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Impact of historic sediment characterisation on predicting polychaete distributions: a case study of so-called muddy habitat shovelhead worms (Annelida: Magelonidae)

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Abstract

Shovelhead worms are common polychaetes around the British Isles and have been recorded in numerous ecological surveys. Yet, understanding of their habitat conditions is poor, based heavily on visual observations of sediments from historical records. In this study, the drivers of abundance and geographical distribution of two morphologically and behaviourally diverse species *Magelona alleni* and *Magelona minuta* are investigated by reanalysing sediment characteristics and depths from museum marine monitoring surveys. Although both species are historically associated with muddy sediments, the records herein suggest that *M. alleni* occurs in an extensive range of sediments, but is more abundant at localities with more than 25% sand. In comparison, *M. minuta* shows a negative linear relationship between grain diameter and abundance, corroborating previous work that the species is abundant in fine-grained mud. The depth records show that while *M. alleni* predominates below 60 m, *M. minuta* is a distinct offshore species. These differences may be attributed to the interspecific variation in morphology and motility between the species: *M. alleni* is stout and tube-dwelling, while *M. minuta* is fragile, small, and fairly motile. To corroborate these findings, sediment grains from tubes of *M. alleni* were classified using the Udden–Wentworth grain size scale and suggest sand is the key component for tube construction. Overall, this study highlights that sediment parameters for *M. alleni* have been misinterpreted and generalised in historical records, emphasising the importance of quantitative sediment analysis in defining the habitat of *Magelona*.

Introduction

The Magelonidae is a small family of marine annelids, consisting of 81 extant species within the genus *Magelona* F. Müller, 1858 (Mortimer and Mackie, 2006; Mortimer *et al.*, 2021a, 2021b). Magelonid worms are recorded in most of the world's regions and the Temperate Northern Atlantic is one of the most diverse in terms of the number of known magelonid species, which could be partially attributed to geographic bias of taxonomic work in the region. Magelonids are generally described to burrow in muddy and sandy substrates (Uebelacker and Jones, 1984; Parapar *et al.*, 2021) primarily in coastal regions and on continental shelves (Hernández-Alcántara and Solís-Weiss, 2009), although several deep-water species are known (Hartman, 1971; Fiege *et al.*, 2000; Aguirrezabalaga *et al.*, 2001).

Magelona species are recorded in numerous ecological studies within British and European waters, and many records of occurrence can be found in databases such as the National Biodiversity Network's (NBN Trust 2023) gateway, Global Biodiversity Information Facility (GBIF 2023), Ocean Biodiversity Information System and accessible through platforms such as the World Register of Marine Species (WoRMS) (WoRMS Editorial Board, 2023). However, the application of this information to the assessment of species-specific habitat conditions is not well understood. In the case of European species, Meißner and Darr (2009) developed habitat models of four magelonid species in the German Bight based on sediment and depth, finding large variations in the environmental predictors most important for abundance and distribution. However, the study area was relatively shallow (<45 m) and *Magelona minuta* Eliason, 1962 was not recorded. Fiege *et al.* (2000) provided locality data for many European records of *Magelona johnstoni* Fiege, Licher and Mackie, 2000 and *Magelona mirabilis* (Johnston, 1865) and subsequent information has been provided for other European magelonids (Mortimer *et al.*, 2011, 2020, 2022; Mills and Mortimer, 2018), but descriptions of environmental parameters are still generalised across the family in most cases.

At present, five *Magleona* species are known to occur in British waters: *M. johnstoni*, *M. mirabilis* (Johnston, 1865), *Magelona filiformis* Wilson, 1959, *Magelona alleni* Wilson, 1958 and *M. minuta*. Mackie *et al.* (2006) and Mortimer and Mackie (2014) reported the former four species to occur both littorally and sublittorally, whilst *M. minuta* has been considered a distinct offshore species (Mortimer and Mackie, 2014; Mills and Mortimer, 2018; Mortimer, 2019). Of the British magelonids, *M. minuta* and *M. alleni* are the most morphologically (Mortimer *et al.*, 2020; Parapar *et al.*, 2021) and behaviourally diverse (Mills and

Mortimer, 2018). *Magelona alleni* is a large, stout species known to construct permanent burrows (Mills and Mortimer, 2019; Mortimer *et al*., 2022), while *M. minuta* is small, fragile (Mills and Mortimer, 2018) and regarded as mobile. Mortimer and Mills (2020) highlighted *M. minuta* to occur in at least 73 works of taxonomic and biotic survey literature by over 60 different authors and numerous ecological reports. They emphasised the species to be dominant in several biological assemblages, the latter being also true for *M. alleni* (e.g., Mackie *et al*., 1995). Despite the regularity with which these two species are recorded, information defining the characteristics of their predominant habitat is still lacking, especially regarding sediment characterisation. This information is critical in predicting occurrence and abundance in future monitoring studies.

