based on the available positions of *L. conchilega* and bivalve reefs from the video survey conducted by van der Have et al. (2019). Selected stations are indicated in Fig. S2.

2.3. Sampling of biota for biodiversity and food web reconstruction

To compare macrobenthic communities across habitats at the Borkum Reef Grounds and Voordelta, sediments were sampled using a 30 cm diameter box corer at 4 stations per habitat, retrieving one sample per station as a single replicate. At the rocky reef, a Hamon grab was used for 3 of the 4 samples due to the coarse sediments (Fig. 1A,B & Figs. S1 & S2). The sampled surface area was 0.07 m^2 for the 30 cm box core and 0.024 m^2 for the Hamon grab on coarse sediment (calculated using Hamon grab specifications and assuming no frame penetration). In total, 4 replicates per habitat were collected at both locations. All samples were immediately sieved onboard through a 1 mm mesh and fixed in buffered 4% formalin. Large boulders and rocks were preserved whole (with fauna attached). Samples were further processed in the laboratory of the Royal Netherlands Institute for Sea Research (NIOZ), where all faunal specimens were picked from the samples and thoroughly scraped from the rocks. Then, they were all identified to the lowest possible taxonomic level by taxonomists, and individuals were counted to assess the richness of taxa and individual density per sample. Individual abundance was converted to ind. m^{-2} based on the sampled surface area.

Mobile fauna was sampled through sets of baited traps of different sizes to capture species of different dimensions. Each set consisted of one squared metal cage (150 × 150 × 75 cm; mesh: 2 cm), to which were

mounted one fyke (60 × 40 × 30 cm; mesh: 2 cm) and one smaller fyke (mesh: 0.5 cm), all baited with pieces of frozen mackerel packed in nylon stockings. Trap sets were equally distributed across the different habitats in both areas. They were deployed on the seafloor for 24 h to minimize the effect of tidal shifts and ensure uniform sampling across habitats. At the Borkum Reef Grounds, 8 sets were deployed on 3 consecutive days, with the sets split across habitat on each day, obtaining a final total of 8 replicates per habitat (Fig. 1B & Fig. S1). At the Voordelta, 6 sets were deployed twice, equally split across the habitats, obtaining a final total of 4 replicates per habitat (Fig. 1C & Fig. S2). Due to adverse weather conditions, the second deployment was left for 48 h instead of 24 h. Upon finding no significant differences in the species collected between 24 and 48 h, the data of the 48 h deployment was corrected by dividing the number of individuals by 2 (Table A1 in the Appendix). All specimens caught inside the traps were counted, identified to the lowest possible taxonomic level, measured, and weighed. Individual abundances were calculated by summing all catches per cage setup, with each setup treated as an individual replicate.

The species lists obtained from the analysis of the benthic macrofauna samples and mobile fauna catches, which span multiple trophic levels, were jointly used to reconstruct food webs for each habitat in both study areas (Table S1).

2.4. Sampling and chemical analyses to complement the food web reconstruction

Stable isotope analysis further identified trophic links among species within food webs. Stable isotope samples for carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) were collected from prevalent species across all habitats in both study areas, including available primary producers. At the Borkum Reef Grounds, stable isotope samples from benthic macrofauna were collected through additional box cores or grabs, consecutive to the sampling for macrobenthic biodiversity at all sampling stations. By contrast, mobile megafauna tissue samples were taken from the catches of baited traps. At the Voordelta, benthic macrofauna for stable isotope collection was sampled with a grab, and scientific SCUBA divers manually collected mobile species from all 3 habitats. In both study areas, 3–5 individuals were targeted per species per habitat. Suspended particulate matter (SPM), water-column particulate organic matter (wPOM), and surface sediments were sampled to obtain primary sources, targeting 3–5 samples per habitat in both study areas. SPM was obtained from the overlaying water of box cores, while wPOM was collected from surface water using a Niskin bottle or a clean bucket.

Sample processing was performed onboard (Borkum Reef Grounds), in the lab, or onshore (Voordelta). For larger animals, tissue samples were taken from muscular tissue, while for smaller invertebrates, the whole body, excluding the guts, was collected. SPM and wPOM water samples were filtered through precombusted Whatman GF/F glass fibre filters until the filter was clogged. Surface sediments were scooped directly from box cores or grabs, ensuring minimal disturbance to sediment structure. Samples were then frozen at −20°C before transferring to the lab.

All samples were freeze-dried in the lab for 48 h and homogenized through pestle and mortar. Small samples containing inorganic carbonates (e.g. filters) were decalcified using drops of 2 M HCl in silver cups. Sub-samples of sediments and animals containing inorganic carbonates (i.e. whole crustaceans) were decalcified using 2 M HCl and measured following Jacob et al. (2005). Finally, samples were weighed in tin cups, or silver cups (for decalcified fractions), and analysed for $\delta^{13}C$ and $\delta^{15}N$ using a Vario ISOTOPE cube elemental analyser, coupled to an isoprime vision isotope ratio mass spectrometer (both Elementar).

2.5. Statistical analysis and food webs networks

Statistical analysis was performed in R (v.4.2.2, R Core Team 2022), through R studio (v.2023.12.0369, RStudio Team 2020). Main community indices such as Shannon-Wiener, Simpson, and Pielou's evenness were calculated using the R package 'vegan' and the 'diversity' function (Oksanen et al. 2022). Taxa richness and abundance were tested for significant differences among reefs and sand habitats. We first applied generalized linear models (GLMs) with gamma, Poisson, or negative-binomial distributions (package 'MASS', Brian et al. 2024). Richness was fitted with a Poisson distribution, ecological indices (Shannon, Simpson's, Pielou's) with a gamma distribution, and individual abundances and abundances of different phyla (macrofauna) or species (mobile) with negative-binomial or Poisson GLMs, respectively. Model selection was based on the lowest Akaike information criterion (package 'car', Fox et al. 2023), and the model fit was checked by examining the residuals for overdispersion. Analysis of variance (ANOVA; package 'car') was then conducted on the selected models to check for significant differences among habitats.

Tukey's HSD post hoc test was performed on the estimated marginal means (package 'emmeans', Lenth 2016) to test which habitats were driving the differences. Differences were considered significant at a threshold of $p < 0.05$. To address potential temporal variations due to differences in deployment durations of the cages at the Voordelta, a generalized linear mixed-effects model ('lme4' package, Bates et al. 2015) with deployment time as a random effect and Poisson distribution was employed, again followed by ANOVA and Tukey's HSD post hoc test. All statistics are reported in Table A1. To assess differences in macrobenthic community composition across habitats, we performed a PERMANOVA using the 'adonis' function (package 'vegan', Oksanen et al. 2022), with 999 permutations and using Bray-Curtis similarity. Furthermore, we performed a principal coordinates analysis (PCoA) and a SIMPER analysis (Text S1).

