



Spatial structure and biodiversity of macrofauna around marine munition dumpsites – A case study from the Baltic Sea

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ABSTRACT

Coastal German waters contain about 1.6 million tons of dumped munition, mostly left after World Wars. This study investigated the benthic macrofauna around the 'Kolberger Heide' munition dumpsite (Baltic Sea). A total of 93 macrofauna grab samples were obtained in the proximity of the munition dumpsite and in reference areas. Environmental variables analysed included the latitude/longitude, depth, terrain ruggedness, sediment grain size distribution, TNT concentration in the bottom water and distance to the centre of munition dumpsite. The overall abundance, biomass and diversity varied among these groups, though demonstrated no clear differences regarding the proximity to munition and modelled near-bottom dissolved TNT. Among individual taxa, however, a total of 16 species demonstrated significant correlation with TNT concentration. Moreover, TNT may serve as a predictor for the distribution of three species: molluscs *Retusa truncatula*, *Varicorbula gibba* and polychaete *Spio goniocephala*. Possible reasons for the species distribution including their biological traits are discussed.

1. Introduction

Discarded military munition (DMM) and unexploded ordnance (UXOs) are found globally in shallow coastal waters. The German Exclusive Economic Zone (EEZ) of the North and Baltic Seas alone already contains about 1.6 million tons of munitions dumped after World War II during the demilitarization (GICH, 2016; Wehner and Frey, 2022). Much of this munition is concentrated in several areas marked as officially designated munition dumpsites, that are prohibited for industrial fishing, constructions or dredging, and generally restrict any bottom contact (Böttcher et al., 2011). Due to these restrictions and the danger of munition in general, these dumpsites are usually out of research focus, so the effect of the UXOs and DMM on local ecosystems remains poorly studied.

The variety of UXOs and DMM known in the German EEZ covers a wide range of munition, from small-calibre firearm cartridges to large bombs and mines containing mostly conventional explosives (Wehner and Frey, 2022). The exact amount and composition of the munition was not properly recorded during the dumping. Moreover, the dumping

occurred sometimes just along the way to the designated areas, so the details for many dumpsites and their surroundings are still not well constrained (Böttcher et al., 2014), although much insight has been gained in the last ten years due to several national and international funded projects; e.g. MERCW ('Modelling of ecological risks related to sea-dumped chemical weapons', <https://cordis.europa.eu/project/id/13408>), CHEMSEA ('Chemical munitions search & assessment', <http://www.chemsea.eu/>), DAIMON ('Decision aid for marine munitions: practical application', <http://www.daimonproject.com/>); UDEMM ('Environmental monitoring for the delaboration of munitions in the sea', <https://udemmm.geomar.de/>); North Sea Wrecks, BASTA ('Boost applied munition detection through Smart data integration and AI workflows', <https://www.basta-munition.eu/>), ExPloTect ('Ex-situ, near-real-time explosive compound detection in seawater', <https://www.explotect.eu/>) and the ongoing CONMAR ('Concepts for conventional marine munition remediation in the German North and Baltic Sea', <https://conmar-munition.eu/>).

Within the Baltic Sea, eight designated dumpsites are mapped, while around 40 more areas are considered to be contaminated and over 20 are

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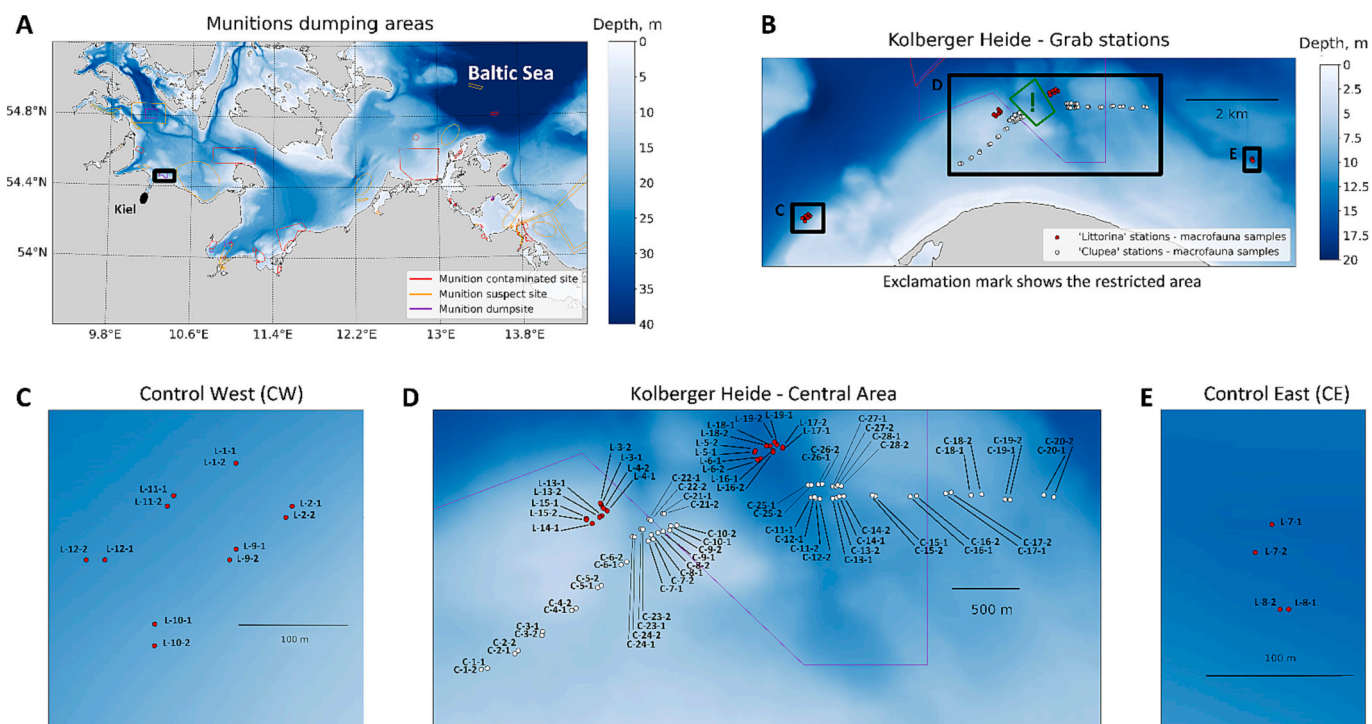


Fig. 1. Study area and stations. A – Western Baltic Sea with munition areas; B – enclosed area of Kolberger Heide; C-E – enclosed areas with individual macrofauna grab samples.

suspected to be contaminated (Munition Cadaster “AmuCad”). According to the German monitoring program BLMP (Bund/Länder Messprogramm), around 300,000 tons of conventional munition and 5000 tons of chemical munition are located within the German waters of the Baltic Sea (Böttcher et al., 2011). The conventional munition represents dozens of different explosive mixtures, but 2,4,6-trinitrotoluene (TNT) is the most abundant component. In most cases, the dumped munition was not fused. However, the danger for the environment remains, as TNT (and its degradation products) are known to have toxic effects on marine organisms, mammals and humans, and is identified as cancerogenic and mutagenic (Lotufo et al., 2017; Beck et al., 2018).

Toxic compounds of the munition may accumulate in some organisms (e.g. bivalves and fishes), potentially entering higher levels of the food chain (Strehse et al., 2017; Appel et al., 2018). The bioaccumulation potential of TNT is not very high due to rapid excretion, though still notable (Lotufo et al., 2009; Lotufo et al., 2016), while its aminated products (ADNT and DANT) can be accumulated to a far greater degree (Lotufo et al., 2016). So far, the influence of TNT and its degradation products has been tested in experiments both in the laboratory and in situ on algae, mussels and fishes (Patel et al., 2004; Schuster et al., 2021; Beck et al., 2022; Brenner et al., 2023; Schuster et al., 2023). At the Kolberger Heide dumpsite (Kiel Bay, Baltic Sea) one or more of these munition compounds were detected in >98 % of organisms with the median level of ~ 1 ng g⁻¹ dry weight, and up to $\sim 4.5 \times 10^6$ ng g⁻¹ in one *Asterias rubens* starfish (Beck et al., 2022). In contrast, concentrations of TNT in the surrounding waters are ~ 30 – 50 ng l⁻¹ and as much as 3 mg l⁻¹ around exposed chunks of explosives (Beck et al., 2019; Greinert, 2019). In the North Sea, over 60 % of the examined dab (*Limanda limanda*) near the wreck of SMS Ariadne showed at least one visible nodule in liver (interpreted as possible tumors), apparently related to the dissolving TNT from the wreckage (Schuster et al., 2023). Different aquatic organisms can tolerate varying dosage of munition compounds. In laboratory experiments an acute toxicity occurs at approximately 10^0 – 10^1 mg l⁻¹ levels (Lotufo et al., 2017), and 50 % lethal concentration (=LC-50) ranges from ~ 1 to 10 mg l⁻¹ for several tested polychaetes, amphipods, bivalves and fishes (Nipper et al., 2009;

Lotufo et al., 2013). Although direct mortality from the intoxication was not observed within the dumpsites, a response in antioxidant enzymes and histochemical biomarkers was clear (Strehse et al., 2020; Schuster et al., 2021; Brenner et al., 2023).

In contrast to the negative effects of toxic substances, the wooden munition boxes and metal shells of the munition represent a hard substratum that is otherwise rare in the Baltic Sea, providing a habitat for foulers and other epifaunal organisms (Edwards and Beldowski, 2016; Kampmeier et al., 2020). Underwater imagery from photo and video investigations shows dense populations of algae, hydroids, mussels and other members of epifauna on the wooden crates, mines, torpedo heads etc. (Beck et al., 2018; Greinert, 2019; Kampmeier et al., 2020).

In terms of the entire ecosystem, the rate and scale of the potential effect of the TNT e.g. on macrofauna biomass, biodiversity patterns or individual macrofauna species distribution, remains unknown. However, the overall structure of the macrofauna in the Baltic Sea, and in this area in particular, is well studied outside of the munition dumpsites. For example, it is known that the area north of Kiel largely consists of communities dominated by infaunal polychaetes and algae (Schiele, 2014; Gogina et al., 2016), with relatively high values of biomass and species richness (~ 100 – 300 g/m² and > 120 species) (Zettler et al., 2008; Gogina et al., 2016).

The dumpsite Kolberger Heide is potentially the most well-studied and mapped dumpsites in the Baltic Sea, and is located ca. 20 km northeast from Kiel, Germany (Kampmeier et al., 2020). This study aims to investigate the influence of munition compounds on the structure and composition of macrofauna within and around the Kolberger Heide dumpsite. We hypothesized that the proximity of the munition may cause gradients in the abundance, biomass or diversity of the macrofauna towards or away from the highest munition concentrations, resulting in changes of certain species distributions.