Both *M. alleni* and *M. minuta* are historically associated with muddy sediments (Wilson, 1958, 1982; McIntyre, 1960; Eliason, 1962; Kirkegaard, 1969; Hartmann-Schröder, 1996; Böggemann, 1997; Mortimer and Mackie, 2014). Even with the magnitude of records available for these species, habitat descriptions are often based largely on information from the original descriptions, despite several uncertainties. For example, information on the type locality for *M. alleni* was not clearly defined by Wilson (1958), the sediment type was based upon visual judgement alone, being noted as abundant in black sandy mud off Rame Head, which Mortimer *et al*. (2021b) concluded to be approximately 60 m deep. The type locality of *M. minuta* was simply described as shelly mud with a small amount of sand (Eliason, 1962). Comparative material from a re-description of *M. minuta* by Mills and Mortimer (2018) suggested the species to also occur in sandy mud, muddy sand, sand, and sandy gravel. However, in the absence of detailed assessment of species-habitat records, this remains unconfirmed.

The current study aims to investigate records of *M. alleni* and *M. minuta* from waters around the British Isles to increase understanding of abundance and geographical distribution patterns. The previous assumption that both species are predominately from muddy sediments is tested by analysing depth and sediment parameters (mud, sand and gravel content, and mean grain diameter) with abundance information. Furthermore, grains from the tubes of *M. alleni* are measured to classify the characteristics of the sediments utilised for tube construction. The use of historical visual assessments against quantitative sediment characterisation for the understanding of polychaete species habitat conditions is discussed. It should be noted that *M. minuta* is an unavailable name because it is an unreplaced junior primary homonym to *Magelona filiformis minuta* Wilson, 1959 (Read and Fauchald, 2023). As a replacement name is required, Mortimer and Mills (2020) applied to the ICZN for the suppression of *Magelona filiformis minuta* in favour of the junior homonym *Magelona minuta*. As the case (3804) is currently open, and no decision has been made, the name *M. minuta* is used herein.

Materials and methods

Samples and data

Reanalysed sediment and depth records of *M. minuta* and *M. alleni* (Figure 1) held at Amgueddfa Cymru – Museum Wales (NMW) (i.e. verified records where species identification has been checked, available at the Mendeley data repository: doi:10.17632/wzt3bsgmky.1) and additional records from other online sources (unverified records from data held within NBN and GBIF databases, accessed online 18 July 2023) were utilised to better understand distribution and abundance patterns around and beyond the British Coast. Verified records were extracted from the BIOMÔR 1 (Mackie *et al*., 1995, 73 stations sampled throughout the southern Irish Sea), BIOMÔR 4 (Mackie *et al*., 2006, 148 stations located at regular intervals throughout the Outer Bristol Channel, including additional locations of geological interest and a number of coincident stations selected to investigate temporal change) and BIOMÔR 5 (Robinson *et al*., 2009, 97 stations in the southern Irish sea, including a few repeat stations from BIOMÔR 1) (Figure 2). Of the stations sampled, magelonids were recorded as present at 44, 30, and 28 stations within the BIOMÔR 1, BIOMÔR 4 and BIOMÔR 5 surveys, respectively. Unverified records extracted from the NBN and GBIF databases covered the entirety of the British coastline (Figure 2).

Data analysis

All surveys with verified records (i.e. BIOMÔR surveys) utilised the same sampling procedure, allowing direct comparison of species abundance at each station. Seabed samples were collected with a 0.1 m^2 modified Van Veen grab and sieved with a 0.5 mm mesh sieve (see Mackie *et al*., 1995; Mackie *et al*., 2006; Robinson *et al*., 2009 for full methodology). Replicate samples were taken at each site; two for the macrofauna and one for sediment analysis. Quantitative parameters on sediment (mud, sand and gravel contents, and mean grain diameter) and depth were extracted from verified records. Sediment data were originally classified using either Buchanan's trigon (1971, 1984) (Mackie *et al*., 1995) or an extension to the Folk's (1954) classification system within the surveys, allowing the subdivision of gravels (Mackie *et al*., 2006; Robinson *et al*., 2009). In the current study, sediment size was reclassified following the Udden–Wentworth grain size scale (Wentworth, 1922) (Table S1). Afterwards, the Krumbein phi (φ) scale, which is defined as a logarithmic phi scale of the Udden–Wentworth scale proposed by Krumbein (1934), was calculated to place emphasis on finer grain sizes (Donoghue, 2016) (Table S1). The Krumbein phi (φ) scale is calculated as the negative logarithm to the base 2 of the particle diameter (in millimetres) and is obtained as follows:

$$D = 2^{-\Phi}$$

where φ is the phi size and D is the grain diameter in millimetres (mm).