Food web networks were reconstructed based on the species found in the different habitats in both study areas. First, a self-constructed interaction matrix was generated based on the total species list obtained for each area (Borkum Reef Grounds and Voordelta). Here, all possible trophic relationships among consumers and their prey were assessed. Primary sources were added manually to the matrix when observed in the box core or seafloor pictures collected during previously performed surveys in the area (sediments, diatoms, phytoplankton, chlorophyte, rhodophyte, phaeophyceae; van der Have et al. 2019). All potential trophic links among species and sources were scored based on the literature (see supplementary data at https://doi.org/10.25850/nioz/7b.b.tj), available databases (i.e. FishBase, GLOBI, BIOTIC), and expert knowledge. Secondly, a single matrix was generated for each habitat at both study areas, removing rare species (non-colonial species with a total abundance of $n < 3$ individuals per habitat) to include only ecologically relevant species interactions. The resulting matrices were further filtered for the most frequently recurring species based on their $\delta^{13}C$ and $\delta^{15}N$ values (Table S2) and stable isotope mixing models, 'SIMMR' (Govan & Parnell 2019). These models were used to calculate the dietary proportion of the ingested consumer. When needed, sources were pooled based on their isotopic signature and taxonomic relatedness to restrain the maximum number of sources per consumer to $n = 10$. When a source contributed less than 5% to the consumer diet, it was removed from the interaction matrix. Finally, classical food web metrics were calculated on the obtained matrices (Table S3), using methods from Borst et al. (2018) and including number of species, link density (links / number of species), connectance (links / number of species^2), and maximum trophic level. Moreover, fractions of basal species (without prey), intermediate species (with prey and predators), and top species (without predators) were also calculated on the obtained matrices (Borst et al. 2018).

3. RESULTS

3.1. Benthic macrofauna and mobile taxa inside and outside reefs

The raw data are available online (see supplementary data at https://doi.org/10.25850/nioz/7b.b.tj). A total of 109 benthic macrofauna taxa and 17 mobile taxa were sampled at the Borkum Reef Grounds, and 117 benthic and 16 mobile taxa at the Voordelta (see Table S1 for abundance per taxa per habitat per area). Taxa richness of benthic macrofauna was significantly higher within reef compared to sand at the Borkum Reef Grounds (1-way ANOVA; $F_{2,9} = 12.48$, $p < 0.01$), while both richness and abundance of individuals of benthic macrofauna were significantly higher within reef habitats than sand in the Voordelta (1-way ANOVA; $F_{2,9} = 56.35$, $p < 0.001$ and $F_{2,9} = 17.11$, $p < 0.001$, respectively; Fig. 2, Table 1 & Table S1). Mobile fauna, however, showed no significant difference among habitats (see Fig. 4). Overall, 55 taxa out of 124 were found exclusively in the *Lanice conchilega* reef, 27 in the rocky reef, and 12 in the sand at the Borkum Reef Grounds. At the Voordelta, 53 taxa out of 130 were found exclusively in the bivalve reef, 27 in the *L. conchilega* reef, and 13 in the sand (Table S1).

At the Borkum Reef Grounds, the *L. conchilega* reef had the highest mean (±SE) number of taxa per sample (32.50 ± 4.86), followed by the rocky reef (29.25 ± 1.31) and the sand habitat (15.25 ± 1.03; Fig. 2A, Table 1). In terms of abundance of individuals, the *L. conchilega* reef also had the highest mean per sample (524 ± 198.15 ind. m^{-2}), followed by sand (218.75 ± 46.61 ind. m^{-2}) and the rocky reef (216 ± 51.51 ind. m^{-2}). The macrobenthic community at the rocky reef, however, was the most diverse (mean Simpson index: 0.85 ± 0.05) and uniformly distributed (mean Shannon index: 2.52 ± 0.2, Pielou's: 0.75 ± 0.07) compared to the other habitats at the Borkum Reef Grounds (Fig. 2B, Table 1).

At the Voordelta, the mean taxa richness was higher at both reefs (bivalve reef: 52.50 ± 0.29, *L. conchilega*: 30 ± 3.81) compared to sand (6.25 ± 1.97; Fig. 2A, Table 1). The mean abundance of individuals was also greater at the bivalve reef (1666.75 ± 364.94 ind. m^{-2}), followed by the *L. conchilega* reef (237.50 ± 81.49 ind.

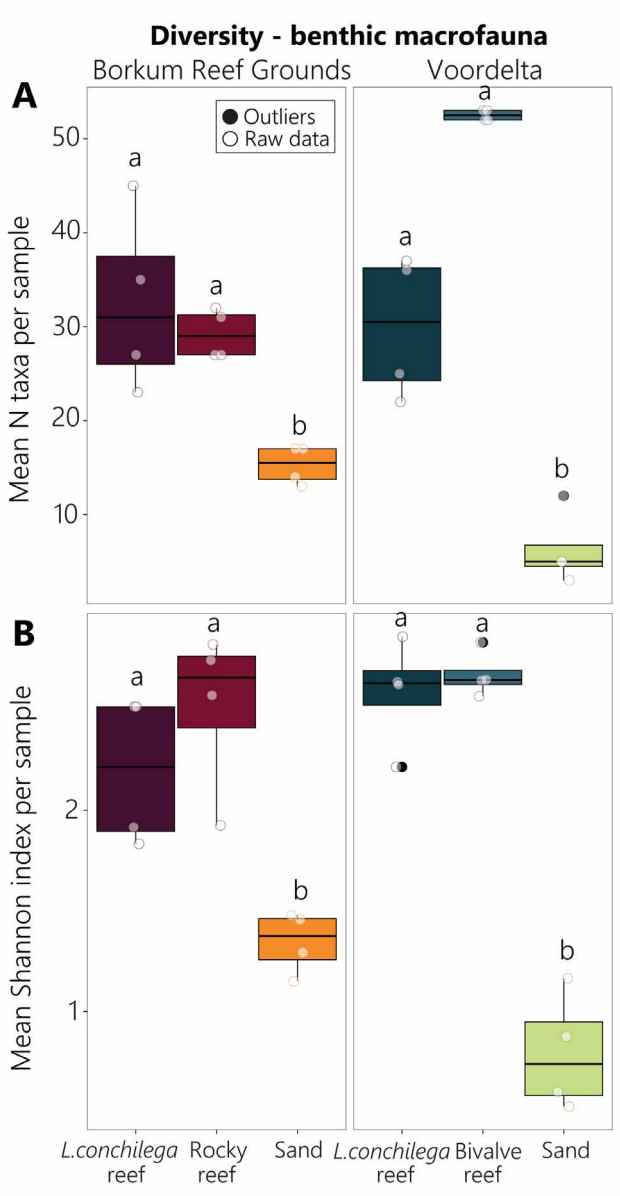

Fig. 2. (A) Taxa richness (number of taxa) per sample and (B) Shannon diversity index per sample, representing taxa distribution within the community of benthic macrofauna across habitat types between the deeper offshore Borkum Reef Grounds and the shallower nearshore Voordelta. Data (n = 4) are shown as raw data points and boxplots with median, interquartile range (25th to 75th percentiles), minimum and maximum values (whiskers), and outliers. Significant differences, obtained with generalized linear model and Tukey post hoc comparison, are marked with lowercase letters

m^{-2}) and sand (76.50 ± 36.65 ind. m^{-2}). Both diversity (Shannon and Simpson's indices) and evenness were higher in reef habitats than sand, although evenness was non-significantly different among habitats (Shannon: 1-way ANOVA; $F_{2,9}$ = 33.09, p < 0.001; Simpson's: 1-way ANOVA; $F_{2,9}$ = 12.6, p < 0.01; Fig. 2B, Table A1).

