SHORT COMMUNICATION

Open Access

Who lives where? Macrobenthic species distribution over sediment types and depth classes in the eastern North Sea

Werner Armonies[*]

Abstract

An extensive data set of macrozoobenthos from the eastern North Sea was evaluated in order to describe the distribution of infaunal species with respect to water depth and median grain size of the sediment. The resulting data are presented for 134 species, in 104 species abundance correlated significantly with water depth, with most species decreasing in abundance towards the hydrographically turbulent shallow areas. This suggests hydrography is a limiting factor for most of the species in this area while very few species only seem to favour the turbulent side of the gradient. With respect to median grain size, two thirds of the species showed significant abundance variations and one third did not. Most of the latter species were either represented by rather poor data or are known to be highly motile. Thus, true sediment generalists seem to be few. Conversely, no species was exclusively restricted to a single sediment type. Significant depth × sediment type interaction terms in a regression model indicate that abundance distribution over sediment types varied with depth level in 60% of the species, indicating that these populations were restricted to a part of their species-specific tolerated ranges in the study area. Hence, the distributional patterns over water depth and sediment types shown here represent realised niches. These data may help to locate populations and, in the light of global change, may serve as a baseline for future comparisons.

Keywords: Macrobenthos, North Sea, Water depth, Sediment type, Hydrography

Background

"You classified *Lagis koreni* as a mud-dweller, how do you know?" – a simple question by a reviewer, but it turned out to be difficult to answer. Whoever has sorted North Sea macrobenthos knows, by experience, that this species is closely associated with very fine sediments. However, citable information about sediment preferences are limited to a few species and I found no comprehensive overview. With respect to water depth, the lack of comprehensive information applies accordingly. The morphological/systematic papers used for species determination

are usually not based on quantitative studies over a range of habitats; therefore, they can only list the habitat types and depth levels where a species has been encountered. For the more abundant species this results in an every-one-everywhere impression.

The quantitative surveys available for the North Sea benthos primarily concentrated on the delimitation of species assemblages. On a large spatial scale (the entire North Sea), sea bottom temperature was identified as a major structuring factor (correlating with water depth and, ultimately, the origin and connection of the water body with southern Lusitanian or northern Atlantic waters [1]). On a smaller spatial scale (the German Bight), sediment composition was the main factor separating the species associations [2] while temperature strongly varies seasonally but shows no correlation with water depth

*Correspondence: Werner.Armonies@awi.de
Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Wattenmeerstation Sylt, Hafenstr. 43, 25992 List, Germany

in these shallow (< 50 m) and well-mixed waters. Instead, hydrodynamic sediment disturbance becomes a major structuring force which strongly correlates with water depth and directly or indirectly influences all physical properties of the sediment [3]. Thus, water depth is important within these shallow waters as well, although most likely as a proxy only for a hydrodynamic-generated combination of physical factors within the sediment.

In order to fill the gap of species-specific information of the dependence on water depth and sediment composition, I evaluated species abundances in the eastern part of the North Sea which had been repeatedly sampled between 2004 and 2011 (Fig. 1) and supplemented by a data set from the shallow waters off the island of Sylt. From a total of 2591 sediment cores, each with individual information on water depth and a granulometric sediment analysis, quantitative distribution over depth classes and sediment types is compiled for the 134 most abundant species. These data represent the species realised niches which may help to locate populations and serve as a baseline for future studies.

Data source and statistical treatment

As a data source I restricted to sediment cores gained from a 0.02 m^2 Reineck-type box-corer that were sieved over 1 mm square meshes without prior fixation. This was done because corer types have different sampling characteristics while mesh size and shape affect the percentage of fauna retained by sieving [4]. A further requirement was information about water depth of the sampled site (which is usually available) and a granulometric sediment analysis for each core (which is usually not available because most sampling protocols restrict to a sediment sample from a single replicate). Finally, I restricted seasonally to samples collected outside the main recruitment season; most sample sets were collected in September/October, i.e. during the annual maximum of diversity. This was done because in many species early recruitment includes water depths and/or sediment types where they cannot not survive, for whatever reason [3, 5]. Thus, the focus of this evaluation is on habitats likely to harbour persistent populations.