2. Materials & methods

2.1. Study area

The Kolberger Heide munition dumpsite is an area of ca. 15 km², located in the eastern part of the Kiel Bay 2 km offshore (Fig. 1). The depth within the area varies from 5 to 20 m. Within this area two restricted sub-areas exist (one major in the central part with most of munition, and one smaller next to the traffic route) which are marked with navigation buoys and ship traffic is strictly prohibited without special permit. Here and further, to avoid the precise location of the munition items, no coordinates will be displayed for the samples and environmental data.

Data on the military-historic background of Kolberger Heide area are described in detail by Kampmeier et al. (2020). Up to now, around 30,000 tons of munition material are assumed to be present there, including mostly conventional munition consisting of gun cartridges, artillery projectiles, grenades, bombs, rockets, anti-tank, anti-personnel, moored and ground mines, torpedo heads and depth charges (*Documents of the German National/Military Archive BaMa folder RM, 1486, n.d.*).

Waters around Kolberger Heide are influenced by the exchange processes between the Baltic and North Sea resulting in a mean bottom salinity around 19 (14 to 24) and temperature around 10 °C (2 to 20 °C), depending on the season (*Baltic Sea Physics Analysis and Forecast, n.d.*). Bottom currents are predominantly in eastward direction, reaching 0.024 ± 0.005 m/s (Kampmeier et al., 2020).

Munition items are generally concentrated within the restricted area, although individual items can also be found outside (Kampmeier et al., 2020). Dissolved TNT in the near-bottom waters varies between 1 and 30 ng l⁻¹ depending on the season, but can reach dozens of µg l⁻¹ near munition items (Greinert, 2019). The sediments are predominantly sands, with a smaller fraction of mud and, sometimes, gravel, pebbles and boulders. The bottom is partly covered by patches of algae and eelgrass (*Zostera marina*) (von Deimling, 2019; Kampmeier et al., 2020).

2.2. Sampling design and environmental parameters

Samples were collected during two expeditions with RV 'Littorina' (expedition L-04-22) and 'Clupea' (expedition Clu-367) in April and July 2022, respectively. Samples were obtained using a 0.1 m² Van Veen grab sampler with three replicates per station; two grabs were taken for the macrofauna and one for sediment grain analysis. Macrofauna grabs were washed through a 1 mm mesh size sieve and fixed with 4 % formaldehyde buffered by hexamethylenetetramine. Sediment samples were frozen onboard.

The sampling design provided several double-transects with a short distance between the stations (ca. 50–100 m). A total of 37 macrofauna samples assigned to 18 stations were taken during L-04-22 and 56 samples assigned to 28 stations were during Clu-367. At the border of the restricted area, the distance between the stations was ca. 50 m; further away the distance increased to ca. 100 m (Fig. 1). Since the exact positioning of the ship was hard to maintain due to current and winds, the distance between individual grab replicates was sometimes significant. Therefore, we decided to analyse the samples on the scale of individual grab samples (Fig. 1).

The water depth was recorded for each grab sample. Sediment grain-sizes were analysed on a 'Laser Particle Sizer Analysette-22 NanoTec' device. The organic and carbonate fractions were not removed prior to the sample treatment. Each sample was screened through a 2 mm sieve into the sample inlet. The data were separated into sand and mud content (> and <62.5 µm individual grain size, respectively).

Data on sediment roughness expressed in Terrain Ruggedness Index (=TRI, Riley et al., 1999) was taken from the multi-beam echosounder data (RESON T50-P multibeam, for details see Kampmeier et al., 2020). The original resolution of 0.25 × 0.25 m was averaged over 5 × 5 m² considering the uncertainties of precise grab positioning on the bottom

relative to the ship GPS-antenna. For visualisation also the hillshade derivative was used.

Because sediment samples were not collected for direct TNT analysis, we used instead the modelled data for the near-bottom water layer taken from the 600 m grid GETM-TNT model developed by the Institute of Baltic Research in Warnemünde (http://thredds-iow.io-warnemuende.de/thredds/catalogs/projects/CONMAR/catalog_GETM600m_TNT.html?dataset=IOW-THREDDS-Baltic_GETM600m_TNT_2022-10-14-15_ysesmean). In addition to the TNT composition, a distance to the munition centre (assumed as the centre of the major restricted area, also corresponded to the highest average sediment ruggedness) was calculated as a more gradual variable compared to 600 m grid of the TNT concentration. Station details, including the depth, sediment composition and TNT concentrations are available in Supplementary Material 1, 2. Detailed description of the GETM-TNT model is available in Supplementary Material 3.

2.3. Statistics

Each macrofaunal organism was identified to the lowest possible taxonomical level, counted and weighed (wet weight = ww). Units of the abundance and biomass were therefore individuals or grams recalculated per 1 m². Taxa names were verified using the World Register of Marine Species database <https://marinespecies.org>. Diversity was estimated using a simple species richness, Shannon index (Shannon and Weaver, 1963), Hurlbert rarefaction per 100 individuals (Hurlbert, 1971), further referred to as 'ES-100' and an extrapolated diversity per 100 individuals following an algorithm provided by Chao et al. (2014), further referred to as 'Hill-100'. Information on biological traits was taken from the database by Clare and Brafield (2022).

The similarity between the samples was estimated using Bray-Curtis similarity based on abundance (Clarke et al., 2006). Raw data were square-root transformed to reduce the dominant taxa bias. Hierarchical cluster analysis was performed with the UPGMA (=group average) algorithm with the similarity profile routine (SIMPROF) at the significance level of 0.05 (Clarke and Warwick, 2001). Identified groups of samples were further tested with Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2005). Non-parametric Kruskal-Wallis test with Dunn's post-hoc pairwise comparisons was performed to verify the differences between the groups of samples in the values of abundance, biomass and diversity (Marshall, 2019). Position of high and low similarity values in the similarity matrix was analysed for stations to reveal the presence of gradients in the community structure. The concentration of higher similarity values along the diagonal indicates the presence of gradients (Pielou, 1983).

Spearman ranked correlations were calculated between the environmental values and the values of abundance, biomass, diversity and individual species abundances. Combined effects of the environmental parameters on samples and species were tested using the canonical correspondence analysis (CCA) (McCune et al., 2002).

To compare the effects of spatial coordinates, depth, sediment parameters and TNT-composition on the macrofauna we developed linear mixed-effect models (LME) for the entire dataset (Kuznetsova et al., 2017). Abundance, biomass and diversity values were included in the models as fixed variables. The number of the grab (1 or 2, see last digit of station labels at Fig. 1) was chosen as random effect. Generalized additive models (GAM) were used for variables with significant LME-results; this was done because an unspecified smooth function can be a better predictor than a linear function (Hastie and Tibshirani, 1987).

Statistical analyses were performed using Primer v6 and Microsoft Excel 2010 software (Clarke and Warwick, 2001). Maps, diversity indices, PERMANOVA analysis, correlations, CCA and models were run and plotted using the original Python 3.8 scripts (with Basemap, Matplotlib, NetCDF4, NumPy, Pandas, Pygam, Scikit-bio, Seaborn packages, Van Rossum and Drake, 2009) and R 4.0.5 (with lme4, lmerTest and gam packages, R Core Team, 2021).

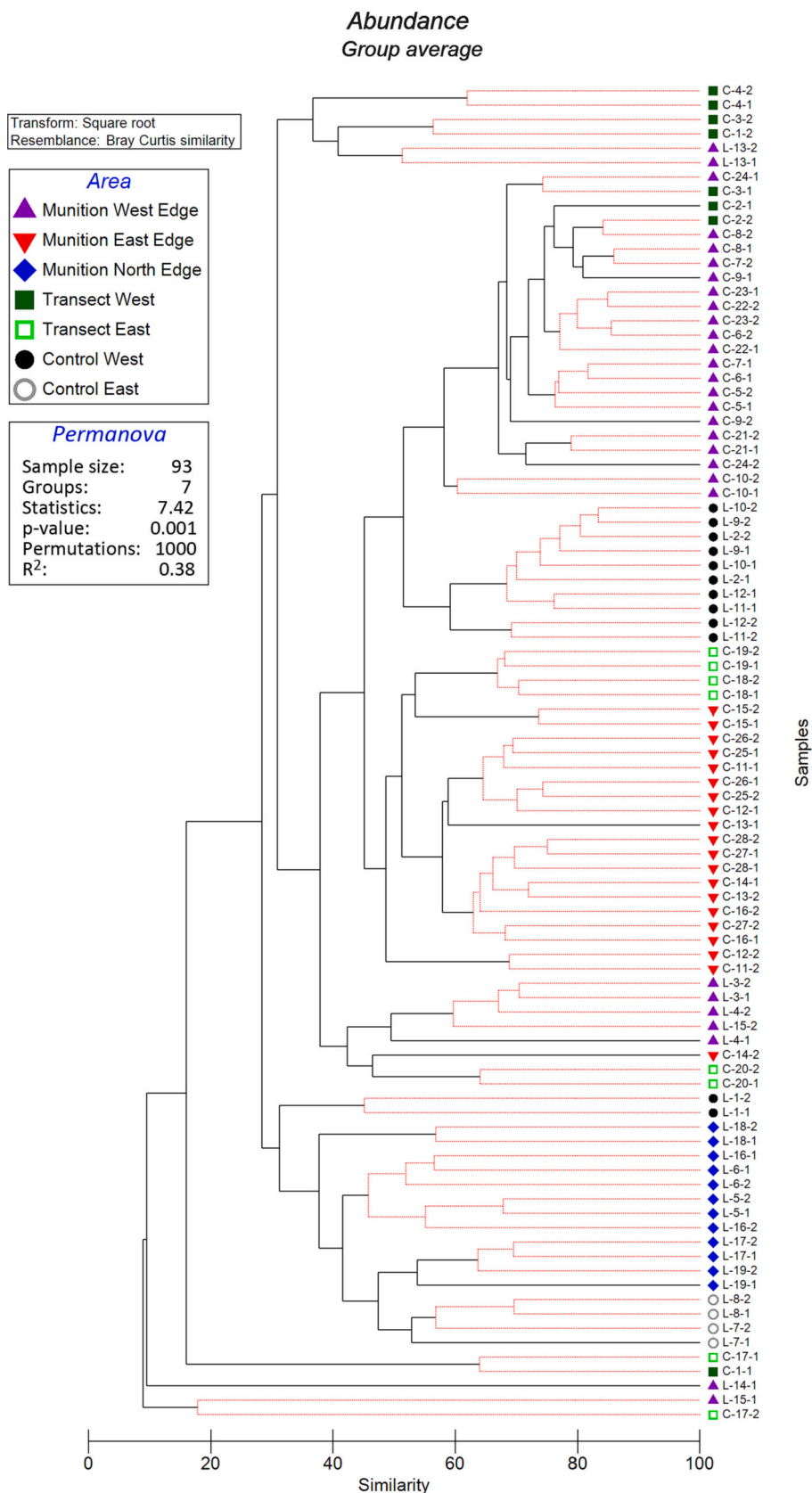


Fig. 2. Cluster dendrograms of the samples using the Bray-Curtis similarity index with SIMPROF and PERMANOVA results based on the abundance square-root transformed data. Red lines indicate branches and nodes not statistically significant at $p < 0.05$. Colour and shape of marker corresponds to the sampling sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Mean values of macrofauna abundance (ind. m⁻²), biomass (g ww m⁻²) and diversity of each sample group and results of the Kruskal-Wallis and Dunn's post-hoc tests for quantitative samples.