All data analysis was carried out in RStudio Version 4.0.3 (R Core Team, 2020). The R code is available from the Mendeley Data Repository at doi:10.17632/wzt3bsgmky.1. Percentage of mud, sand and gravel, together with depth and mean grain diameter for stations where at least one of the two species occurred (Mackie *et al*., 1995, 2006; Robinson *et al*., 2009 for *M. alleni*; Mackie *et al*., 1995; Robinson *et al*., 2009 for *M. minuta*) were investigated using linear regression analyses to understand the relationship between sediment parameters and abundance. This was coupled with principal component analysis (PCA) to allow the number of environmental variables under investigation to be reduced and further explore species–habitat relationships.

Image stacking

To classify the key characteristics of the sediments utilised for tube construction by *M. alleni*, tube samples were initially mounted on a glass slide. Images were subsequently taken using a Canon EOS 6D 20.2 MP DSLR camera attached to a Nikon Optiphot 2 Trinocular Microscope. Afterwards, the resulting images were stacked using HeliconFocus v6.22 (HeliconSoft Ltd) software. The maximum diameter for grains unobstructed (i.e., grain boundaries that were clearly observed) were measured

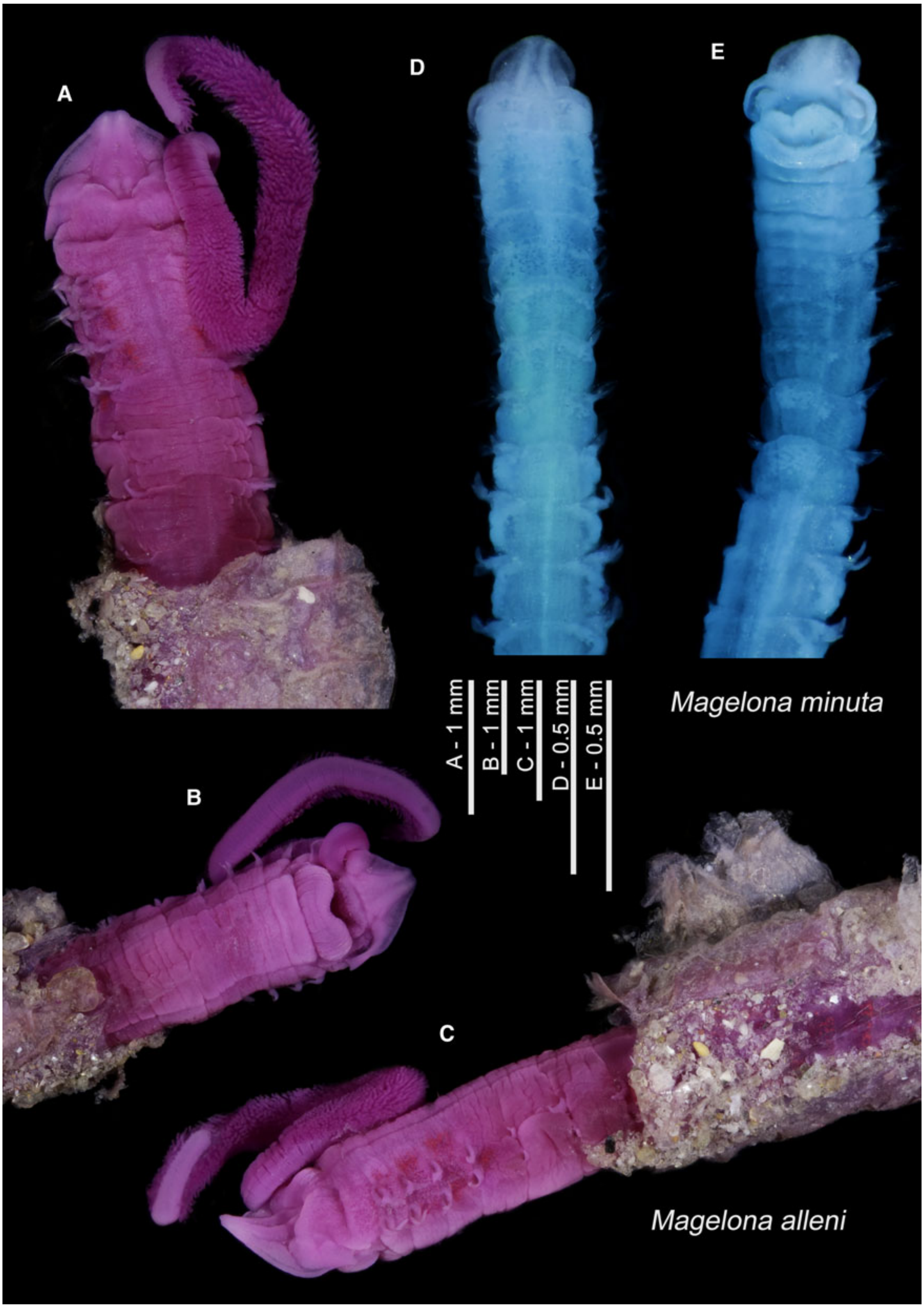

Figure 1. Anterior regions of the shovel head worms *Magelona alleni* (NMW.Z. 1991.075.1574, stained with Rose Bengal) and *Magelona minuta* (NMW.Z.1991.075.1584, stained with Methyl Green); (A) dorsal view of prostomium and chaetigers 1–7 (Left hand palp missing, tube apparent), (B) same, ventral view, (C) same, lateral view, (D) dorsal view of prostomium and chaetigers 1–12 (palps lost), (E) ventral view of prostomium (burrowing organ slightly everted) and chaetiger 1–11 (palp stubs visible).

under a petrographic microscope and reported as the Udden–Wentworth grain size scale. A similar methodology using the same equipment was also employed to take images of the anterior abdominal segments of both *M. alleni* and *M. minuta* for comparison of morphology.

Results

Distributions

This study looked at the distribution of two morphologically (Figure 1) and behaviourally diverse species of magelonid – *M.*

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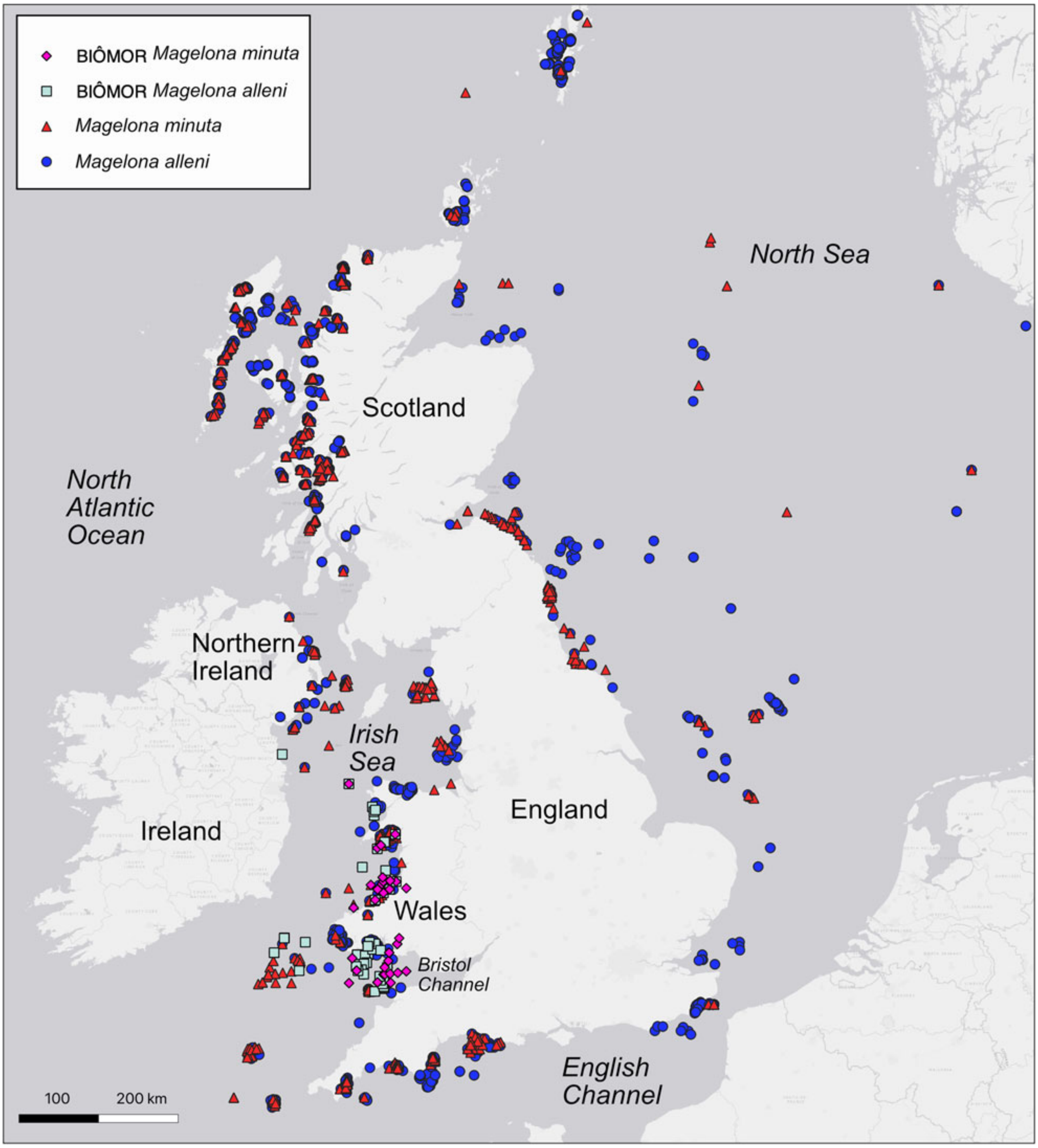