At both locations, the *L. conchilega* reef primarily increased the abundance of infaunal taxa from the phyla Annelida (both when including and excluding *L. conchilega* individuals from the analysis), Arthropoda, and Mollusca. The rocky reef and the bivalve reef displayed a more even effect across phyla; however, they also increased the abundance of sessile epifaunal taxa such as anemones, Hydrozoa (Cnidaria), and Bryozoa (both when including and excluding *Ostreaedulis*, *Magallana gigas* and *Mytilus edulis* from the analysis; Table 1, Fig. 3, Figs. S3 & S4).

At both locations, the composition of macrobenthic communities varied significantly among habitats, as confirmed by the PERMANOVA (Borkum Reef Grounds: pseudo-$F_{2,9}$ = 7.45, p < 0.001; Voordelta: pseudo-$F_{2,9}$ = 8.42, p < 0.001). Results of the SIMPER analysis and PCoA are given in Text S1, Fig. S5, and Tables S4 & S5.

Overall, mobile communities were consistent throughout habitats at both locations, and differences were mostly limited to single species. Taxa richness was comparable among habitats at both the Borkum Reef Grounds and the Voordelta (Table 2). At the Borkum Reef Grounds, the mean abundance of individuals per trap setup was significantly higher at the rocky reef (13.25 ± 2.85 ind. $trap^{-1}$) compared to sand (9.13 ± 2.34 ind. $trap^{-1}$) but was the lowest at the *L. conchilega* (9.00 ± 1.27 ind. $trap^{-1}$; Table 1 & Table A1). At the Voordelta, mean total abundance of individuals was significantly lower at the bivalve reefs (30 ± 2.89 ind. $trap^{-1}$) than at *L. conchilega* reef (48.50 ± 4.57 ind. $trap^{-1}$) and sand (40.88 ± 5.04 ind. $trap^{-1}$). Some reef-associated species were found with significantly higher abundances among reef habitats at both locations. At the Borkum Reef Grounds, mean individual abundances of the edible crab *Cancer pagurus* were higher among reef habitats (*L. conchilega* reef: 3.5 ± 1.77 ind. $sample^{-1}$; rocks: 6.12 ± 1.24 ind. $sample^{-1}$) than sand (2.00 ± 0.53 ind. $sample^{-1}$), while the velvet swimming crab *Necora puber* was only observed on the rocky reef (1.25 ± 0.29 ind. $sample^{-1}$; Fig. 4A, Table A1 & Table S1). Pouting *Trisopterus luscus* was also found with higher mean abundances of individuals among reef habitats (*L. conchilega* reef: 0.37 ± 0.37 ind. $sample^{-1}$; rocks: 3.65 ± 1.97 ind. $sample^{-1}$) than sand (0.12 ± 0.12 ind. $sample^{-1}$) at the same location. At the Voordelta, both *C. pagurus* and *N. puber* were observed only on the bivalve reef (0.12 ± 0.12 and 0.12 ± 0.12 ind. $sample^{-1}$), while the shore crab *Carcinus maenas* was observed with higher abundances in the *L. conchilega* reef (43.50 ± 3.80 ind. $sample^{-1}$), followed by sand (5.00 ± 1.08 ind. $sample^{-1}$) and the bivalve reef (22.12 ± 2.97 ind. $sample^{-1}$; Fig. 4B, Table A1 & Table S1).

Table 1. Comparison of faunal assemblages through calculated community indices between habitat types among the deeper offshore Borkum Reef Grounds and the shallower nearshore Voordelta. Values are expressed as means ± SE. Richness is expressed as mean number of taxa per sample, while abundance is expressed as mean number of individuals per m^2 (calculated first per sample and then converted per unit area). Diversity indices were calculated per sample and then averaged

Habitat	Richness	(±) SE	Abundance	(±) SE	Shannon	(±) SE	Simpson	(±) SE	Evenness	(±) SE
Benthic macrofauna										
Borkum Reef Grounds										
Lanice conchilega	32.50	4.86	7485.71	2830.78	2.19	0.19	0.77	0.06	0.64	0.06
Rocks	29.25	1.31	1782.89	1073.19	2.52	0.20	0.85	0.05	0.75	0.07
Sand	15.25	1.03	3125.00	665.92	1.34	0.08	0.62	0.04	0.49	0.03
Voordelta										
L. conchilega	30.00	3.81	3392.86	5213.44	2.58	0.13	0.86	0.04	0.77	0.06
Bivalves	52.50	0.29	23810.71	364.94	2.67	0.06	0.88	0.01	0.67	0.01
Sand	6.25	1.97	1092.86	523.64	0.79	0.14	0.39	0.08	0.49	0.11
Mobile fauna										
Borkum Reef Grounds										
L. conchilega	3.88	0.67	9.00	1.27	1.11	0.17	0.59	0.07	0.86	0.04
Rocks	4.25	0.37	13.25	2.85	1.11	0.04	0.59	0.02	0.79	0.04
Sand	4.00	0.71	9.13	2.34	1.06	0.24	0.53	0.12	–	–
Voordelta										
L. conchilega	3.75	0.85	48.50	4.57	0.41	0.14	0.18	0.06	0.30	0.08
Bivalves	4.25	0.48	30.00	2.89	0.77	0.13	0.40	0.08	0.55	0.08
Sand	5.00	1.08	40.88	5.04	0.88	0.13	0.45	0.05	0.57	0.03

3.2. Food web properties inside and outside reefs

Several food web parameters responded to the presence of a reef habitat at both the Borkum Reef Grounds and the Voordelta. The number of species within the networks increased within reefs compared to sand (*L. conchilega* reef: +126%, rocky reef: +87% at the Borkum Reef Grounds; *L. conchilega* reef: +176%, bivalve reef: +312% at the Voordelta; Table 2), resulting in a higher link density (*L. conchilega* reef: +52%, rocky reef: +28% at the Borkum Reef Grounds; *L. conchilega* reef: +166%, bivalve reef: +150% at the Voordelta; Table 2). Connectance decreased by 33% at both reef habitats at the Borkum Reef Grounds compared to sand (Table 2). Similarly, at the Voordelta, connectance decreased by 5% at the *L. conchilega* reef and 41% at the bivalve reef compared to sand (Table 2). The maximum trophic level was higher in the reef habitats than in the sand at the Borkum Reef Grounds (Fig. 5A) but was higher in the sand habitat at the Voordelta (Fig. 5B).