| Parameter | Mean values and SD | | | | | | | Kruskal-Wallis | | Dunn's post-hoc comparisons |
|------------------|--------------------|--------------|--------------|---------------|--------------|--------------|--------------|----------------|----------|---|
| | MWE (1) | MEE (2) | MNE (3) | TW (4) | TE (5) | CW (6) | CE (7) | Statistics | p-value | |
| Total abundance | 7326 ± 4835 | 3118 ± 846 | 1415 ± 492 | 11,324 ± 6942 | 6600 ± 8382 | 9162 ± 4762 | 2330 ± 1368 | 28.87 | 6.45E-05 | 1-3; 2-3; 2-4; 2-6; 3-4; 3-5; 3-6; 4-7; 6-7 |
| Total biomass | 23.2 ± 22.4 | 31.3 ± 38.6 | 20.3 ± 29.4 | 115.1 ± 247.5 | 47.6 ± 99.1 | 36.9 ± 14.7 | 98.8 ± 136.4 | 12.09 | 0.06 | 1-6; 2-6; 3-6; 5-6 |
| Species richness | 24 ± 7 | 29 ± 9 | 26 ± 8 | 32 ± 10 | 35 ± 15 | 31 ± 8 | 34 ± 8 | 16.74 | 0.01 | 1-4; 1-5; 1-6; 1-7; 3-5 |
| Shannon index | 1.71 ± 0.58 | 2.00 ± 0.34 | 2.23 ± 0.59 | 1.78 ± 0.53 | 2.39 ± 0.44 | 1.75 ± 0.36 | 2.58 ± 0.36 | 21.73 | 1.36E-03 | 1-3; 1-5; 1-7; 3-6; 4-5; 4-7; 5-6; 6-7 |
| ES-100 | 13.13 ± 5.97 | 17.26 ± 4.50 | 21.95 ± 6.15 | 14.13 ± 5.23 | 19.21 ± 6.36 | 13.69 ± 1.80 | 24.73 ± 3.36 | 30.21 | 3.59E-05 | 1-2; 1-3; 1-5; 1-7; 2-7; 3-4; 3-6; 4-7; 5-6; 6-7 |
| Hill-100 | 13.72 ± 6.43 | 17.26 ± 4.50 | 22.3 ± 5.82 | 14.13 ± 5.23 | 19.66 ± 5.15 | 13.82 ± 1.95 | 24.73 ± 3.36 | 29.24 | 5.49E-05 | 1-2; 1-3; 1-5; 1-7; 2-3; 2-7; 3-4; 3-6; 4-7; 5-6; 6-7 |

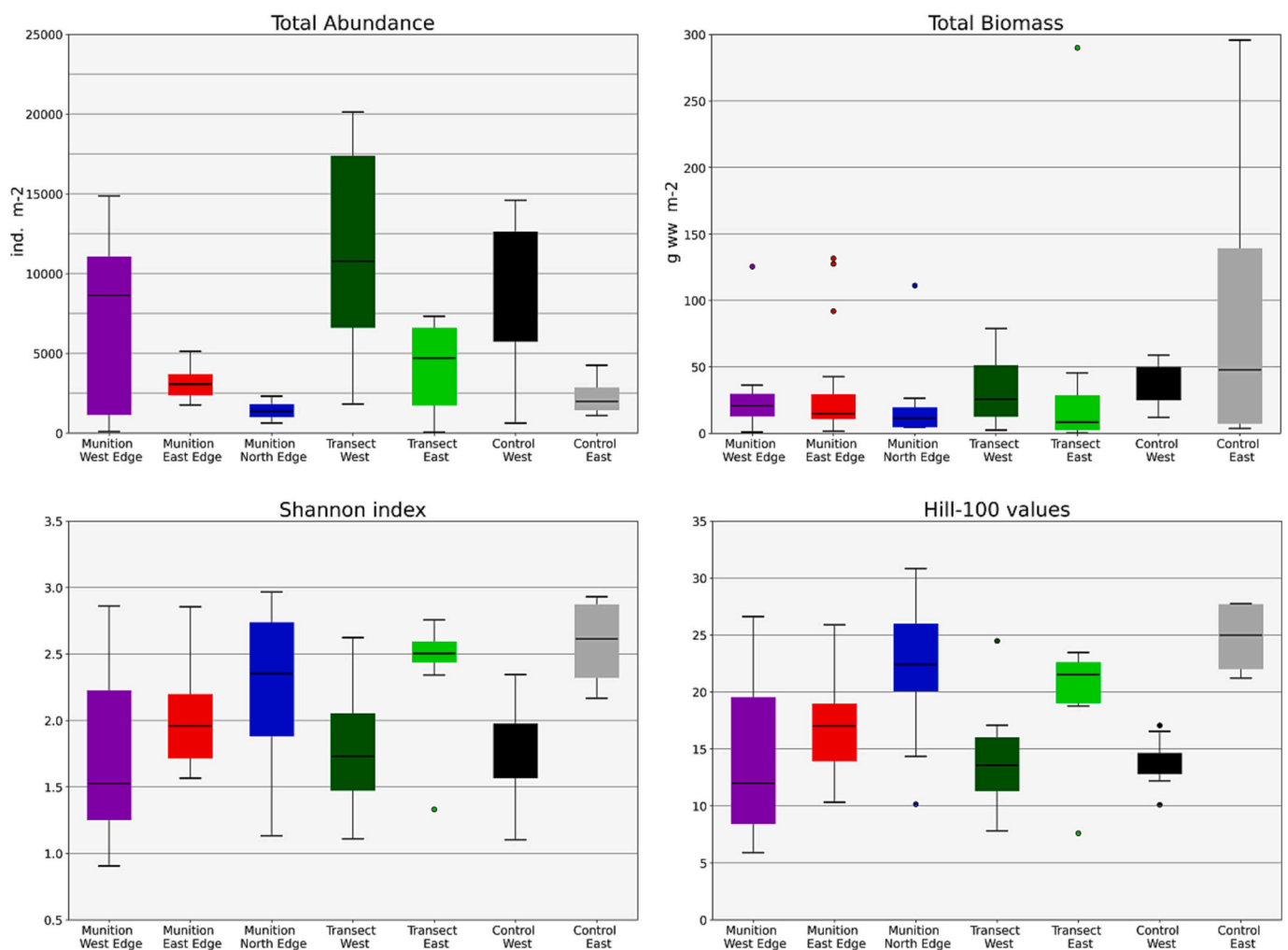


Fig. 3. Standard boxplots for macrofauna abundance, biomass and diversity for different sample groups. A – Total abundance; B – Total biomass; C – Shannon index; D – Hill-100 values. Colours are the same as in Fig. 2.

3. Results

3.1. Macrofauna structure and composition

A total of 152 macrofauna taxa were identified in the samples. Values of abundance and biomass varied from 100 ind. m⁻² (sample L-15-1) to 26,390 ind. m⁻² (sample C-17-1) and from 0.94 g ww m⁻² (L-14-1) to 724.79 g ww m⁻² (C-1-1). Number of species per sample was less

variable, ranging from 5 (L-15-1) to 50 (C-17-1). Shannon indices differed from 0.91 (C-8-1) to 2.97 (L-6-2), ES-100 differed from 5 (L-15-1) to 31 (L-6-2) and Hill-100 differed from 6 (L-15-1) to 31 (L-6-2).

Cluster analysis revealed several groups of samples that largely corresponded to geographic areas of sampling, identified as ‘Munition West Edge’ (=MWE), ‘Munition East Edge’ (=MEE) and ‘Munition North Edge’ (=MNE) located near the very munition dumpsite, ‘Transect West’ (=TW) and ‘Transect East’ (TE) located at the further ends of continuous

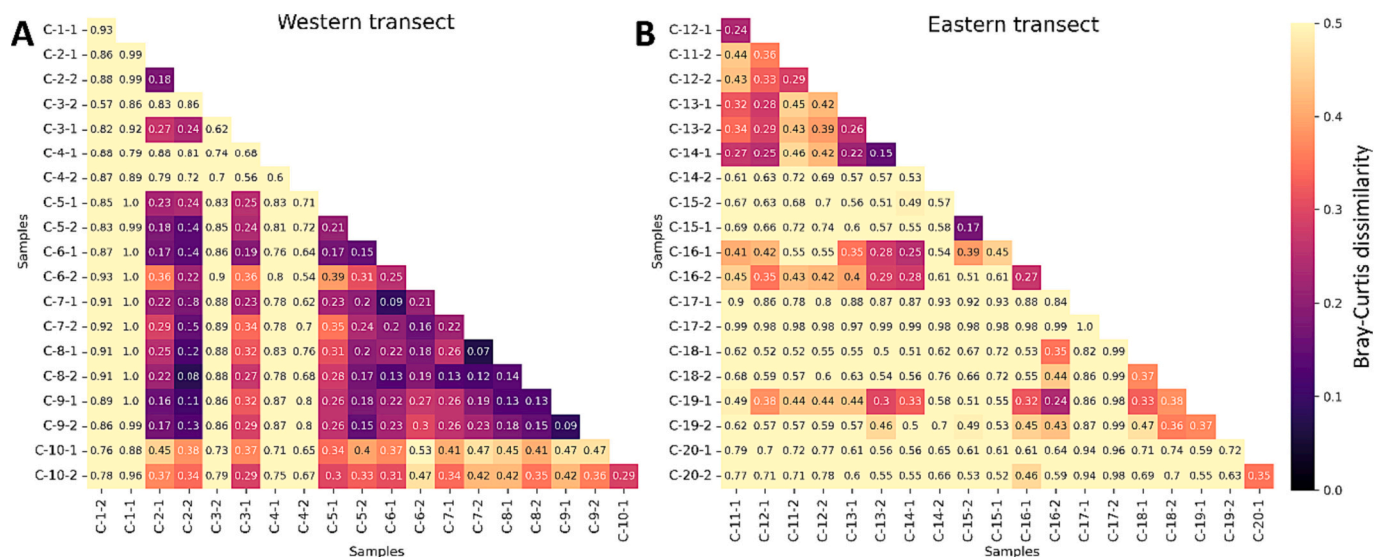


Fig. 4. Heatmaps of the Bray-Curtis dissimilarity matrices for the transects west off the munition dumpsite (A, samples C-1-1 – C-10-2) and east off the munition dumpsite (B, samples C-11-1 – C-20-2).