Figure 2. Map of occurrences of *Magelona minuta* and *Magelona alleni* from verified records held at Amgueddfa Cymru – Museum Wales (ACNMW) and unverified records from additional sources (NBN, GBIF).

alleni and *M. minuta*. The combined distribution maps of the records (verified and unverified) of both species show a broadly continuous distribution around the British Coast (Figure 2). Yet, there is a distinct lack of records in the English Channel (approximately Weymouth to Brighten for the former species, and a larger gap from Whitby, Yorkshire in the North Sea to Weymouth for the latter).

Quantitative data

Verified survey data from BIOMÔR records for *M. alleni* showed it to be present in sediments classified as mud to sandy gravel. These sediments ranged from a mud content of between 0.00 and 53.93% (Figure 3a), sand 0.00–98.87% (Figure 3b) and gravel 0.00–96.03% (Figure 3c). Mean grain diameter was between 0.12 and 0.48 mm (Figure 3d), corresponding to fine to coarse sand (Udden–Wentworth scale, 1–3 φ Krumbein phi scale). Occurrences (16) were more frequent in sediments with higher sand contents (80.66–99.56%), less mud (0.00–10.58%) and shallow depths (11–58 m), although abundance at each locality was not strongly influenced by any of the investigated parameters (Figure 3). Total depth range was 11–113 m, but occurrences were higher between 0 and 60 m and the highest abundances (up to 38 individuals per 0.1 m^2) occurred between 11 and 32 m.

Verified survey data for *M. minuta* revealed the species occurs in mud to sandy gravel. Mud content was between 0.23 and

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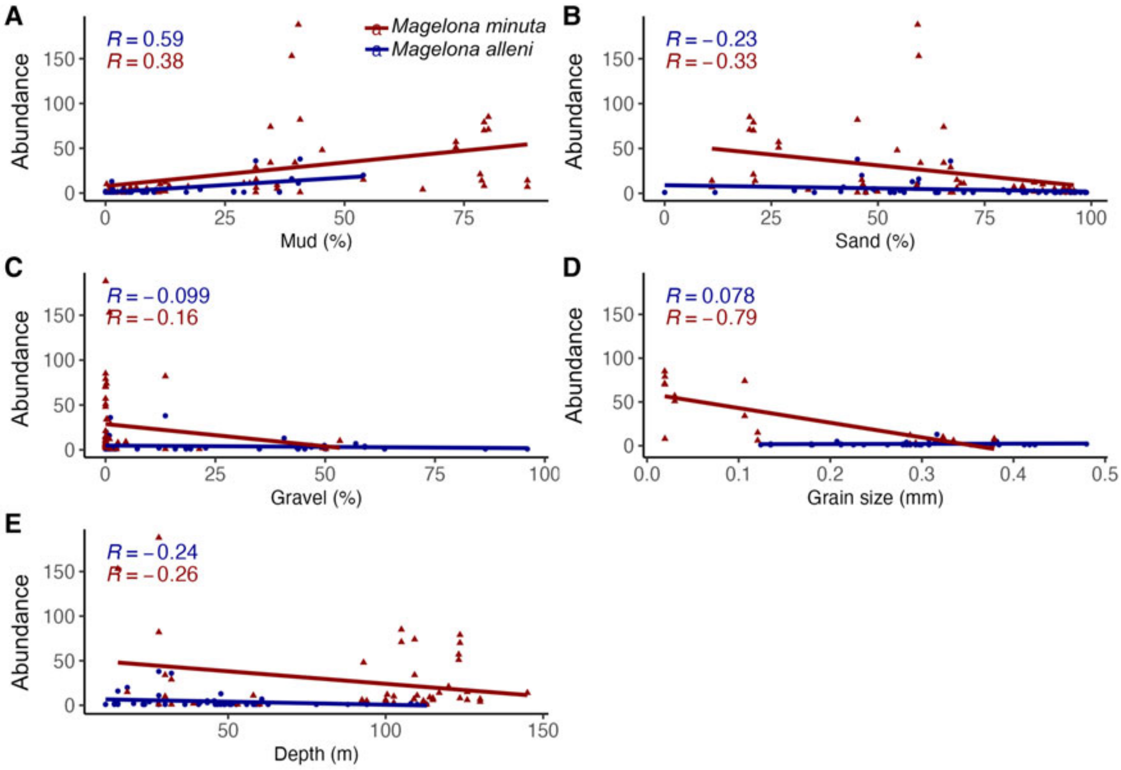

Figure 3. Linear regression analyses and correlation coefficient (R values) abundance per 0.1 m^2 of *Magelona alleni* and *Magelona minuta* at each station vs (A) mud (%), (B) sand (%), (C) gravel (%), (D) mean grain diameter (grain size) (mm), (E) Depth (m).