Overall, the fraction of intermediate species increased among reef habitats (*L. conchilega* reef: +13%, rocky reef: +10% at the Borkum Reef Grounds; *L. conchilega* and bivalve reefs: +34% at the Voordelta; Table 2). Conversely, the fraction of basal species decreased among reefs (*L. conchilega* reef: −53%, rocky reef: −46% at the Borkum Reef Grounds; *L. conchilega* and bivalve reefs: −50% at the Voordelta) and so did the fraction of top species (*L. conchilega* reef: −33%, rocky reef: −22% at the Borkum Reef Grounds; *L. conchilega* and bivalve reefs: −78% at the Voordelta; Table 2).

4. DISCUSSION

The ecological functioning of subtidal reefs in temperate seas and their food webs has remained relatively underexplored. We provide a unique analysis of the reef effect on biodiversity and food web complexity of 2 subtidal temperate reef types (i.e. geogenic versus biogenic reefs), as is needed to enable more informed decision-making in future restoration and conservation projects. By comparing the faunal communities and food web structure of geogenic and biogenic reefs in a shallow (i.e. nearshore Voordelta) and deeper (i.e. offshore Borkum Reef Grounds) area of the North Sea, we confirmed that independent of location, reefs greatly enhance biodiversity and the abundance of macrobenthic communities compared to sandy seafloors. We observed that reefs shape characteristic communities depending on their structural origin, with biogenic ones creating intermediate communities between sand and geogenic reefs. Our results showed that the reef presence impacted only certain mobile species but favoured commercially valuable ones like *Cancer pagurus* and *Trisopterus*

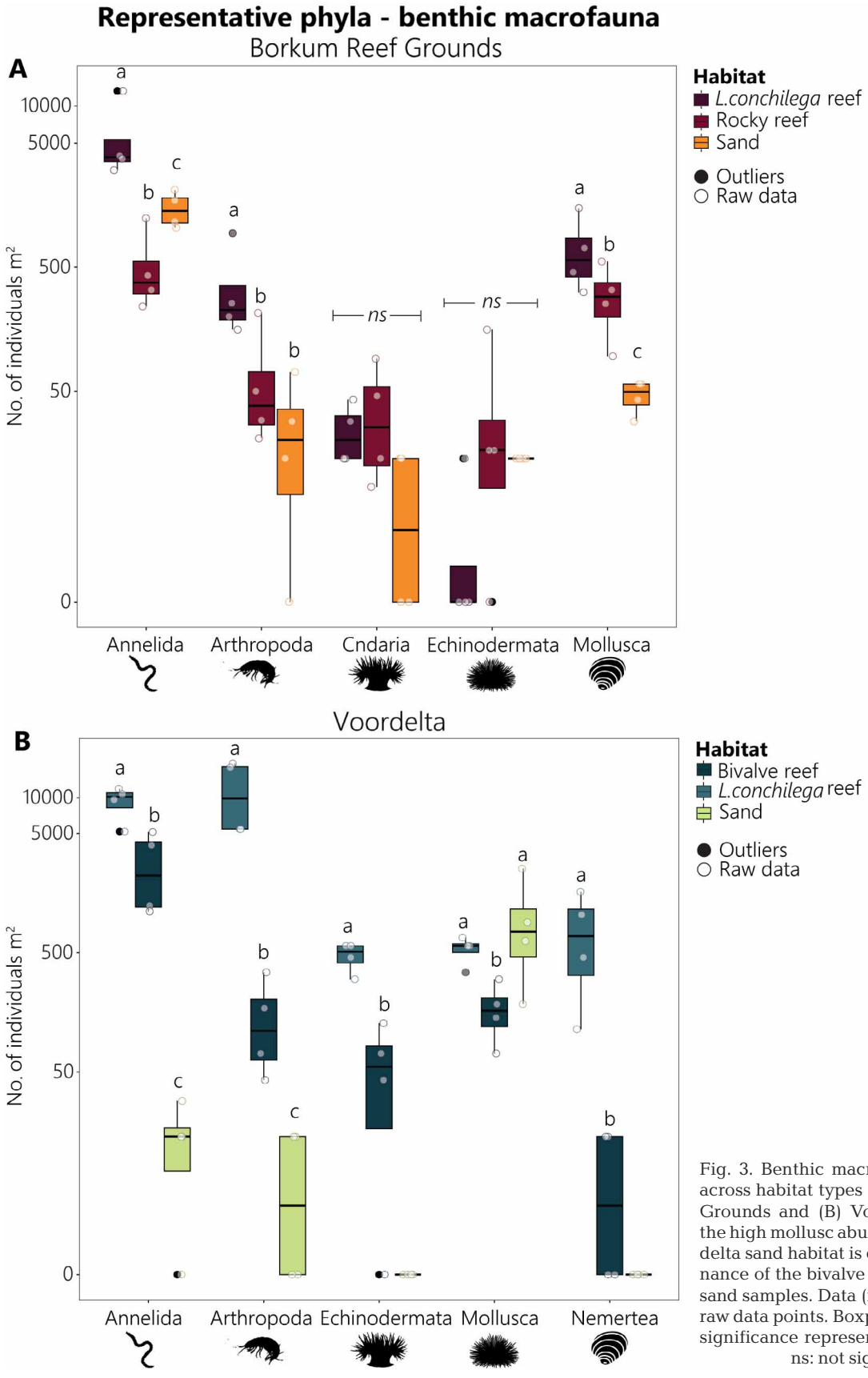

Fig. 3. Benthic macrofauna abundance across habitat types at (A) Borkum Reef Grounds and (B) Voordelta. Note that the high mollusc abundance in the Voordelta sand habitat is driven by the dominance of the bivalve *Mulinia lateralis* in sand samples. Data (n = 4) are shown as raw data points. Boxplot parameters and significance representation as in Fig. 2. ns: not significant

Table 2. Comparison of food web networks through calculated metrics between habitat types among the deeper offshore Borkum Reef Grounds and the shallower nearshore Voordelta. Richness (number of species), link density (number of links per species), and connectance (number of links per species^2) are provided. Fraction of top (species without predators), intermediate (species with prey and predators), and basal (species with no prey) species as well as the fractions of herbivores (species that consume only basal species), omnivores (species that consume other species including basal species) and carnivores (species that consume other but not basal species) are shown. Values are expressed as mean (n = 4 replicates)

Habitat	Richness	Link density	Connectance	Top	Intermediate	Basal	Herbivores	Omnivores	Carnivores
Borkum Reef Grounds									
Lanice conchilega	52	7.29	0.14	0.06	0.88	0.06	0.29	0.50	0.15
Rocks	43	6.14	0.14	0.07	0.86	0.07	0.16	0.63	0.14
Sand	23	4.78	0.21	0.09	0.78	0.13	0.26	0.61	0.00
Voordelta									
L. conchilega	47	7.49	0.16	0.04	0.87	0.09	0.32	0.49	0.11
Bivalves	70	7.07	0.10	0.04	0.87	0.09	0.31	0.51	0.09
Sand	17	2.82	0.17	0.18	0.65	0.18	0.12	0.53	0.18

luscus. Regardless of the reef type (geogenic or biogenic), reefs greatly increased the complexity of food webs in terms of taxa richness, link density, and saturation, potentially enhancing species redundancy and resistance to species loss. Overall, our findings emphasize the ecological importance of temperate reefs and the need for their conservation. By advancing knowledge on their functioning, particularly in relation to food webs, we aim to support future restoration efforts.