‘Clupea’ transects, and ‘Control West’ (=CW) and ‘Control East’ (=CE) located in the background areas ca. 1 km away from the dumpsite. Samples were grouped according to the geographical position (Fig. 2). PERMANOVA showed significant results with p -value = 0.001 (Fig. 2). Non-parametric Kruskal-Wallis test found significant differences between some groups in terms of the community parameters, including abundance, biomass and diversity metrics, although no significant differences between the background and areas close to the dumpsite were found (Table 1, Fig. 3).

Dominant taxa were similar in each sample group and included *Scoloplos armiger*, *Pygospio elegans* and *Spio gonocephala* polychaetes and *Peringia ulvae* gastropods. At certain stations, epifaunal species played a major role in terms of abundance and biomass, including *Mytilus edulis* bivalves and *Electra pilosa* and *Alcyonidium* spp. bryozoans. Heatmaps of Bray-Curtis dissimilarity were plotted separately for the samples, aligned in continuous transect west from the munition dumpsite and, correspondingly, east from the dumpsite (Fig. 4).

The pairs of samples with higher similarity were distributed unevenly along each of the transects. Particularly, the most similar values tended to be concentrated in the lower right corner of the western transect (samples C-5-1 – C-9-2) and along the diagonal at the eastern transect (Fig. 4).

3.2. Environmental parameters

The depth in the study area varies from 4 to 15 m, with the average value of 8.9 m. Samples taken near the western edge of the munition dump site were the shallowest, with 4 to 8 m depth. Other stations were deeper, with 9 to 15 m. Sediment grain-size composition varied for the sand and mud content with 76.2 % \pm 17.3 SD and 23.8 % \pm 17.3 SD, respectively. The sampling areas identified by cluster analysis showed no significant difference in grain size. TNT-concentrations of the water had the greatest variance with mean values of $2.88 \pm 0.95 \text{ ng l}^{-1}$ at the control sites and $30.60 \pm 4.59 \text{ ng l}^{-1}$ at the ‘MWE’, ‘MNE’ and ‘MEE’ regions (Fig. 5A). TRI (terrain ruggedness index) data were available only for 15 samples, as not all areas were mapped so far with the MBES. (Fig. 5B, C).

3.3. Environmental influence

The results of canonical correspondence analysis plotted in Fig. 6 show the concentration of CCA-points along two directions – one

corresponding to the lower TNT-concentrations and shallower depths, the another one corresponding to a higher mud content and greater depth (higher mud content and greater depth go hand in hand in this area). However, the sum of the CCA1 and CCA2 explains <65 %, so the described trends are of moderate significance (Fig. 6).

Spearman ranked correlations were found to be most significant between depth and different diversity values as well as total abundance (Fig. 7). Longitude as a variable showed a similar, though lower correlation. The sand content was also correlated with the total abundance. The TNT-concentration showed no reliable correlation with any of the community characteristics. The distance to the centre of the restricted area was correlated with the abundance and biomass values (Fig. 7).

Among individual taxa multiple environmental parameters demonstrated significant correlation values for many species (Fig. 8). Specifically, the depth and sand content were strongly correlated with 33 and 25 taxa, respectively. Latitude and longitude were correlated with only 18 and 19 taxa, respectively. Regarding the munition, a total of 16 species demonstrated significant correlation with the TNT-concentration and 11 species – with the distance to the restricted area (Fig. 8).

Correlation coefficients for TNT were mostly negative, except for distance, indicating that most species tend to be less abundant in the proximity of the munition. The values of total abundance, biomass, diversity and the abundances of the 16 TNT-correlated taxa were further tested in linear mixed-effect model (Table 2).

For the abundance, biomass, and diversity, only depth showed significant results for the ES-100 and Hill-100 diversity indices. All other environmental parameters demonstrated p -values above 0.05 (Table 2). Among the 16 species tested, only three showed significant results. The TNT concentrations may be a predictor for the distribution of the gastropod *Retusa truncatula* and the bivalve *Varicorbula gibba*, which were lacking from samples with higher TNT concentrations. On the contrary, the polychaete *Spio gonocephala* was more abundant in the proximity of the munition area, although the p -value was only slightly below 0.05 (Fig. 8, Table 2). For these three species a linear generalized additive model was developed and plotted to visualize the relation of their abundance with TNT (Fig. 9, Table 3). Summary of the GAM-models showed significant p -values for all the fitted models. The approximate R^2 values were in average higher for the log-transformed data (Table 3), which we chose for plotting (Fig. 9).

No common biological features were obvious for the taxa correlated with TNT concentration. For the three species confirmed by the LME-

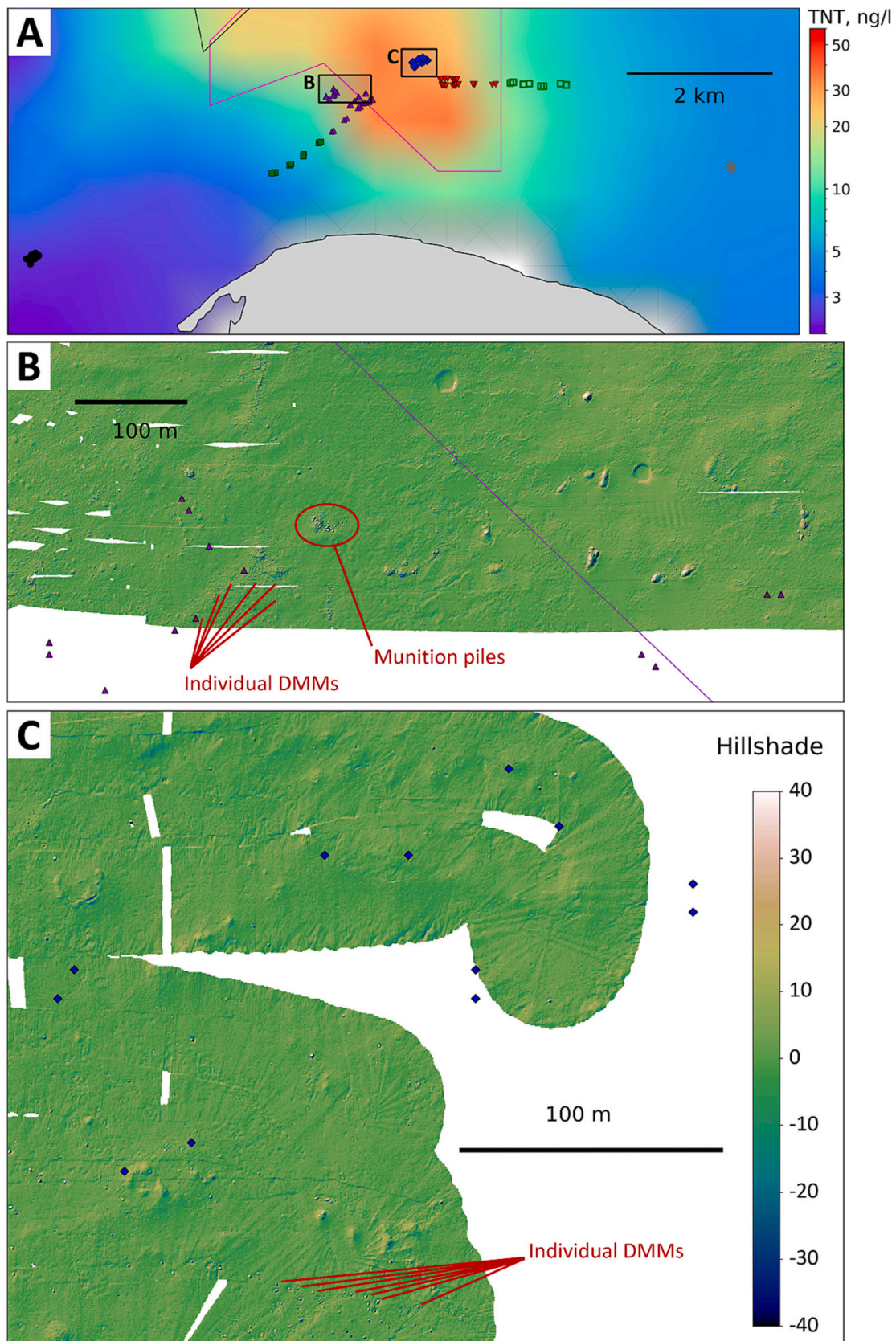


Fig. 5. Stations on the background of mapped TNT-concentration (A) and the seafloor morphology represented as hillshade data of the sub-areas B and C. Certain munition piles and individual DMMs are marked; munition areas and station markers and their colours are the same as in previous figures.