88.26% (Figure 3a) and sand 11.07–95.90% (Figure 3b). The percentage of gravel was lower than that observed for *M. alleni*, ranging between 0.00 and 53.34% (Figure 3c). The highest abundances (over 100 individuals per 0.1 m^2) for the species occurred in sediments with very little to no gravel (0.00–0.87%) and at least 59.30% sand. Depths ranged between 15 and 145 m, but occurrences were recorded more frequently from deeper waters (>100 m). Mean grain diameter ranged between 0.02 and 0.38 mm (Figure 3d), corresponding to medium silt to coarse sand on the Udden–Wentworth scale (1–6 φ Krumbein phi scale). Grain size strongly influenced abundance ($R = -0.79$) and more individuals were found in sediments with small mean grain diameters (mud to sandy mud). Overall, there were higher abundances recorded at stations of *M. minuta* than *M. alleni*.

PCA was used to explore relationships between investigated environmental variables for both species. PCA defined two principal components covering 83.3% of the cumulative variance (Figure 4). PC1 accounted for 46.3% of the variance, with the highest negative association of gravel and highest positive association of mud. PC2 accounted for 37.0% of the variance, with highest positive association of sand and highest negative association of gravel. Most data points that represented records of *M. minuta* were situated in the top right quadrant with loadings from mud and depth, while most data points for *M. alleni* were within the left quadrants, with loadings from sand and gravel.

Sediment characteristics of Magelona alleni *tubes*

The diameter measurements for the majority of sediment grains used to construct the tubes of *M. alleni* (Figure 5) correspond to fine sand on the Udden–Wentworth scale (3 φ Krumbein phi scale). Measurements ranged between 0.06 and 0.43 mm (2–5 φ Krumbein phi scale) (coarse silt-to-medium sand) (Table S2). Overall, the mean diameter was 0.22 mm and the median diameter 0.20 mm (fine sand).

Discussion

This study has shown that *M. alleni* occurs in an extensive range of sediments ranging from mud to sandy gravel. Despite previous reports that it is mostly a muddy sediment species (Wilson, 1958, 1982; McIntyre, 1960; Hartmann-Schröder, 1996; Mortimer and Mackie, 2014), it is recorded herein more frequently at localities with a high percentage of sand. Although *M. minuta* was also found to occur in mud to sandy gravel, a strong negative linear relationship between mean grain diameter and abundance corroborates previous descriptions of the species inhabiting finer sediments with small grain sizes (Eliason, 1962; Mortimer and Mackie, 2014). Noteworthy, the observation of *M. minuta* in coarser sediments occurred at only three stations within the current dataset, suggesting that this is infrequent. It has been previously noted that gravelly sediments in the Southern Irish Sea can comprise of a cobble and shell pavement with mud and sand embedded between the stones which is sufficient for burrowing benthic organisms to live in (Rees, 1993; Mackie *et al*., 2006). This may explain the infrequent records of *M. minuta* in coarser sediments as visual assessments from the three stations (Mackie *et al*., 2006:12) indicates the presence of some mud within the samples.

An ecological modelling study that investigated the distribution of magelonids in the German Bight (Meißner and Darr, 2009) has previously shown that the most suitable habitats for *M. alleni* are sands with elevated mud contents at depths between 30 and 40 m. The records herein show that although *M. alleni* is found within mud, most occurrences are documented to be under 10% mud and it is not an important predictor of distribution and abundance compared to the records from the German Bight.