The resulting data matrix includes 2591 sediment cores sampled between 2004 and 2011 (see Additional file 1). The statistical evaluation includes tests for significance and graphs. One-way ANOVAs were calculated to test for abundance variations over classes of water depth and median grains size, respectively, with H_0 assuming no effect of these factors. In addition, the explanatory power of correlations was tested by a multiple regression model with univariate tests of significance for water depth, median grain size, and water depth x grain size interactions. As this is a linear model, it gives more emphasis on linear trends while ANOVAs just tested for differences

Fig. 1 Study area; inset shows repeatedly sampled sites
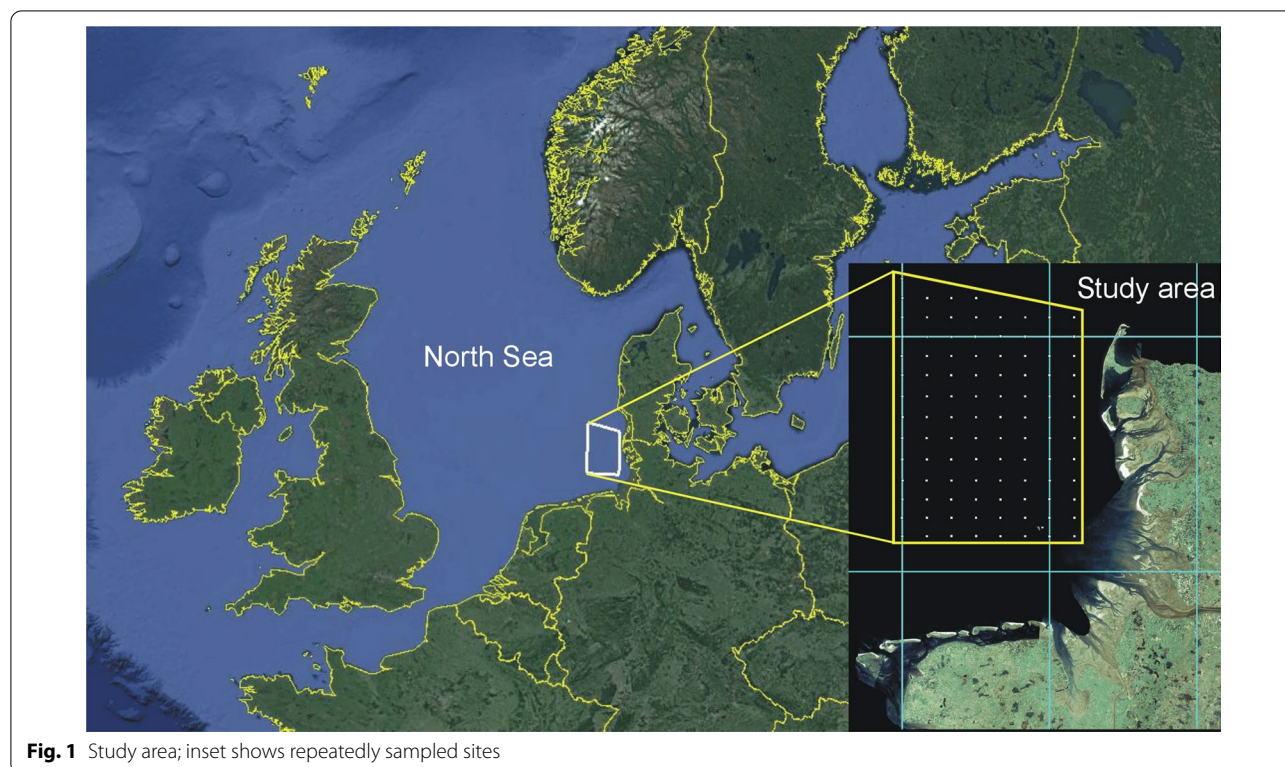
among classes. Accordingly, the results differed when abundance peaked in the middle of the studied gradients of water depth or median grain size.

While linear regression directly used the measured water depth and grains sizes, ANOVAs and the graphical presentations are based on classes of water depth (10 m intervals) and median grain size. For the latter, I used the Wentworth [6] classes mud (median < 62 μm), very fine sand (63 – 125 μm), fine sand (125 – 250 μm), medium sand (250 – 500 μm), coarse sand (500 – 1,000 μm), and very coarse sand (1,000 – 2,000 μm) which are also commonly used for field classification of sediment types. Figures showing mean abundance with 95% confidence intervals per depth class, respectively grain size class, are given for each species in the Additional file 1. In addition, distribution over habitat types is shown by contour plots (water depth × sediment class × abundance) based on water depth in finer (5 m intervals) depth classes; the resulting abundance pattern was calculated by distance-weighted least squares following the standard procedures of STATISTICA®6.1 software.