Canonical Correspondence Analysis

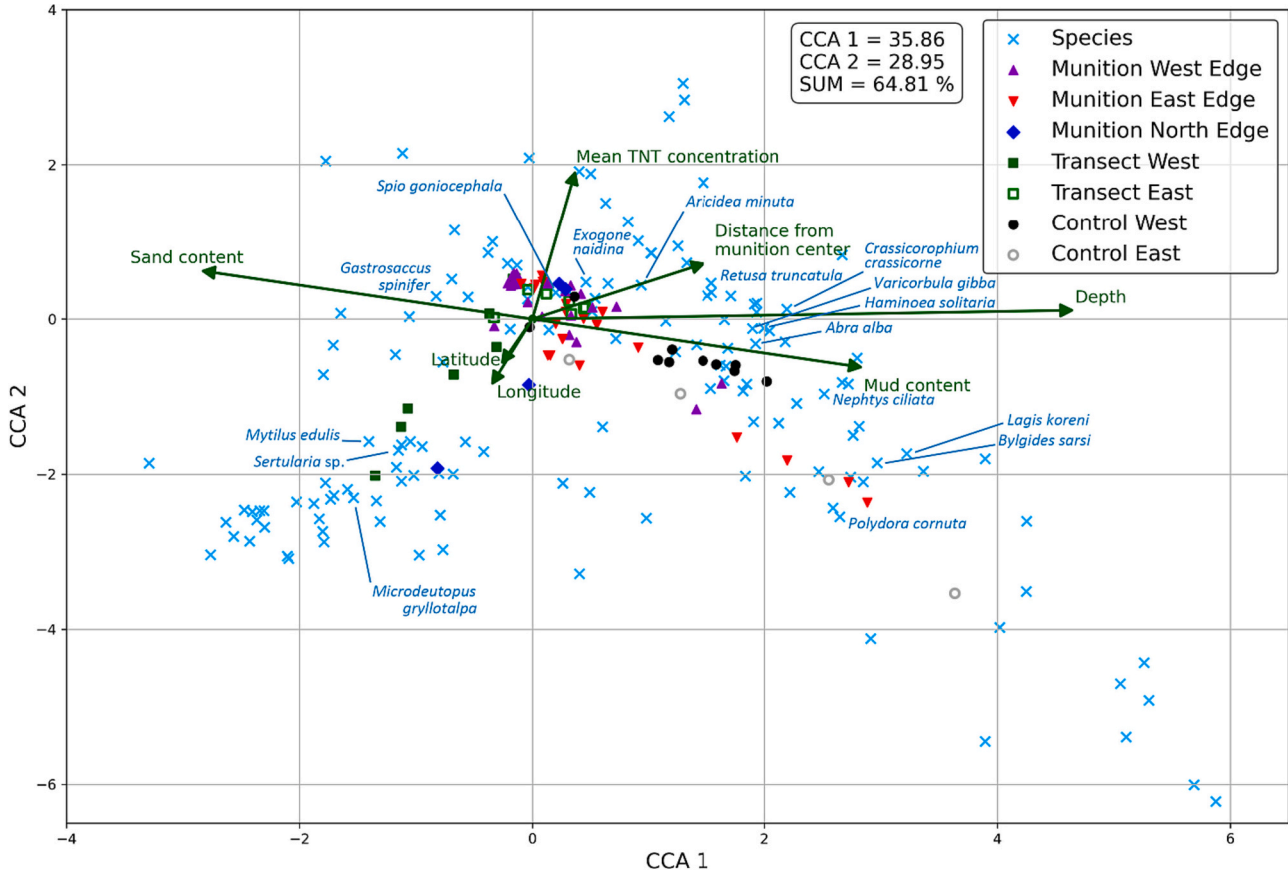


Fig. 6. Canonical correspondence analysis of samples and species along the vectors of Latitude, Longitude, Mud content, Depth, Sand and TNT-concentration and distance from the munition centre. Environmental vectors are shown as green arrows; species are shown as blue crosses, samples are shown as markers with the same colours and shapes as in Fig. 2. 16 species correlated with the TNT-concentration are shown. CCA-statistics (%) are given in the inset box. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

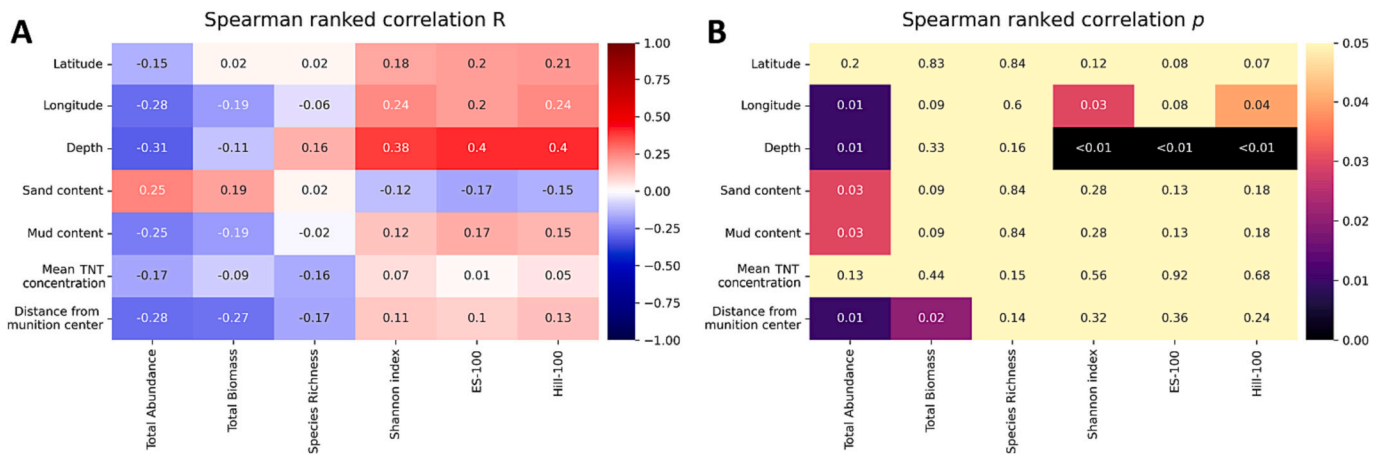


Fig. 7. Spearman ranked correlation of the community characteristics (abundance, biomass and diversity) with the environmental variables. A – R-values for the community characteristics; B – p-values for the community characteristics.

model results (*Spio gonocephala*, *Varicorbula gibba* and *Retusa truncatula*), the biological traits varied greatly and included different kinds of size classes (from <10 mm to 100 mm), morphology (soft-bodied / with exoskeleton), reproduction modes (benthic direct / planktotrophic development), living habits (surface/burrows) feeding modes (predator / suspension-feeder / deposit-feeder), etc. (Table 4, Fig. 9). For other 13

TNT-correlated taxa the differences were also significant and no common trend was found (Table 4).

4. Discussion

The Baltic Sea is one of the most extensively studied seas, with first

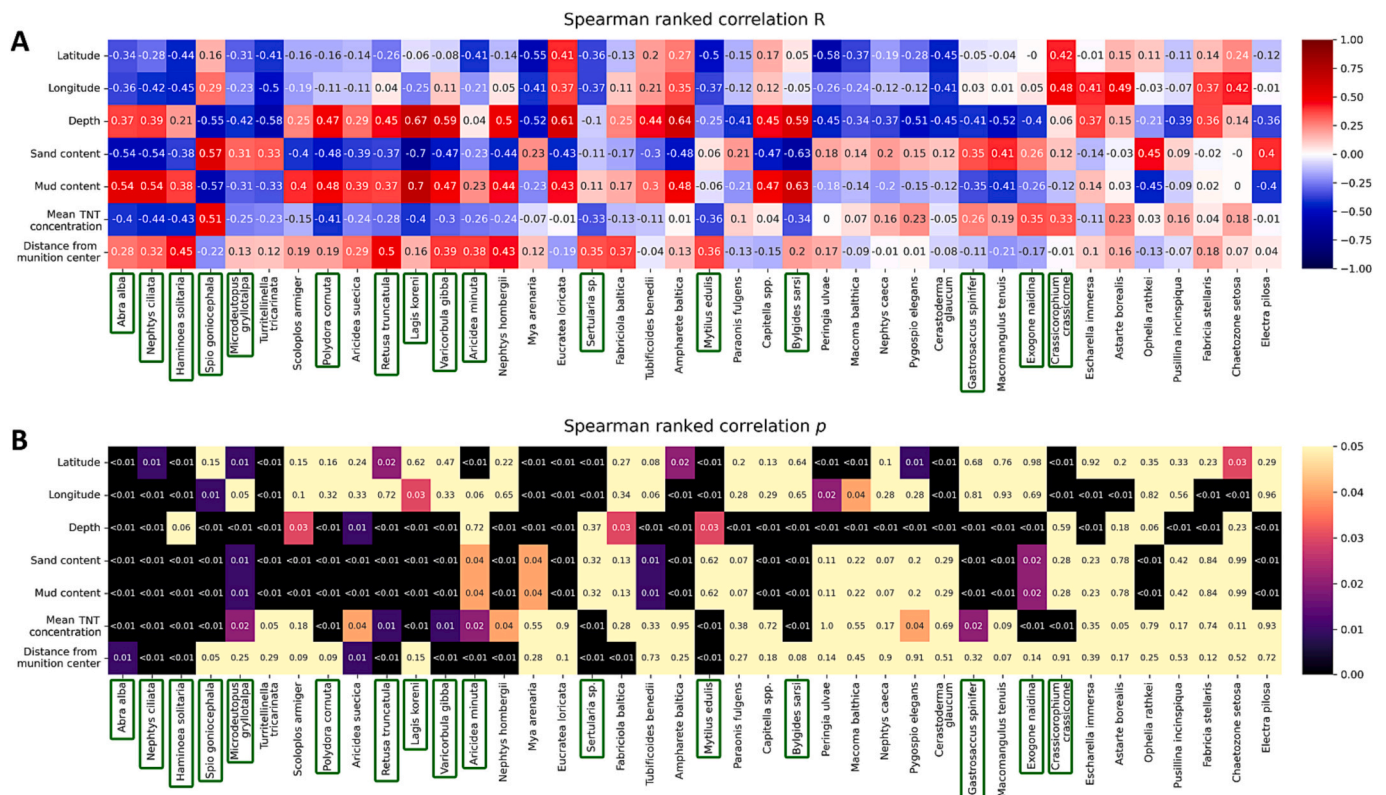


Fig. 8. Spearman ranked correlation of individual species abundances with the environmental variables. A – R-values for the individual species abundances; B – p-values for the individual species abundances. 16 species significantly correlated with the TNT-concentration are marked with green rectangles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

benthic biota samples collected during the eighteenth century. More systematic, although mostly qualitative studies on benthos were initiated in the nineteenth century (Martin, 2000; Leppäkoski, 2001). The data on macrofauna occurrence and distribution are accumulated in various resources, including the HELCOM monitoring data (<https://helcom.fi/action-areas/monitoring-and-assessment/>), and the Baltic Sea Alien Species Database (<http://www.corpi.ku.lt/nemo/>). During the past 30 years, the Leibniz Institute for Baltic Sea Research (IOW) has been sampling different regions of the Baltic Sea with regular observational stations as part of the regular monitoring.

The spatial structure of macrofauna communities in the Baltic Sea has been studied over a few decades, including modelling the large- (hundreds of km) and medium-scale (several km) distribution of individual species (Gogina and Zettler, 2010; Schiele, 2014; Zettler et al., 2014). The area of Kolberger Heide and its surroundings are known to be inhabited by a variety of mostly infaunal organisms with the dominance of polychaetes (mostly *Pygospio elegans* and *Dipolydora quadrilobata*) and molluscs (*Peringia ulvae* and *Arctica islandica*) with relatively high values of abundance, biomass and diversity compared to the average in the South-Western Baltic Sea (Josefson and Hansen, 2004; Zettler et al., 2008; Schiele, 2014; Gogina et al., 2016). However, no patterns relative to the munition dumpsite have been described there yet. Only a few studies were focused on the influence of the Baltic Sea munition dumpsites specifically, and these were located in the south-central Baltic Sea close to chemical munition dumpsites in the Bornholm Basin (Beldowski et al., 2016). The majority of chemical munition has been dumped in deep areas like the Gotland or Bornholm deeps, where oxygen is depleted or almost absent, so the amount of macrofauna data is very low. In some cases, only 3 to 4 species were reported from the deeper stations, in others, only meiofaunal taxa were present (Kotwicki et al., 2016; Czub et al., 2018; Lang et al., 2018). In the current dataset, the species list included a total of 152 taxa with 5 to 50 per sample,

which allowed us to look at similarities between samples at higher resolution.