4.1. Reef effects on macrobenthic communities

Our results showed that temperate reefs greatly enhanced macrobenthic biodiversity and abundance compared to sandy environments. Additionally, we found that the structural origin of the reef influenced the community composition, which varied among the different reef types. At the rocky reef, we observed an increased proportion of sessile epifauna (e.g. anemones, bryozoans, hydrozoans), along with higher richness and evenness but lower individual abundance compared to the other habitats at the Borkum Reef Grounds. Like macrobenthic communities from other stony habitats in the southern North Sea (e.g. the Cleaver Bank), they included rare, long-lived, and large-growing species but with low abundance (e.g. Paguridae, *Upogebia deltaura*, *Obelia bidentata* and various anemones; Bos et al. 2011, Jager et al. 2018). Several studies on subtidal and intertidal *Lanice conchilega* reefs have described these reefs as ephemeral, intermediate habitats between rocky reefs and sandy environments, classified as part of the sandy habitats (Coolen et al. 2015). As such, they were thought only to attract species naturally occurring in the surroundings without establishing a distinct community (Rabaut et al. 2007, 2009, Callaway et al. 2010, De Smet et al. 2015a). However, we found that the *L. conchilega* reefs at both the Borkum Reef Grounds and at the Voordelta hosted 49 and 20%, respectively, of the total taxa found in both areas and demonstrated a solid effect in not just increasing biodiversity but in shaping distinct communities. We hypothesize that in subtidal conditions, *L. conchilega* might persist with more stability than the intertidal and thus, over time, facilitate the development of unique benthic communities. However, no research has yet been conducted on this topic.

European flat oyster reefs are considered functionally extinct in the North Sea (zu Ermgassen et al. 2024), yet we found that they can serve as a hotspot of benthic biodiversity. In our study, the bivalve bed supported 43% of the total richness and hosted taxa typical of sand and hard substrates. This is comparable to studies on the benthic communities of subtidal horse mussel reefs *Modiolus modiolus*, where both infaunal and epifaunal species benefit from the reef presence (Rees et al. 2008, Sanderson et al. 2008, Fariñas-Franco et al. 2016). Bivalve reefs are characterized by alternating patches of elevated rock-like shell aggregations and sand, creating a mosaic of habitats that promote diversity and stability in benthic faunal assemblages (Kovalenko et al. 2012, Romoth et al. 2023). Moreover, this mosaic not only provides complex hard structures with substrates for species attachment but also enriches the sediments between clumps. Filter-feeding bivalves produce biodeposits which increase the available organic matter in the sediments, supporting infaunal communities as

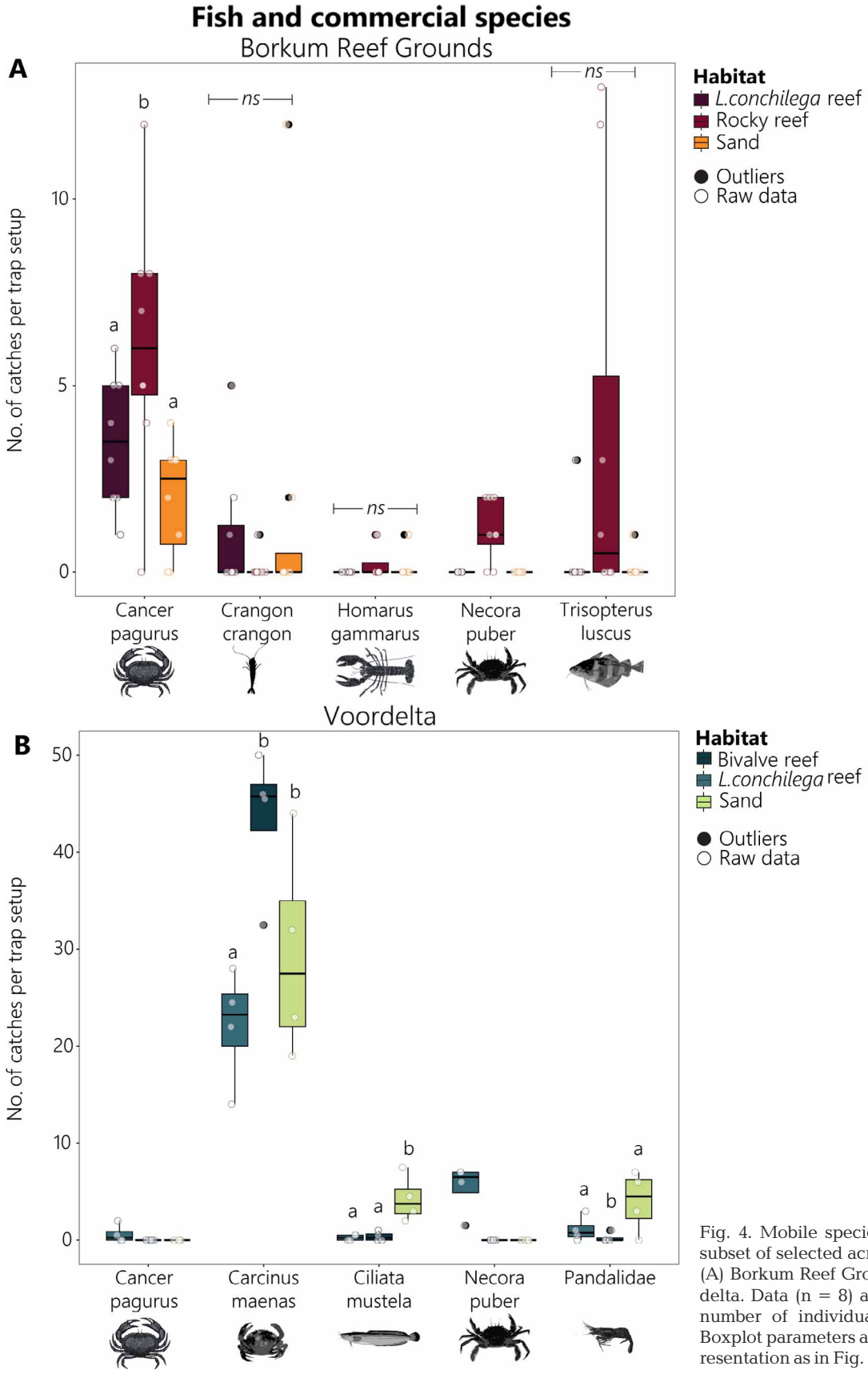

Fig. 4. Mobile species abundance for a subset of selected across habitat types at (A) Borkum Reef Grounds and (B) Voordelta. Data (n = 8) are presented as the number of individuals per trap setup. Boxplot parameters and significance representation as in Fig. 2. ns: not significant