Results

ANOVAs revealed significant ($p < 0.05$) effects of water depth for 104 species (Table 1); most species increased in abundance towards deeper waters or peaked in intermediate water depths while few species showed an opposite trend (see Additional file 1). Sediment composition caused significant abundance variations in 95 out of 134 species while there was no significant effect ($p > 0.05$) in 39 species. However, species with a significant effect of sediment composition were recorded from 280 localities, on average, while those without had been found in an average of 36 localities, only. Similarly, species showing a significant depth effect had an average of 261 records versus an average of 36 records in species without a significant effect. The lack of significant effects may thus be due to a lack of data (Fig. 2).

Multiple regressions gave similar results (Table 1); in 102 species water depth or sediment type or both contributed significantly to abundance variations. In 80

species the depth × median grain size interaction term was significant, i.e. abundance distribution over sediment types varied with depth level. This is interpreted as a sign for restriction of the populations to a part of their species-specific tolerated ranges.

Explanations for the supplementary figures

Three graphs are given for each of the 134 most abundant species in the Additional file 1 material that all adhere to the following example (Fig. 3). The first two graphs show abundance (mean ± 95% confidence intervals) over classes of water depth and median grain size, respectively. The third graph estimates the realised niche in a depth class × sediment type matrix. Abundance always refers to the original sampling units of 200 cm^2 surface area, i.e. 1/50 m^2, and is a mean of the 2004 to 2011 period. Three tables give additional information. 'Data base' gives the numbers of localities, of individuals recorded, and overall presence in the data set; these data allow for an estimate of the reliability of the data with respect to the present species. 'Univariate ANOVA' gives the p-values for the one-way ANOVAs, with $p < 0.05$ (highlighted in red) indicating significant deviations from the null-hypothesis assuming to effects of water depth and median grain size, respectively. Finally, the results of multiple regression analyses are given which are more sensitive than ANOVAs for linear trends, again with factors highlighted in red if significant ($p < 0.05$). In some cases, there are further comments on the species, e.g. on restrictions caused by the sampling device. Thus, for the *Lanice conchilega* example in Fig. 3 this means we have an excellent data base and both water depth and median grain size significantly affect abundances. The figures show maximum abundances in fine sand and in the 20 – 30 m depth range.
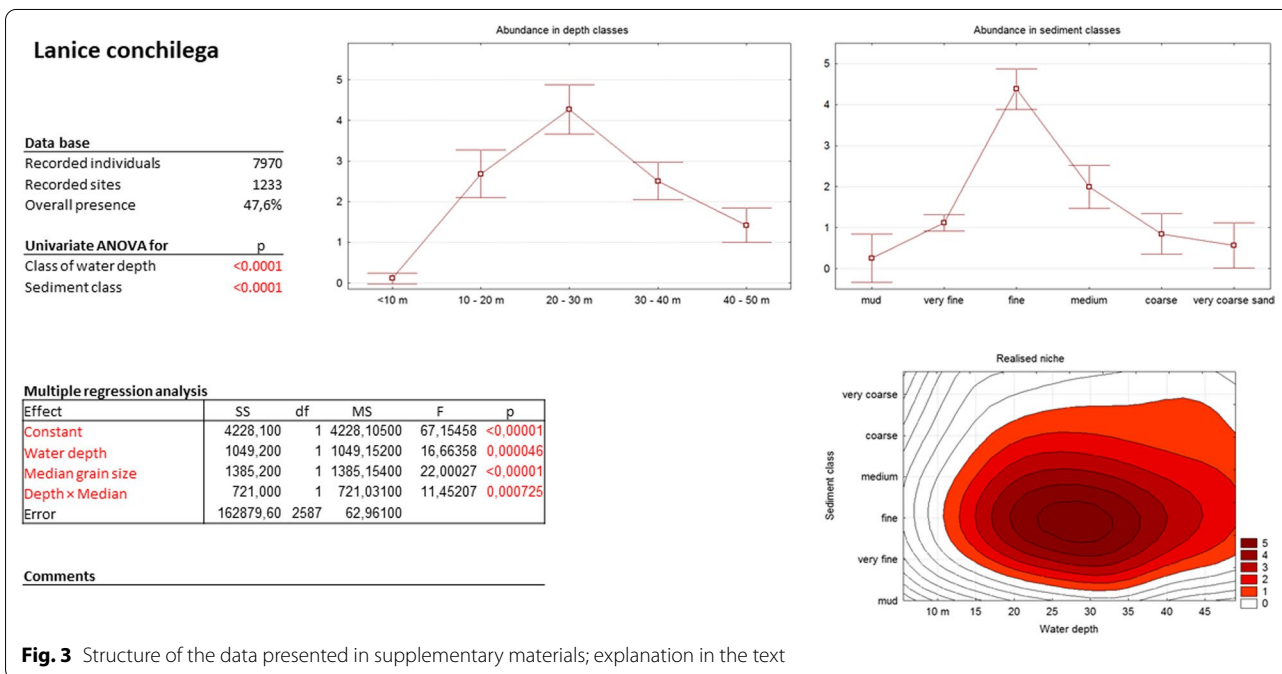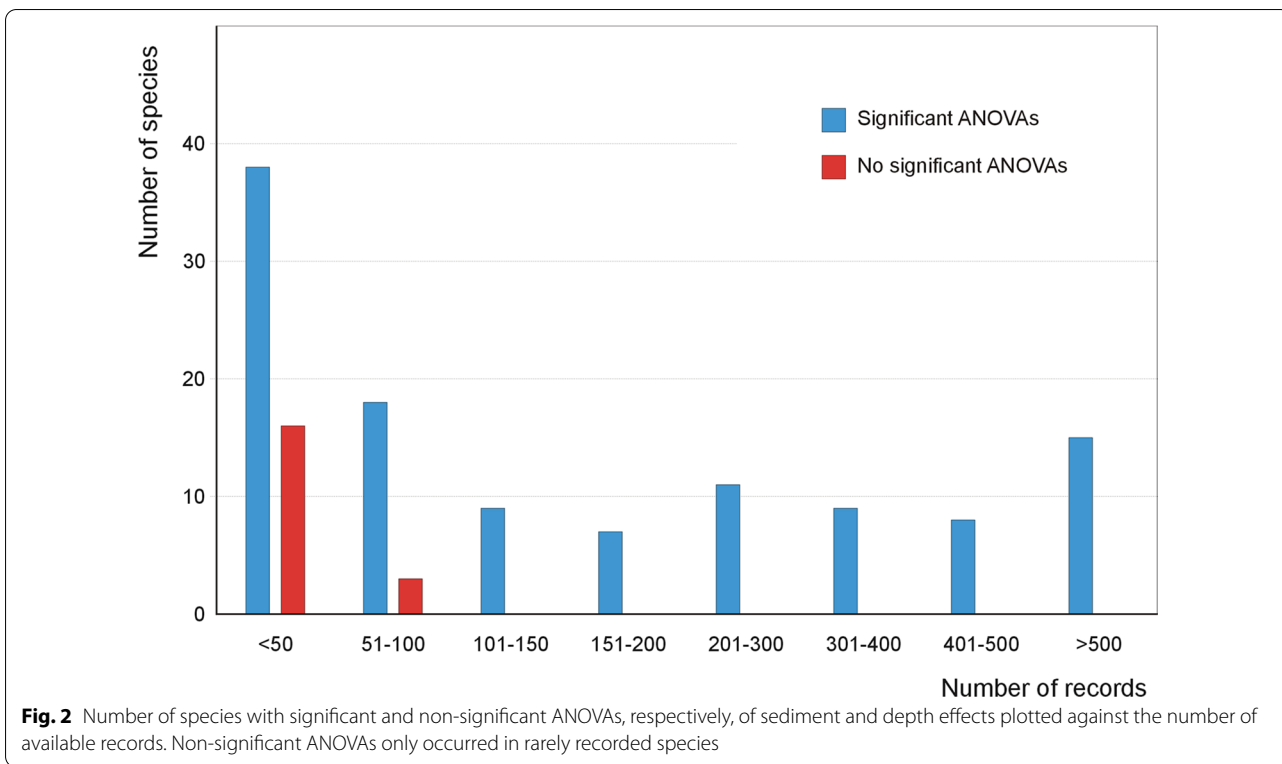
Discussion

Seasonally, the data evaluated here basically represent autumn (September and October) conditions, only a single data set derived from April. During summer,