Apart from the Baltic Sea, existing benthic studies cover only a tiny fraction of the existing global munition dumpsites (Munition Cadastre; Thiel, 2003). For example, several studies took place in the Atlantic Ocean, e.g. in the North-Eastern part off the US coast around conventional munition (Mahadevan, 1977) and radioactive dumpsites (Reish, 1981), in the Adriatic Sea around a chemical munition dumping area (dos Santos et al., 2023), and in the Pacific Ocean near Hawaii and California around both chemical and conventional munition dumpsites (Hilbig and Blake, 2006; Edwards et al., 2016). Overall, the mentioned investigations showed either minor or no differences in benthic communities between areas affected by the munition and the background. One of the possible reasons might be the station planning, as the munition influence disappears quickly with distance. For example, Greinert (2019) showed that even at a few meters distance from the source, the TNT concentration drops by several orders of magnitude from 20 to 25 µg l⁻¹, to 10–30 ng l⁻¹, most likely due to rapid mixing and dilution. For other munition compounds, also present in the study area, the concentrations are usually even lower. The explosives RDX and HMX show 3- and 60-fold lower solubility than TNT (Beck et al., 2018). Concentrations acutely toxic to the benthic fauna start from approximately ~mg l⁻¹ levels which are rarely observed in situ (Beck et al., 2018; Maser and Strehse, 2021). Over longer exposure time, low concentrations of munition compounds may cause sublethal effects such as reduced growth and reproduction, impaired development, and damage to the nervous, immune and blood (Gong et al., 2007), although this is less well studied. At lower concentrations, negative health may still occur in biota, compromising species function in the ecosystem and enhancing sensitivity to other environmental disturbances. Accordingly, a lower distance between the individual samples is required. Our study is therefore the first to describe certain gradients in macrofauna

Table 2
Summary of linear mixed-effects model results with ANOVA for fixed effects (random parameter – number of grab).

| Source (fixed variables) | No. of observations | Estimated slope | Sum of squares | Mean of squares | Denominator df | F value | t value | p value | Comment |
|---------------------------|---------------------|-----------------|----------------|-----------------|----------------|---------|---------|---------|--------------------|
| Total abundance | Latitude | 93 | -361.90 | 1047.90 | 1047.90 | 91.00 | 0.00 | -0.06 | 0.9521 |
| | Longitude | 93 | 701.58 | 80,280 | 80,280 | 90.99 | 0.28 | 0.53 | 0.5987 |
| | Depth | 93 | -19.98 | 401,645 | 401,645 | 90.96 | 1.41 | -1.19 | 0.2377 |
| | TRI | 15 | 6683 | 18,491 | 18,491 | 0.62 | 0.04 | 0.208 | 0.8836 |
| | Sand content | 78 | 8.09 | 1,382,921 | 1,382,921 | 4.71 | 4.61 | 2.15 | 0.0879 |
| | Mud content | 78 | -9.09 | 1,403,230 | 1,403,230 | 5.48 | 4.68 | -2.16 | 0.0781 |
| | TNT concentration | 93 | -8.41 | 1,001,966 | 1,001,966 | 3.28 | 3.62 | -1.90 | 0.1455 |
| | Distance | 93 | -25.32 | 268,237 | 268,237 | 91.00 | 0.94 | -0.97 | 0.3352 |
| | Latitude | 93 | 94.57 | 71.57 | 71.57 | 91.00 | 0.97 | 0.98 | 0.3283 |
| | Longitude | 93 | 18.22 | 54.19 | 54.19 | 91.00 | 0.73 | 0.85 | 0.3953 |
| Total biomass | Depth | 93 | 0.20 | 40.57 | 40.57 | 91.00 | 0.54 | 0.74 | 0.4623 |
| | TRI | 15 | -273 | 59.54 | 59.54 | 13.00 | 0.16 | -0.40 | 0.6991 |
| | Sand content | 78 | 0.08 | 125.85 | 125.85 | 1.86 | 1.51 | 1.23 | 0.3524 |
| | Mud content | 78 | -0.08 | 93.67 | 93.67 | 1.09 | 1.13 | -1.06 | 0.4697 |
| | TNT concentration | 93 | -0.07 | 64.39 | 64.39 | 1.42 | 0.87 | -0.93 | 0.4812 |
| | Distance | 93 | -0.23 | 22.77 | 22.77 | 91.00 | 0.31 | -0.55 | 0.5821 |
| | Latitude | 93 | 52.40 | 21.97 | 21.97 | 90.95 | 0.24 | 0.50 | 0.6219 |
| | Longitude | 93 | 11.21 | 20.50 | 20.50 | 90.55 | 0.23 | 0.48 | 0.6338 |
| | Depth | 93 | 0.35 | 124.68 | 124.68 | 91.00 | 1.41 | 1.19 | 0.2386 |
| | TRI | 15 | 190 | 28.83 | 28.83 | 13.00 | 0.37 | 0.61 | 0.5537 |
| Species richness | Sand content | 78 | 0.03 | 19.94 | 19.94 | 50.29 | 0.22 | 0.47 | 0.6433 |
| | Mud content | 78 | -0.29 | 12.03 | 12.03 | 0.50 | 0.13 | -0.36 | 0.8156 |
| | TNT concentration | 93 | -0.11 | 166.95 | 166.95 | 91.00 | 1.89 | -1.38 | 0.1721 |
| | Distance | 93 | 0.02 | 0.26 | 0.26 | 91.00 | 0.00 | 0.05 | 0.9571 |
| | Latitude | 93 | 2.63 | 0.06 | 0.06 | 90.99 | 0.18 | 0.43 | 0.6689 |
| | Longitude | 93 | 0.97 | 0.15 | 0.15 | 90.56 | 0.51 | 0.72 | 0.4764 |
| | Depth | 93 | 0.05 | 1.89 | 1.89 | 1.00 | 6.98 | 2.64 | 0.2299 |
| | TRI | 15 | -16.32 | 0.21 | 0.21 | 13.00 | 0.63 | -0.79 | 0.4419 |
| | Sand content | 78 | -2.54E-03 | 0.13 | 0.13 | 2.74 | 0.39 | -0.63 | 0.5788 |
| | Mud content | 78 | 2.54E-03 | 0.15 | 0.15 | 76.00 | 0.45 | 0.67 | 0.5054 |
| Shannon index | TNT concentration | 93 | 2.86E-03 | 0.12 | 0.12 | 79.90 | 0.41 | 0.64 | 0.5239 |
| | Distance | 93 | 0.03 | 0.32 | 0.32 | 1.00 | 1.09 | 1.05 | 0.4858 |
| | Latitude | 93 | 43.21 | 14.94 | 14.94 | 90.94 | 0.39 | 0.62 | 0.5344 |
| | Longitude | 93 | 6.26 | 6.40 | 6.40 | 90.57 | 0.17 | 0.41 | 0.6845 |
| | Depth | 93 | 0.52 | 273.44 | 273.44 | 91.00 | 7.69 | 2.77 | 0.0067 |
| | TRI | 15 | 99.05 | 2.01 | 2.01 | 0.76 | 0.05 | 0.22 | 0.8705 |
| | Sand content | 78 | -0.04 | 40.52 | 40.52 | 2.58 | 0.99 | -0.99 | 0.4040 |
| | Mud content | 78 | 0.04 | 46.69 | 46.69 | 76.00 | 1.14 | 1.07 | 0.2894 |
| | TNT concentration | 93 | 0.02 | 5.75 | 5.75 | 90.90 | 0.15 | 0.39 | 0.7000 |
| | Distance | 93 | 0.27 | 27.63 | 27.63 | 1.02 | 0.72 | 0.85 | 0.5491 |
| ES-100 | Latitude | 93 | 41.85 | 14.01 | 14.01 | 90.90 | 0.37 | 0.61 | 0.5463 |
| | Longitude | 93 | 8.83 | 12.72 | 12.72 | 90.41 | 0.33 | 0.58 | 0.5654 |
| | Depth | 93 | 0.56 | 311.09 | 311.09 | 91.00 | 8.91 | 2.98 | 0.0037 |
| | TRI | 15 | 99.08 | 2.02 | 2.02 | 0.76 | 0.05 | 0.22 | 0.8705 |
| | Sand content | 78 | -0.04 | 34.94 | 34.94 | 76.00 | 0.85 | -0.92 | 0.3594 |
| | Mud content | 78 | 0.04 | 34.94 | 34.94 | 76.00 | 0.85 | 0.92 | 0.3594 |
| | TNT concentration | 93 | 0.03 | 15.30 | 15.30 | 90.99 | 0.40 | 0.63 | 0.5284 |
| | Distance | 93 | 0.31 | 39.05 | 39.05 | 1.23 | 1.03 | 1.02 | 0.4688 |
| | TNT concentration | 31 | -0.10 | 43.02 | 43.02 | 1.78 | 6.37 | -2.52 | 0.1425 |
| | TNT concentration | 13 | -0.02 | 0.48 | 0.48 | 11.00 | 0.78 | -1.00 | 0.3950 |
| Nephtys ciliata | TNT concentration | 6 | - | - | - | - | - | - | Not enough samples |
| | TNT concentration | 73 | 0.51 | 3066.70 | 3066.70 | 50.96 | 4.35 | 2.09 | 0.0420 |
| Haminoea solitaria | TNT concentration | 21 | -0.21 | 79.94 | 79.94 | 17.48 | 0.46 | -0.68 | 0.5058 |
| | TNT concentration | 24 | 0.02 | 1.88 | 1.88 | 22.00 | 0.03 | 0.19 | 0.8542 |
| Spio goniocephala | TNT concentration | 38 | -0.58 | 2446.30 | 2446.30 | 35.99 | 19.78 | -4.45 | 8.02E-05 |
| | TNT concentration | 27 | -0.14 | 83.98 | 83.98 | 25.00 | 3.44 | -1.86 | 0.0755 |
| Microdeutopus gryllotalpa | TNT concentration | 37 | -0.20 | 249.73 | 249.73 | 35.00 | 16.39 | -4.05 | 2.71E-04 |
| | TNT concentration | 27 | -0.14 | 83.98 | 83.98 | 25.00 | 3.44 | -1.86 | 0.0755 |
| Polydora cornuta | TNT concentration | 37 | -0.20 | 249.73 | 249.73 | 35.00 | 16.39 | -4.05 | 2.71E-04 |
| | TNT concentration | 27 | -0.14 | 83.98 | 83.98 | 25.00 | 3.44 | -1.86 | 0.0755 |
| Retusa truncatula | TNT concentration | 27 | -0.14 | 83.98 | 83.98 | 25.00 | 3.44 | -1.86 | 0.0755 |
| | TNT concentration | 37 | -0.20 | 249.73 | 249.73 | 35.00 | 16.39 | -4.05 | 2.71E-04 |
| Lagis koreni | TNT concentration | 27 | -0.14 | 83.98 | 83.98 | 25.00 | 3.44 | -1.86 | 0.0755 |
| | TNT concentration | 37 | -0.20 | 249.73 | 249.73 | 35.00 | 16.39 | -4.05 | 2.71E-04 |
| Varicorbula gibba | TNT concentration | 27 | -0.14 | 83.98 | 83.98 | 25.00 | 3.44 | -1.86 | 0.0755 |
| | TNT concentration | 37 | -0.20 | 249.73 | 249.73 | 35.00 | 16.39 | -4.05 | 2.71E-04 |