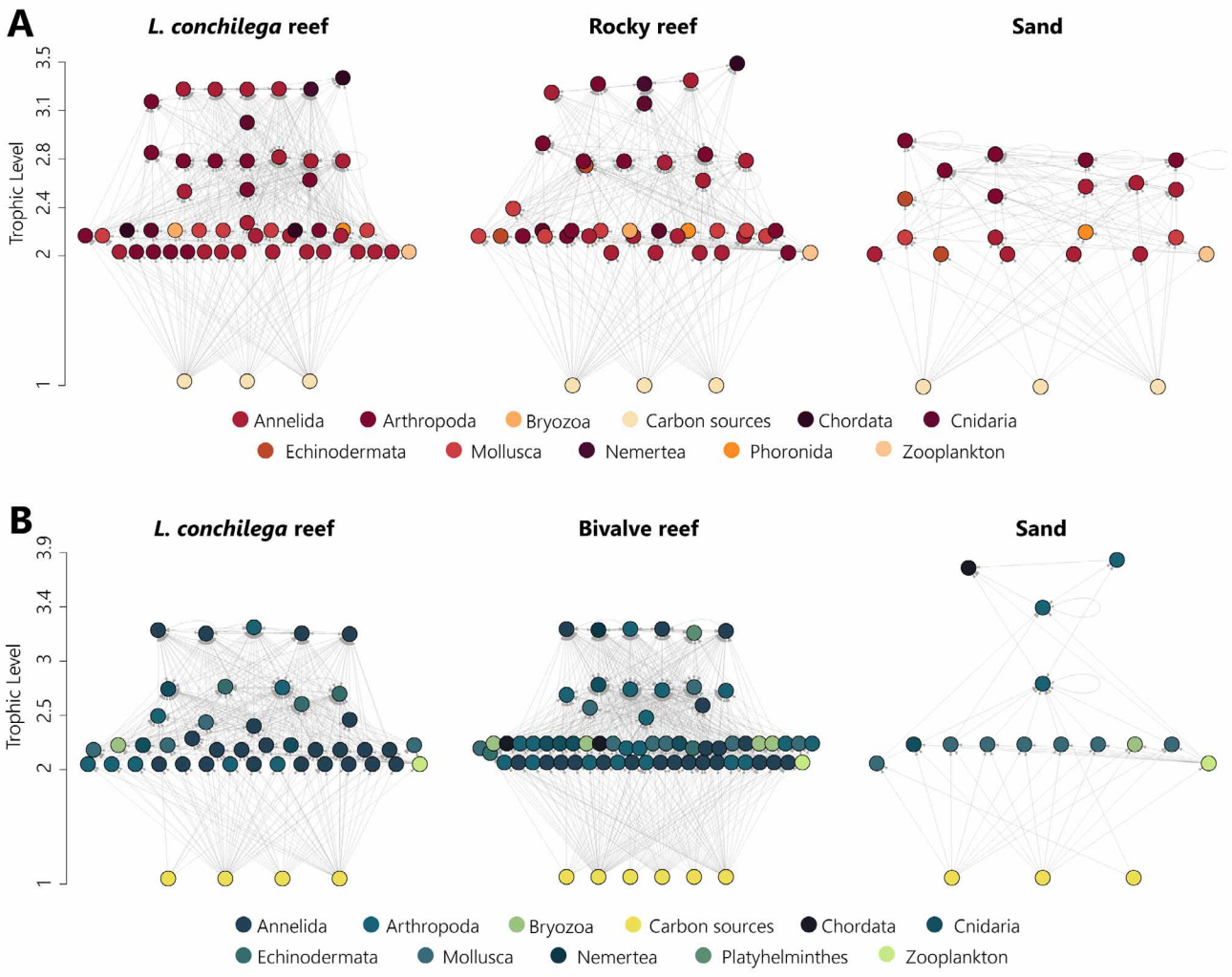

Fig. 5. Comparison of food web network habitat types at (A) Borkum Reef Grounds and (B) Voordelta. Closed circles (nodes) represent species, with colour indicating their respective phylum. The line between nodes (links) represents trophic interaction among taxa. Trophic levels increase from the basal species at the bottom (carbon sources) to the top (top predators)

well (Rees et al. 2008). Of note, the Voordelta sand was dominated by the invasive species *Mulinia lateralis*, with few other typical soft-bottom species present. This small bivalve, relatively new to the North Sea, lives buried in the sediments and is known for its rapid turnover and growth (Craeymeersch et al. 2019, Klunder et al. 2019 and references within, Gismann et al. 2023). Its high abundance relative to the other taxa may be interesting to investigate in future studies. Nevertheless, the striking differences observed between the oyster reef and the sandy reference indicate that a mixed shellfish reef can greatly increase benthic biodiversity even at relatively limited scales. Hence, maintaining and reintroducing natural reefs could significantly contribute to restoring some of the North Sea's former biodiversity levels.

4.2. Reef effects on mobile communities

The effect of reefs on mobile fauna was not strong and was limited to only a few species, including the commercial species of crab *C. pagurus* and *Necora puber*. Both species favoured reefs with higher structural complexity, like rocky and bivalve reefs. Similar results have been observed in other structurally complex habitats — both natural, like the Cleaver Bank (Robinson & Tully 2000, Bos et al. 2011, Jager et al. 2018), and artificial, such as shipwrecks and platform foundations, including offshore wind farms (OWFs; Krone et al. 2013, 2017). Moreover, some *C. pagurus* individuals were observed resting among the tubes of the *L. conchilega* reef while we were filming the seabed (C. Coral pers. obs.), suggesting that its inter-

mediate characteristics may provide shelter to this species. Baited trap methodology likely affected the outcome, as it filters the catches by mesh size and targets feeding individuals, potentially excluding juveniles or non-feeding ones, which would still rely on the reef habitat but primarily for shelter. Moreover, crabs might prefer fresh prey from the reefs over the bait (Calderwood et al. 2015). Juvenile crabs are known to prefer sheltered habitats like mussel beds (Young & Elliott 2020 and references within). Indeed, we collected some small-sized individuals in our sediment samples, particularly *Carcinus maenas*, *Liocarcinus holsatus*, and *L. depurator*, which were found exclusively within reef habitats at both locations, suggesting that juveniles could be a valuable focus for future studies. Although our results should be interpreted considering the limitations of our sampling methods, we observed that temperate reefs, biogenic and geogenic, may serve as habitats for crab species commonly found in other structurally complex habitats. These included some commercially valuable species and may highlight the ecological importance of temperate reefs.