Table 1 Effects of water depth and mean grain size ('sediment') on the distributional ranges of species

	ANOVA on		Linear regression model		
	Depth classes	Sediment classes	Water depth [m]	Median grain size [μm]	Depth × grain size interaction
Significant effect	104	95	76	73	80
Both factors significant	84		46		
No significant effect	30	39	58	61	54
No significant model	18		24		

Numbers of species showing significant effects in one-way ANOVAs and in a linear regression model with univariate test of significance, respectively

Fig. 2 Number of species with significant and non-significant ANOVAs, respectively, of sediment and depth effects plotted against the number of available records. Non-significant ANOVAs only occurred in rarely recorded species

Fig. 3 Structure of the data presented in supplementary materials; explanation in the text

abundance of recruits may strongly deviate from the patterns described here because larvae often settled in areas where they could not survive until autumn, with summer storm events as a probable cause for the decline in many species [3]. Thus, summer sampling including recent settlers may result in different patterns.

Grab type and size may also affect the distributional patterns detected: due to different sieving characteristics of large and small sediment volumes, the average abundances of species derived from the small-sized box cores used here may deviate from data obtained from larger grabs. Generally, larger cores are expected to better represent large-sized fauna while small cores may better represent the small-sized fauna because they require less vigorous sieve movements, with less risks of smashing small individuals, and sieving is faster, which means less time for the smaller individuals to escape through the meshes. This particularly applies to coarse grained sediments.

All data evaluated here come from the eastern North Sea off the North Frisian Islands from water depths between 10 and some 50 m. A majority of species correlated with water depth which may be mainly caused by local hydrography restricting many species towards the more turbulent shallows [3]. Thus, the resulting distributional patterns over depth classes are shaped by hydrography and can only be generalised to hydrographically similar parts of the North Sea. The study area is characterised by an extended slope to 50 m depth; from local bathymetry [7] I therefore assume the data derived from here may also be transferable to the adjoining Danish coastline in the north, and down to the Netherlands towards the south. Whether or not they also fit for the SE of the British coast or even the entire eastern coast of Britain with a far steeper slope remains to be tested.

Hydrography of the adjoining Wadden Sea is quite different from the North Sea because the chain of shelter Islands strongly reduces wave heights while tidal currents are reduced in the shallow parts of the Wadden Sea but may be enhanced in the tidal inlets. Together with other factors such as a higher variability of temperature and salinity, this causes major differences in the levels of water depth and sediment type exploited by a species. Hence, the range of factors that actually limit the distributional ranges of a species may be different which, in the end, is the reason for differences in faunal composition between the Wadden Sea and the adjoining North Sea. This is also seen in the *Lanice conchilega* example above. While abundance of this species sharply dropped close to zero in the shallows of the wave-exposed study area, this species may be highly abundant in the shallows of the Wadden Sea, with winter frost as a limiting factor for its onshore distribution [8]. Likewise, the results from the eastern North Sea cannot be generalised for the Baltic Sea because hydrography (in particular, tidal range) is different and because salinity is strongly decreased. The latter factor is known to cause dislocations towards deeper water in many species (brackish water submergence, [9, 10].

With respect to sediment composition, most species show clear preferences but are not confined to a single class of grain size, i.e. there seem to be no sediment-type specialists among the macrobenthic species of the study area. However, there are two restrictions to that statement. One the one hand, we do not know how the areas surrounding the species-specific high-abundance spots contribute to population recruitment; in some cases, abundance may be too low for a self-sustaining sub-population, so these areas may depend on recruits deriving from the high-abundance areas. On the other hand, this evaluation only included species that had been recorded 10 times, at least, in the current data set. However, the more a species is restricted to a single habitat type, the lower is the chance to record this species. Thus, sediment-type specialists may have passed this evaluation undetected.

Since the non-existence of an effect is impossible to proof, we do not know whether there are sediment-type generalists in a strict sense. But the data show that some species tolerate rather wide ranges of sediment types, mostly coinciding with a good swimming ability. Accordingly, crustaceans are particularly frequent among these species.