(continued on next page)

Table 2 (continued)

| Source (fixed variables) | No. of observations | Estimated slope | Sum of squares | Mean of squares | Denominator df | F value | t value | p value | Comment |
|--|---------------------|-----------------|----------------|-----------------|----------------|---------|---------|---------|---------|
| <i>Aricidea minuta</i> TNT concentration | 49 | -0.11 | 78.51 | 78.51 | 1.32 | 8.95 | -2.99 | 0.1537 | |
| <i>Sertularia</i> sp. TNT concentration | 8 | -0.02 | 0.03 | 0.03 | 0.17 | 0.02 | -0.15 | 0.9473 | |
| <i>Mytilus edulis</i> TNT concentration | 58 | -1.85 | 23,977 | 23,977 | 2.29 | 0.83 | -0.91 | 0.4480 | |
| <i>Bylgides sarsi</i> TNT concentration | 32 | 3.53E-03 | 0.04 | 0.04 | 1.48 | 0.07 | 0.27 | 0.8207 | |
| <i>Gastrosaccus spinifer</i> TNT concentration | 23 | -0.01 | 0.44 | 0.44 | 0.99 | 0.72 | -0.85 | 0.5546 | |
| <i>Exogone naidina</i> TNT concentration | 64 | 0.05 | 25.21 | 25.21 | 27.17 | 0.26 | 0.52 | 0.6110 | |
| <i>Crassicorophium crassicorne</i> TNT concentration | 25 | 0.03 | 1.61 | 1.61 | 1.25 | 0.49 | 0.70 | 0.5902 | |

Start in right column indicate the significance: 0 '****' – <0.001; '***' – 0.001-0.01; '**' – 0.01-0.05; '.' – 0.05-0.1. Taxa with p-values <0.05 are marked with bold. The order of taxa is the same as in Fig. 8.

structure.

In terms of total macrofauna abundance, biomass and diversity values, no gradients or other relationships were found in this study relative to the munition presence. Previously, the Baltic Sea macrofauna species composition and spatial structure on the larger scale was analysed multiple times (Gogina and Zettler, 2010; Schiele, 2014; Zettler et al., 2014; Gogina et al., 2016). No significant differences related to the munition dumpsites were reported. In our samples, the overall species composition was similar to the previous studies, including the most abundant taxa: *Scoloplos armiger*, *Pygospio elegans*, *Spio gonocephala* polychaetes, *Peringia ulvae* gastropods, etc. (Schiele, 2014; HELCOM Checklist 2.0 of Baltic Sea Macrospecies, n.d.). Only depth has shown some reliable correlation with the diversity indices (Fig. 7, Table 2). This could be an indirect sign of a healthy community, as significant changes in diversity are often observed in polluted areas (Thiel, 2003; Rosenberg et al., 2004). However, the lack of clear dependencies can be also explained by the low resolution of the TNT data (600 m resolution, Fig. 5A) and by the scattering of the munition piles. In particular, some DMMS or even large piles of the munition can be found outside the designated restricted area of Kolberger Heide, as seen in Fig. 5B (see also Kampmeier et al., 2020), thus making less sense in marking 'distance to munition centre' as a parameter for each sample. Another possible reason for the lack of diversity gradients is the ecology and biogeography of the Baltic Sea. The species richness there is very poor comparing to e.g. the neighbouring North Sea and other true marine environments (Ojaveer et al., 2010), and therefore the resolution of the Baltic Sea data may be lower. Some previous studies revealed a generally higher diversity within the oyster reef habits and mussel beds in the Western Baltic Sea compared to bare sediment areas (Norling and Kautsky, 2008; Hollander et al., 2015). Various species of molluscs and crustaceans are known to be generally attracted to hard substrata, while polychaete species that prefer fine sediments remain more abundant away from the hard substrata. However, those studies sampled directly from oyster or mussel grounds, whereas the current study did not collect samples from the hard munition substrates. Same sampling design conducted at one of the North Sea munition dumpsites can bring different patterns of macrofauna diversity.

In terms of individual species composition, some differences and gradients were observed. The overall similarity structure corresponded to the locations of the sampling sites, even at a scale of hundreds of meters, e.g. depending on the direction to the munition concentration centre ('Munition West Edge' vs. 'Munition East Edge') (Fig. 2). On the other hand, some traces of horizontal gradient were visible by the similarity matrices (Fig. 4). The individual species distribution showed even more clear relation with the distribution of *Retusa truncatula*, *Varicorbula gibba* and *Spio gonocephala* being possibly predicted by the TNT concentration (Fig. 9). These species are not dominant, though widely

distributed throughout the Western Baltic Sea, as well as the North Sea and the entire North-East Atlantic (Hayward and Ryland, 1990; Hrs-Brenko, 2006; Bick et al., 2010; Schiele, 2014;). Research focused on the biology of these species is scarce. *Varicorbula gibba* and *Spio* spp. were previously studied for environmental tolerance and various anthropogenic impacts. Specifically, *Varicorbula gibba* was reported to occur in constantly and occasionally eutrophic areas and is considered to be an indicator of environmental instability caused by pollution, low oxygen content, or increased turbidity (Hrs-Brenko, 2006; Sabatini and Ballerstedt, 2008). *Spio* cf. *filicornis* (a close relative of *S. gonocephala*) was reported to be a disturbance-tolerant and pollution-tolerant species (Samuelson, 2001). *Retusa truncatula*, has been shown to increase in abundance shortly after experimental sediment digging comparing to other members of benthic community indicating that it is less affected by this disturbance (Carvalho et al., 2013). Withstanding the environmental disturbances seems to be an obvious common ecological ability for the three mentioned species. However, this is hardly applicable for the Kolberger Heide area, as they demonstrated opposite trends in relation to the TNT concentration (which in our samples was 19 ± 13 ng l⁻¹ – clearly lower than the toxic level). The biological traits for these three species were also very different and represented a variety of living habits, feeding modes and reproductive strategy.

A tolerance to environmental disturbances and pollution are well known for other taxa present in our samples, e.g. for *Capitella* spp. (Grassle and Grassle, 1976), although no correlations were found for them in this study. The reasons that *Spio gonocephala* abundance increased and *Retusa truncatula* and *Varicorbula gibba* abundance decreased with TNT concentration is most likely related to other environmental variables or biological interactions within the ecosystem.

Interestingly, munition dumpsites are known to attract certain fish species, specifically the Baltic cod (*Gadus morhua*) and different species of flatfishes (Kampmeier et al., 2020; Maser and Strehse, 2021; Beck et al., 2022). The abundance of fish is probably due to the structure of the munition piles with lots of crevices and caverns where fish can hide, and by restricted fishing activity. Similar patterns are also observed around offshore wind farms (Stenberg et al., 2015; Glarou et al., 2020), and large amounts of hard substrate are otherwise rare in the German Baltic Sea (Kampmeier et al., 2020). In addition, the polychaete *Spio gonocephala*, was more abundant around munition in the bare sediment and may be an important food source for fish (Surugiu, 2006; Haase et al., 2020).

The sample resolution we obtained for this study allowed to retrieve certain regularities in local structure of the macrofauna, including TNT-related patterns of species distribution. However, to support the conclusions we have, benthic fauna samples from the closest surroundings (<1 m) of the TNT-source would be valuable, as the concentration of munition compounds drops rapidly to the apparently non-dangerous