Despite limited fish catches in our study, differences in abundance were evident for a few species among habitats at both locations. Notably, *T. luscus* abundance was higher in the reef habitats at the Borkum Reef Grounds. This species, which is commercialized for human consumption or as fishing bait, is commonly associated with reef habitats and rocky grounds, where it forages on benthic macrofaunal species (Heessen et al. 2015). Additionally, 2 demersal fish species, *Mullus surmuletus* and *Ciliata mustela*, typically found among sandy or rocky habitats (Heessen et al. 2015), were also recorded in the *L. conchilega* reef at the Borkum Reef Grounds. By contrast, at the Voordelta, nearly 90% of all fish specimens were collected in the sand habitat and belonged to *C. mustela*, with only a few individuals on the biogenic reefs. This supports the idea that biogenic reefs create an intermediate habitat between rocky reefs and soft substrates, potentially hosting species from both environments. However, given the limitations of our data set, further research on this matter is needed. Previous studies using different methods at both locations documented at least 6 fish species within reefs at the Borkum Reef Grounds (Coolen et al. 2015) and 25 species within the bivalve reef at the Voordelta (van der Have et al. 2019). Thus, we believe that our methodology, which targeted bottom-dwelling species attracted to the used bait and influenced by mesh size (Hinlo et al. 2017), may have influenced the results observed at both locations. Nevertheless, our findings, in combination with the existing literature, offer some interesting insight into the potential of temperate biogenic reefs as fish habitats.

4.3. Reef effects on food web networks

Habitat complexity increased within the studied reef ecosystems, which in turn enhances taxa richness. This leads to a higher number of trophic interactions among species, or, in other words, a higher number of links per species (link density), thereby increasing the complexity of the food web network (Borst et al. 2018, Nauta et al. 2023b). Food web complexity has been linked to robustness, a measure of a network's ability to withstand species loss, and is often used as indication of its stability and resilience; that is, the capacity of a system to resist (stability) or recover (resilience) from an impact (e.g. the loss of a species; Dunne et al. 2002a, 2004, Allesina & Tang 2012, Nauta et al. 2023a,b, Keyes et al. 2024). Our study found that the complexity of food webs was enhanced within reef habitats, in terms of both species richness and link density, at both studied locations. Conversely, connectance (the fraction of realized links among all possible links) decreased within reef habitats. Lower connectance is characteristic of more complex networks, as an increased number of species reduces the probability of the saturation of all links and is also linked to decreased ecosystem robustness (Dunne et al. 2002a,b, Nauta et al. 2023b). Our results align with previous studies on intertidal temperate reefs (van der Zee et al. 2016, Christianen et al. 2017, Borst et al. 2018, Nauta et al. 2023a, Witte et al. 2024), ultimately expanding this knowledge on subtidal habitats. Overall, we observed that the reef presence enhanced food web robustness, regardless of the reef origin (geogenic or biogenic; bivalve or *L. conchilega*), indicating their potential to increase network stability and resilience to species loss.

We found that reefs particularly affected the intermediate species fraction, which was predominant compared to the top and basal species fractions. Several factors may explain these findings. Firstly, subtidal environments support limited primary productivity compared to intertidal ones and thus rely more on the photic zone's primary productivity (Brockmann et al. 1990). Particularly, the depth of the Borkum Reef Grounds seafloor (26 m) limits macroalgal growth and primary production, hence the proportion for basal species. Secondly, the presence of a complex structure like a reef, on the other hand, reduces the water bottom flow, increasing the precipitation of plumes

and particles and enhancing the local nutrient availability for herbivores, detritivores, and other intermediate consumers (Lindenbaum et al. 2008, Fodrie et al. 2017, Lee et al. 2020). Thirdly, some intermediate species like small arthropods and worms adapt their diets to the availability of resources (Chartosia et al. 2010, Jumars et al. 2015) and thus thrive in habitats with high food resources like reefs (Klecka & Boukal, 2014, Borst et al. 2018).

Additionally, the structural complexity of reef habitats provides a competitive advantage for smaller intermediate predators, enabling them to hide in interstitial spaces that are inaccessible to larger predators (Kovalenko et al. 2012). Lastly, the fraction of top species, which includes fish and larger crabs, appeared underestimated in our data set, with hardly more than 3 individuals per species per habitat. Both reef types increased the proportion of top species and extended the food web length (trophic level) at the Borkum Reef Grounds. By contrast, at the Voordelta, sand habitats exhibited a higher trophic level. However, we argue that the limited catches of mobile species have partially influenced these results and thus should be interpreted with caution at both locations. Overall, by integrating food web metrics into our habitat comparisons, we linked the effects of reefs to enhanced trophic interactions and attributed these effects to specific trophic groups within the food web (Christianen et al. 2017, Nauta et al. 2023b, Witte et al. 2024).

4.4. Take-home messages and overarching conclusions

Our study enhanced our understanding of how temperate subtidal reefs can bolster marine biodiversity, potentially contributing to more complex and stable food webs and more resilient habitats. Our results, compared (to some extent) to studies on the biodiversity of other complex artificial structures like offshore platform foundations, can thus offer a solid baseline for future restoration projects within these environments. The current planned expansion of OWFs (from 23 GW in 2018 to 342–562 GW in 2040 worldwide; Li et al. 2022) presents new opportunities for designing nature-inclusive solutions that incorporate native temperate reefs (Pearce et al. 2014, Kamermans et al. 2018). Our findings contribute to the knowledge needed for such efforts while emphasizing the importance of the conservation of temperate reefs. The planning of new infrastructures should carefully consider the presence of these essential ecosystems. Our findings underline that not only do bivalve reefs contribute to increased biodiversity and food web complexity, but polychaeta reefs including *L. conchilega* also have a similar effect and have their own unique community. Although our research focussed on *L. conchilega*, the tube-building worm *Sabellaria spinulosa* likely fulfils similar functions by creating 3-dimensional structures (van der Reijden et al. 2019). The differences in species assemblages observed between the reef types suggest that if the area is suitable, future restoration projects could consider a mixed restoration approach, including different reef-building species to maximize diversity on a local scale. Finally, by demonstrating that subtidal reefs of different types facilitate different unique communities, we advocate for the protection of all types of temperate reefs to maintain the biodiversity and robustness of marine ecosystems.

Overall, our study provides foundational knowledge on the ecology of subtidal temperate reefs in the North Sea, setting a baseline for food web studies. We have provided evidence that the presence of a biogenic or geogenic reef fosters rich and complex faunal communities, including commercially relevant species. In particular, our findings highlight how biogenic reefs create intermediate habitats between sand and geogenic reefs and thus can support unique and rich faunal assemblages. By providing resource-rich habitats and enhancing taxa richness, reefs promote more complex food web networks, increasing their stability and resilience to species loss. Although limited, we observed some positive influence of reef presence on fish abundance within deeper water (Borkum Reef Grounds). We advise that future research targeting the role of reefs in supporting fish stocks should focus on long-term monitoring of fish populations around restored reefs to better understand their role as fish habitats. Finally, our study underlines the importance of incorporating reef restoration projects within the scope of MPAs. Such integration could optimize seabed usage, enhance biodiversity, and contribute to the stability of marine ecosystems. These insights are crucial for guiding future restoration efforts, ensuring that marine biodiversity and ecosystem resilience are maintained in the face of increasing anthropogenic pressures.

Data availability. The data used for this study is available at https://doi.org/10.25850/nioz/7b.b.tj.