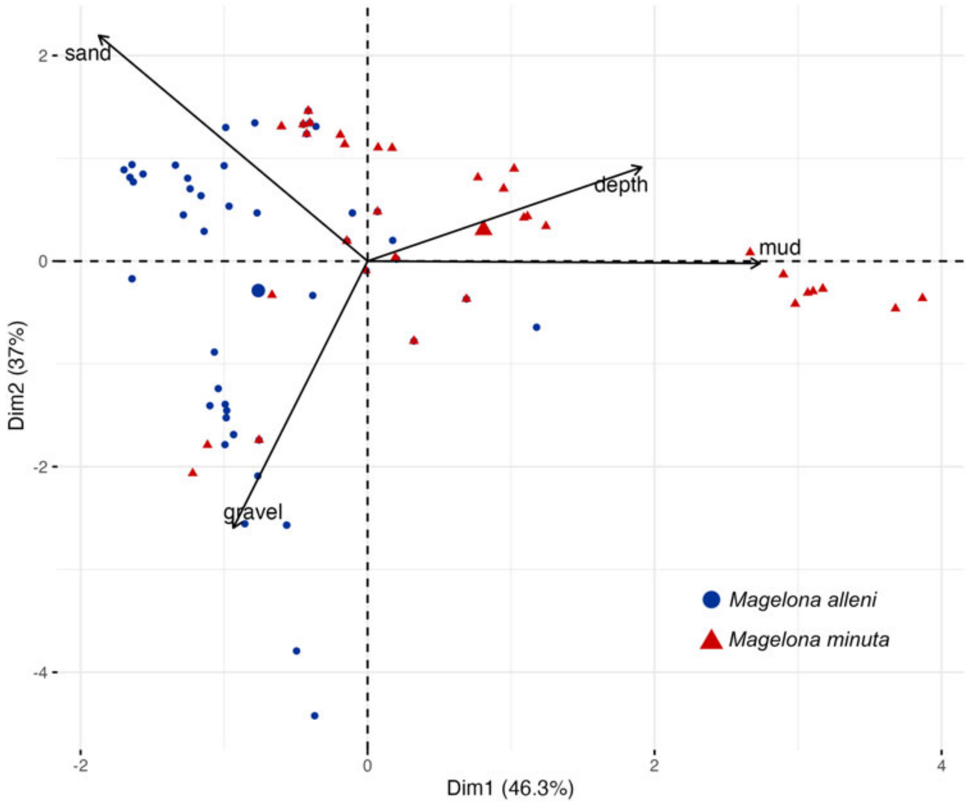

Figure 4. Principal component analysis of environmental variables for occurrences of *Magelona alleni* and *Magelona minuta*: mud (%),sand (%)gravel (%),depth (m). Black arrows show the loading of each variable and points show PCA scores. Point sizes represent quality of representation. Superimposed 95% confidence ellipsoids contain group points.

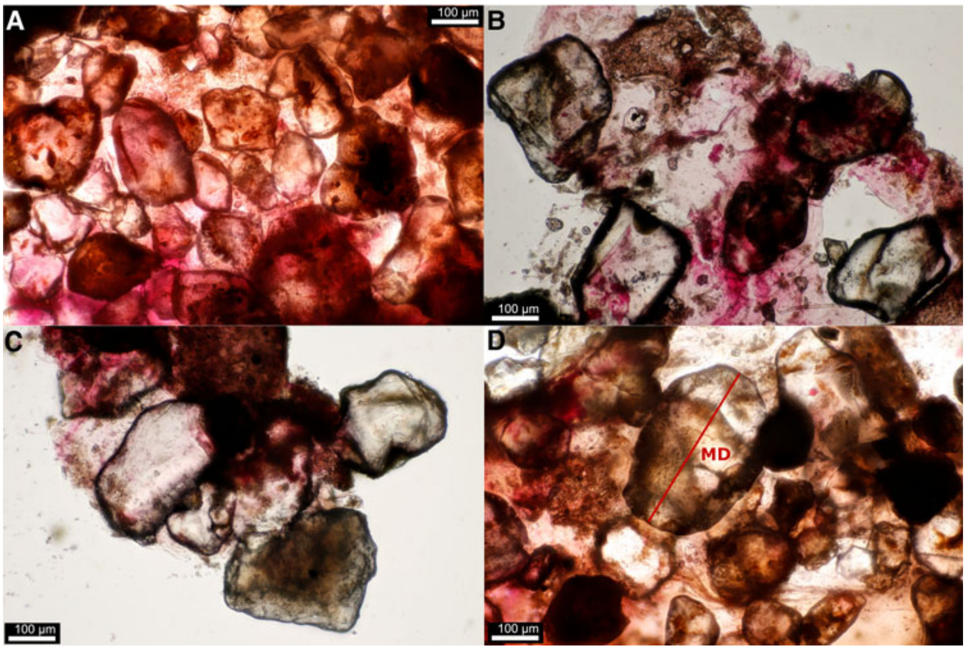

Figure 5. *Magelona alleni* tubes with sediment covering. The maximum diameter of unobstructed grains was measured where grain edges can be clearly seen.

Despite the differences in the range of depth data between the German Bight and the current study, with depths reaching 45 m in Meißner and Darr (2009), compared to over 100 m here, the results are generally similar and show *M. alleni* is abundant around 30 m, but occurrences are more frequent at approximately 50 m.

In comparison to *M. alleni*, the current results found that *M. minuta* is an offshore species, recorded more frequently over 100 m. Although the species has been reported at deeper depths up to 1000 m off the Gulf of Taranto (Fiege *et al.*, 2000) and *M.* cf. *minuta* at over 4000 m from Greenland (discussed in Mills and Mortimer, 2018), verification of these records is needed, due to their distance from the type locality. It is likely that several undescribed species are present which may account for these records.