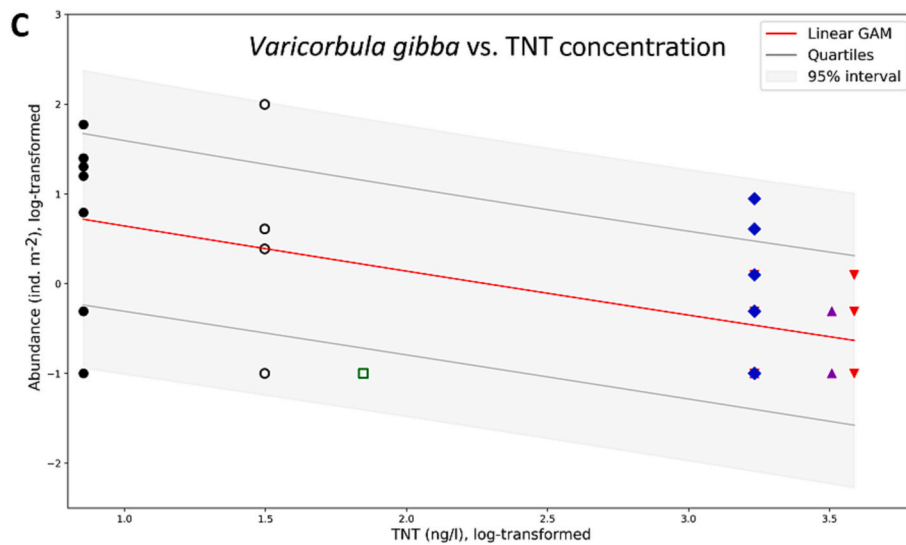
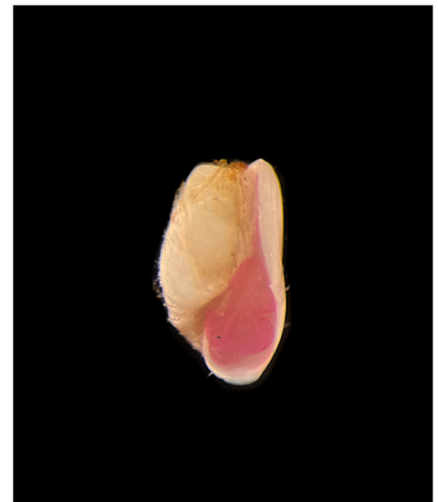
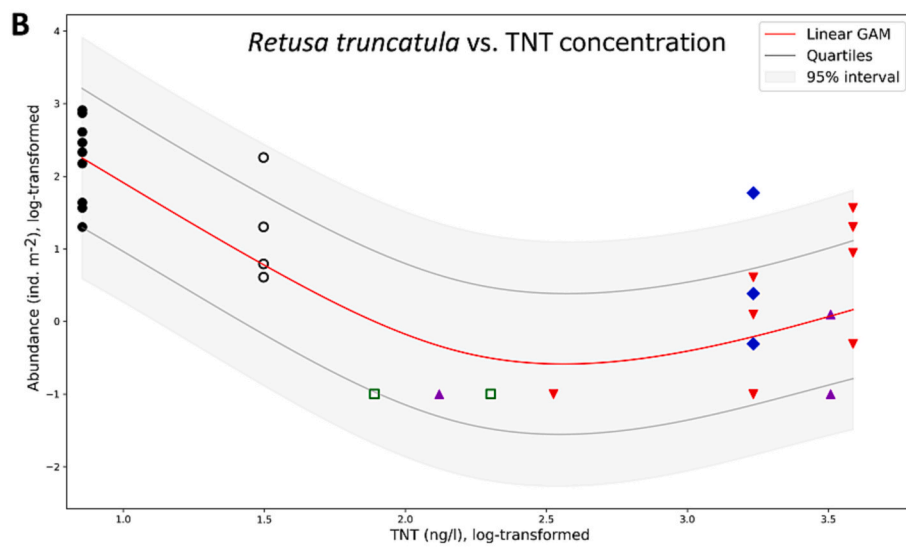
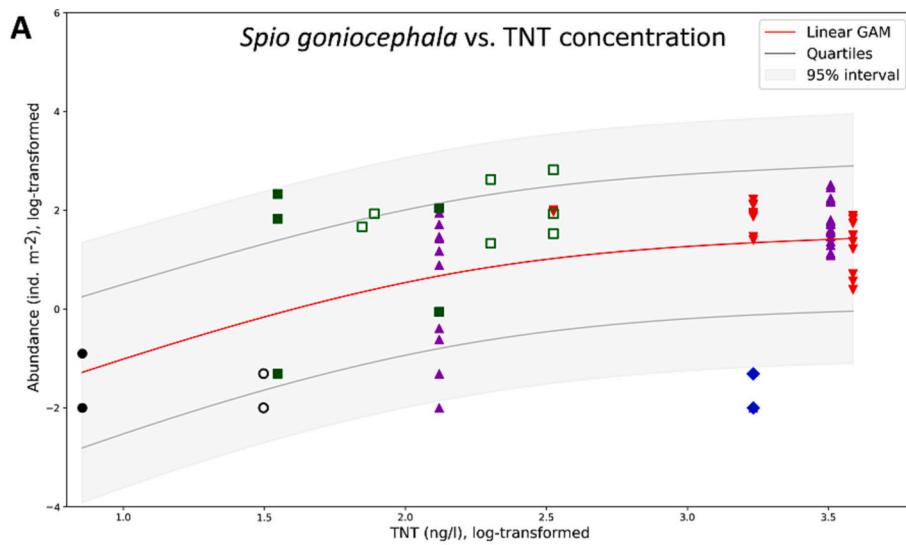


Fig. 9. Generalized additive models plotted for the abundance of three species vs. TNT-concentrations. A – *Spio gonocephala*; B – *Retusa truncatula*; C – *Varicorbula gibba*. Colours and shapes of markers are same as in Figs. 2 and 4. Photos by A. Vedenin.

Table 3
Summary of generalized additive models for three species vs. TNT-concentration.

| Variables | | | No. of observations | Approximate R ² | Ref. df | F value | p value |
|--------------------------|-------------------|-----------------|---------------------|----------------------------|---------|---------|----------|
| <i>Spio gonocephala</i> | TNT concentration | Untransformed | 93 | 0.30 | 5.97 | 7.49 | 3.24E-06 |
| | | Log-transformed | 73 | 0.44 | 7.95 | 8.17 | <2E-16 |
| <i>Retusa truncatula</i> | TNT concentration | Untransformed | 93 | 0.54 | 6.03 | 18.74 | <2E-16 |
| | | Log-transformed | 38 | 0.66 | 4.22 | 17.83 | <2E-16 |
| <i>Varicorbula gibba</i> | TNT concentration | Untransformed | 93 | 0.35 | 4.54 | 10.94 | 3.40E-07 |
| | | Log-transformed | 37 | 0.33 | 1.00 | 18.74 | 1.19E-04 |

Table 4
Biological trait description of the 16 TNT-correlated taxa. Three genera with significant LME-model p-values are marked with bold. Data taken from [Clare and Brafield \(2022\)](#). Order of taxa is the same as in [Fig. 8](#) and [Table 2](#).

| Genus | Size (mm) | Morphology | Lifespan (years) | Egg development | Larva development | Living habit | Sediment position | Feeding mode | Mobility | Bioturbation |
|---------------------------|-----------|-------------|------------------|-----------------|-------------------|-----------------|---------------------|----------------------------|---------------|--------------------|
| <i>Abra</i> | 10–20 | Exoskeleton | 1–3 | Pelagic | Planktotrophic | Burrow-dwelling | Shallow infauna | Suspension/predator | Sessile | Diffusive mixing |
| <i>Nephtys</i> | 20–200 | Soft bodied | 3–10 | Pelagic | Planktotrophic | Free-living | Shallow/mid infauna | Scavenger/predator | Swim/burrower | Diffusive mixing |
| <i>Haminoea</i> | <10 | Exoskeleton | 1–3 | | | Free-living | Shallow infauna | | Crawl | Diffusive mixing |
| <i>Spio</i> | 10–100 | Soft bodied | 1–3 | Brooded | Planktotrophic | Burrow-dwelling | Shallow infauna | Surface deposit | Sessile | Surface deposition |
| <i>Microdeutopus</i> | <10 | Exoskeleton | 1–3 | Brooded | Benthic direct | Tube-dwelling | Shallow infauna | Surface deposit | Swim/crawl | Surface deposition |
| <i>Polydora</i> | 10–100 | Soft bodied | 1–3 | Brooded | Planktotrophic | Tube-dwelling | Shallow infauna | Surface deposit | Sessile | Surface deposition |
| <i>Retusa</i> | <10 | Exoskeleton | 1–3 | Benthic | Benthic direct | Free-living | Shallow infauna | Predator | Crawl | Diffusive mixing |
| <i>Lagis</i> | 20–100 | Soft bodied | 1–3 | Pelagic | Planktotrophic | Tube-dwelling | Shallow infauna | Subsurface deposit | Sessile | Upward conveyor |
| <i>Varicorbula</i> | 10–20 | Exoskeleton | 1–3 | Pelagic | Planktotrophic | Burrow-dwelling | Shallow infauna | Suspension/predator | Sessile | Surface deposition |
| <i>Aricidea</i> | <100 | Soft bodied | 1–3 | Brooded | Benthic direct | Free-living | Shallow infauna | Surface deposit | Burrower | Diffusive mixing |
| <i>Sertularia</i> | >500 | Stalked | 3–10 | Asexual/pelagic | Planktotrophic | Attached | Surface | Suspension/predator | Sessile | None |
| <i>Mytilus</i> | 20–100 | Exoskeleton | >10 | Pelagic | Planktotrophic | Attached | Surface | Suspension/predator | Sessile | Surface deposition |
| <i>Bylgides</i> | 20–100 | Soft bodied | 3–10 | Pelagic | Planktotrophic | Free-living | Surface | Predator | Crawl | Surface deposition |
| <i>Gastrosaccus</i> | 10–100 | Exoskeleton | 1–3 | Brooded | Benthic direct | Free-living | Surface | Suspension/surface deposit | Swim | Surface deposition |
| <i>Exogone</i> | <10 | Soft bodied | 1–3 | Brooded | Benthic direct | Free-living | Surface | Surface deposit | Crawl | Surface deposition |
| <i>Crassicorophium</i> | <10 | Exoskeleton | <1 | Brooded | Benthic direct | Tube-dwelling | Shallow infauna | Suspension | Swim/crawl | Surface deposition |

concentrations away from the source ([Beck et al., 2018](#); [Greiner, 2019](#)). Direct measurements of TNT and other MC content in the upper layers of sediment will be necessary to confirm the observed correlations, as these values may differ from the TNT concentration in the near-bottom water. This was shown for other munition compounds, depending on their solubility or tendency to partition to sediment surface ([Briggs et al., 2016](#)). Specifically, TNT is known to rapidly sorb from solution to the sediment, especially in association with sediment organic carbon ([Brannon et al., 2005](#)). On the other hand, sediment concentrations of TNT can be >50 times lower than that in the water ([Bünning et al., 2021](#)). The dissolved TNT concentration modelled in this study represents annual mean levels with 600-m area resolution. Sediment TNT levels may vary significantly over a scale of meters, depending on the sediment structure and proximity and type of nearby munition items. Direct TNT measurements in sediments are crucial in future studies examining effects on spatial patterns of macrofauna species.

Some benthic organisms, including the starfishes *Asterias rubens* or mussels *Mytilus edulis*, can be found on surfaces of exposed explosives, where dissolved TNT concentrations approach the LC-50 threshold ([Beck et al., 2019](#); [Maser and Strehse, 2021](#)). The TNT measured in their tissues can be also very high, as shown for the starfishes *Asterias rubens* (over 4.5 mg/g dry weight in one sample), and unidentified macroalgae

(3.9 µg/g wet weight) and sponges (4.3 µg/g weight) ([Beck et al., 2022](#), Appendix A). At the same time, nothing is known about smaller macrofaunal organisms (including *Retusa truncatula*, *Varicorbula gibba* and *Spio gonocephala*, discussed above), which are undetectable by underwater photography and have not yet been measured for TNT or other munition compounds. The rate of accumulation of various munition compounds is also unknown for these species regarding their different biological traits ([Table 4](#)). Grab sampling from a research vessel is not possible with sufficient precision to collect samples directly adjacent to munition objects, and future studies may require smaller sediment cores taken by scientific divers. This may also reveal other patterns, e.g. for total biomass or diversity values, if they significantly change only under extreme values of the TNT concentration.

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CRediT authorship contribution statement

A.A. Vedenin: Conceptualization, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **I. Kröncke:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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