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Appendix

Table A1. Results of main statistical tests performed on the data set. ns: non-significant. Different letters indicate statistically significant differences based on post hoc tests

	Mean ± SE			Statistics		
	L. conchilega reef (L)	Rocky reef (R)	Sand (S)	*F*	p	Post hoc groups (L, R, S)
Borkum Reef Grounds						
Benthic macrofauna: diversity indices						
Taxa richness (sample)	32.50 ± 4.86	29.25 ± 1.31	15.25 ± 1.03	$F_{2,9} = 12.48$	<0.01	a, a, b
Individual abundance (m^2)	7485.71 ± 2830.78	1782.89 ± 1073.19	3125.00 ± 665.92	$F_{2,9} = 2.86$	0.109	ns
Shannon	2.19 ± 0.19	2.52 ± 0.20	1.34 ± 0.08	$F_{2,9} = 18.04$	<0.001	a, a, b
Simpson's	0.77 ± 0.06	0.85 ± 0.05	0.62 ± 0.04	$F_{2,9} = 5.76$	<0.05	a, b, a
Evenness	0.64 ± 0.06	0.75 ± 0.07	0.49 ± 0.03	$F_{2,9} = 6.42$	<0.05	a, b, a
Benthic macrofauna: community composition (ind. m^{-2})						
Annelida	5992.86 ± 2415.13	560.71 ± 230.58	1510.71 ± 246.43	$F_{2,9} = 11.26$	<0.01	a, b, c
Arthropoda	389.29 ± 185.66	78.57 ± 45.65	38.10 ± 17.17	$F_{2,9} = 5.83$	<0.05	a, b, b
Cnidaria	25.00 ± 6.84	40.03 ± 19.08	7.14 ± 4.12	$F_{2,9} = 1.27$	0.086	ns
Mollusca	746.43 ± 264.47	309.08 ± 95.93	46.43 ± 6.84	$F_{2,9} = 18.76$	<0.001	a, b, c
Nemertea	114.29 ± 53.77	83.63 ± 54.27	0.00	$F_{2,9} = 21.08$	<0.001	ns
Phoronida	14.29 ± 14.29	652.98 ± 625.32	2023.81 ± 314.97	$F_{2,9} = 4.89$	<0.05	a, b, b
Mobile fauna: diversity indices						
Taxa richness (sample)	3.88 ± 0.67	4.2 ± 0.37	4.00 ± 0.71	$F_{2,21} = 0.10$	0.91	ns
Individual abundance (sample)	9.00 ± 1.27	13.25 ± 2.85	9.13 ± 2.34	$F_{2,21} = 1.15$	0.34	ns
Mobile fauna: species composition (ind. $sample^{-1}$)						
Asterias rubens	0.00	0.62 ± 0.18	1.63 ± 0.86	$F_{2,21} = 10.35$	<0.001	
Cancer pagurus	3.5 ±1.77	6.12 ± 1.24	2.00 ± 0.53	$F_{2,21} = 6.64$	<0.01	a, b, a
Crangon crangon	1.00 ± 0.62	0.13 ± 0.12	1.75 ± 1.48	$F_{2,21} = 2.17$	0.14	ns
Liocarcinus depurator	1.12 ± 0.51	0.25 ± 0.16	0.62 ± 0.32	$F_{2,21} = 1.78$	0.19	ns
Liocarcinus holsatus	1.62 ± 0.56	0.37 ± 0.26	0.50 ± 0.33	$F_{2,21} = 2.67$	0.09	ns
Macropodia	0.25 ± 0.16	0.25 ± 0.16	1.50 ± 0.42	$F_{2,21} = 6.54$	<0.01	a, a, b

	L. conchilega reef (L)	Bivalve reef (B)	Sand (S)	*F*	p	Post hoc groups (L, B, S)
Voordelta						
Benthic macrofauna: diversity indices						
Taxa richness (sample)	30.00 ± 3.81	52.50 ± 0.29	6.25 ± 1.97	$F_{2,9} = 56.35$	<0.001	a, a, b
Individual abundance (m^2)	3392.86 ± 1164.15	23810.71 ± 5213.44	1092.86 ± 523.64	$F_{2,9} = 17.11$	<0.001	a, b, c
Shannon	2.58 ± 0.13	2.76 ± 0.06	0.79 ± 0.14	$F_{2,9} = 33.09$	<0.001	a, a, b
Simpson's	0.86 ± 0.04	0.88 ± 0.01	0.39 ± 0.08	$F_{2,9} = 12.6$	<0.01	a, a, b
Evenness	0.77 ± 0.06	0.67 ± 0.01	0.49 ± 0.11	$F_{2,9} = 2.91$	0.106	ns
Benthic macrofauna: community composition (ind. m^{-2})						
Annelida	2878.57 ± 1009.86	9357.14 ± 1460.34	14.29 ± 5.83	$F_{2,9} = 51.79$	<0.001	a, b, c
Arthropoda	157.14 ± 67.76	12035.71 ± 3809.77	7.14 ± 4.12	$F_{2,9} = 44.56$	<0.001	a, b, c
Cnidaria	100.00 ± 81.02	300.00 ± 30.30	0.00	$F_{2,9} = 23.78$	<0.001	
Echinodermata	60.71 ± 26.96	475.00 ± 64.26	0.00	$F_{2,9} = 87.24$	<0.001	
Mollusca	175.00 ± 47.87	539.29 ± 69.59	1064.29 ± 514.37	$F_{2,9} = 6.73$	<0.05	a, b, a
Nemertea	7.14 ± 4.12	810.71 ± 333.27	0.00	$F_{2,9} = 60.31$	<0.001	
Mobile fauna: 24 vs. 48 h deployment						
Taxa richness 24 h (sample)	3.50 ± 0.50	3.50 ± 0.50	5.00 ± 2.50	$F_{1,10} = 0.12$	0.74	ns
Taxa richness 48 h (sample)	4.00 ± 2.00	5.00 ± 0.00	4.50 ± 0.50			
Individual abundance 24 h (sample)	55.00 ± 5.00	34.00 ± 4.00	43.00 ± 11.00	$F_{1,19} = 10.16$	<0.01	
Individual abundance 48 h (sample)	84.00 ± 8.00	52.00 ± 3.00	77.50 ± 9.50			
Mobile fauna: diversity indices						
Taxa richness (sample)	3.75 ± 0.85	4.25 ± 0.45	5.00 ± 1.08	NA	0.69	ns
Individual abundance (sample)	48.50 ± 4.57	30.00 ± 2.89	40.88 ± 5.04	NA	<0.001	a, b, a
Mobile fauna: species composition (ind. $sample^{-1}$)						
Carcinus maenas	43.50 ± 3.80	22.12 ± 2.97	29.5 ± 5.54	NA	<0.001	a, a, b
Ciliata mustela	0.75 ± 0.35	0.50 ± 0.00	4.25 ± 2.40	NA	<0.001	a, a, b
Pandalidae	1.00	1.5 ± 1.32	5.33 ± 2.08	NA	<0.05	a, a, b

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