Although the records herein indicate both species share some overlap in sediment and depth parameters, the highest species abundances generally occur at localities where they are not in sympatry. Noteworthy, stations where both species co-occur may relate to elevated sand contents for *M. alleni*, but grain sizes that are sufficiently small for *M. minuta*. This may explain the observed gaps in distribution around the British Coast. For example, seabed sediments within the English Channel, where an obvious absence of records exists, show gravels with smaller patches of sandy gravel (British Geological Survey, 1987). This may hint that gravel contents within the region are restrictive for both species. Whilst an absence of records could also be related to several other factors such as a lack of sampling, other magelonid species such as *M. mirabilis* have been recorded within these areas (e.g., NBN atlas). However, the caveat that sediment type and depth alone cannot explain the extent of a macrofaunal community assemblage is acknowledged and additional physical, chemical and biological parameters must be accounted for (e.g., McBreen *et al.*, 2008). Characterising complete habitat type is beyond the scope of this study, whose key objective is to highlight if widely used historical occurrence records from original species descriptions of *Magelona* are reliable predicators of distribution.

It is proposed that the variation in sediment and abundance between species records may be linked to interspecific variation in behaviour and morphology. *Magelona alleni* is the only known species in British waters that constructs permanent burrows lined with layered tubes (Mills and Mortimer, 2019). On analysis of the grain size of sediments attached to tubes of *M. alleni,* fine sand was identified as the most common. Even with the caveat that some grains may have been dislodged from the tube during collection, handling and preservation, it is likely that sand grains are required for tube construction. Although other tube-dwelling magelonids are known (Mortimer *et al.*, 2012; Mortimer, 2019, Mortimer *et al.*, 2022), most species are relatively active, likely burrowing continually through sediments (Jones, 1968; Fauchald and Jumars, 1979; Mortimer and Mackie, 2014; Jumars *et al.*, 2015). For example, *M. minuta* is a non-tubicolous, fairly motile species. The elevated mud contents and smaller grains associated with this species may relate to the small size and notable fragility of the species, compared to *M. alleni*, a robust and stout species (Parapar *et al.*, 2021; Mortimer *et al.*, 2022). McIntosh (1911) described a partiality to fine sand for *Magelona*, noting 'larger sharp fragments of coarse gravel and sand might injure either snout or proboscis' (N.B. referring to the prostomium and burrowing organ), which is likely for *M. minuta*. Investigation of more tube-dwelling magelonid species would be useful to further explore the relationship between life history and sediment requirements.

The current study has demonstrated that sediment type of benthic infaunal polychaetes is easily misinterpreted, especially in concern to historic works that relied upon visual estimation of sediment grain size. These mistakes are often perpetuated in taxonomic and ecological works, compounding the issue, particularly when that data comes from erroneously identified species. This gives a false interpretation for those using that data for species identification. The example herein that *M. minuta* has been recorded from sediments ranging from mud to sandy gravel doesn't reflect the full picture that coarser sediments are at the edge of the species' sediment range. Overall, these findings will add further clarity to habitat and distribution patterns for *Magelona* species, and additionally highlight the implications of interspecific variation for species within the family. The assumption that magelonids are active burrowers is based upon a small number of species. However, it has become increasingly obvious that this is incorrect for some species. Future work should aim to build upon historical data by using quantitative records of sediment and depth for further *Magelona* species and analysing additional environmental variables that are known to be important predictors of abundance and distribution.

Conclusions

- *Magelona alleni* occurs in a range of sediments but needs sand for tube building.
- Grain size strongly influenced the abundance of *M. minuta* and this may be linked to its small body size.
- Sand is the most important variable for *M. alleni*, whilst mud and depth are the most important for *M. minuta.*
- Historic visual assessments have led to misinterpretations of habitat preferences for *M. alleni*. However, an integrated approach is useful as visual assessments can provide additional data on the heterogeneity of sediments.
- These two species overlap in terms of depth records, but *M. alleni* is more abundant at less than 60 m, compared to *M. minuta* present more frequently at over 100 m depths.
- Whilst there is much data openly available concerning records of occurrence for magelonid species, it is important to amalgamate findings so that we can understand more about species-specific environmental parameters.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315423000814.

Data availability. The data that support the findings of this study are openly available in the Mendeley data repository at https://doi.org/10.17632/wzt3bsgmky.1.

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Author's contributions. KM1 and KM2 equally contributed to creation and design of the study. KM1 contributed to data analyses. KM2 contributed to access and analysis of *Magelona* spp. records and specimens. Both authors contributed to drafting, commenting, and reading the manuscript.

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Competing interests. None.

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