While the water depth occupied by a species in the study area is closely linked with local hydrography, the sediment types occupied may be easier generalised beyond the local level. This is expected because species-specific properties such as mode of movement, tube-building, food type and food acquisition may already restrict each species to a specific spectrum of sediment types. As an example, the polychaete *Lanice conchilega* mentioned above builds a tube from fine sand grains; accordingly, problems may arise both in pure mud and coarse sand if there are not enough sand grains of a fitting size available. However, median grain size is a rough classification of sediment type; other aspects of sediment composition such as mud content or sorting may be equally important for some species. In *Lanice conchilega*, for example, a fine sand content of a few percent may be enough to enable tube building in both mud and very coarse sand. Accordingly, poorly sorted coarse sand may be suitable while very well sorted coarse sand may not, despite of equal median diameters of the sand grains.

Generally, sediment sorting is thought to reflect sediment mobility [11] and hence hydrodynamic forcing. Thus, hydrodynamics affects the benthic fauna both

directly and indirectly by shaping the properties of the sedimentary environment, though probably at different temporal scales. For direct effects, I propose short-term extremes like storm driven sediment disturbance to exert the strongest effect while the longer-term dynamics determines sediment composition. Thus, for some species the apparent sediment 'preferences' may be merely a proxy for the longer-term hydrodynamics of their environment and the physical factors associated with hydrodynamics.

Conclusions

In the eastern North Sea, the levels of water depth occupied by macrobenthic species are strongly limited by local hydrography. Most species concentrate in species-specific sediment types, with highly motile species tending to use a broader spectrum than more sessile species. Since some aspects of sediment types also depend on local hydrography, this may be a key factor for macrobenthic species, with sediment composition a proxy for hydrodynamics.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s10152-021-00552-1.

Additional file 1: The file 'Supplementary material.xlsx' contains the sources of original data, the criteria of data selection for the current evaluation, the resulting data matrix analysed here, some basic statistics including an overview of ANOVA and regression results, the species list, and a set of tables and figures for each of the 134 most abundant species.

Declarations

Ethics approval and consent to participate
Not applicable—the study is based on published data.

Consent for publication
Not applicable.

Competing interests
The author declares that he has no competing interests.

References

1. Künitzer A, Basford D, Craeymeersch JA, Dewarumez JM, Dörjes J, Duineveld GCA, Eleftheriou A, Heip C, Herman P, Kingston P, Niermann U, Rachor E, Rumohr H, de Wilde PAJ. The benthic infauna of the North Sea: species distribution and assemblages. ICES J Mar Sci. 1992;49:127–43.
2. Salzwedel H, Rachor E, Gerdes D. Benthic macrofauna communities in the German Bight. Veröff Inst Meeresf Bremerhaven. 1985;20:199–267.
3. Armonies W, Buschbaum C, Hellwig-Armonies M. The seaward limit of wave effects on coastal macrobenthos. Helgol Mar Res. 2014;68:1–16. https://doi.org/10.1007/s10152-013-0364-1.
4. Rumohr H. Soft bottom macrofauna: collection, treatment, and quality assurance of samples. ICES Tech Mar Environ Sci. 1999;27:19.
5. Armonies W, Reise K. Empty habitat in coastal sediments for populations of macrozoobenthos. Helgol Mar Res. 2003;56:279–87. https://doi.org/10.1007/s10152-002-0129-8.
6. Wentworth CK. A scale of grade and class terms for clastic sediments. J Geol 1922;30:377–392. http://www.jstor.org/stable/30063207.
7. EMODnet Bathymetry Consortium (https://doi.org/10.12770/bb6a87dd-e579-4036-abe1-e649cea9881a). EMODnet Bathymetry Viewing and Download service, version of December 2020. https://portal.emodnet-bathymetry.eu.
8. Strasser M, Pieloth U. Recolonization pattern of the polychaete *Lanice conchilega* on an intertidal sand flat following the severe winter of 1995/96. Helgol Mar Res. 2001;55:176–81. https://doi.org/10.1007/s101520100081.
9. Remane A. Einführung in die zoologische Ökologie der Nord- und Ostsee. Tierwelt der Nord- und Ostsee I, S. 1–238. Leipzig: Akademische Verlagsgesellschaft. 1940.
10. Remmert H. Über die Besiedlung des Brackwasserbeckens der Ostsee durch Meerestiere unterschiedlicher ökologischer Herkunft. Oecologia. 1968;1:296–303. https://doi.org/10.1007/BF00386686.
11. Weston DP. Macrobenthos-sediment relationships on the continental shelf off Cape Hatteras, North Carolina. Cont Shelf Res. 1988;8:267–86. https://doi.org/10.1016/0278-4343(88)90033-7.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.