Responses to the reviewers

We are grateful to the reviewers for their time and feedback regarding this long-lasting and heavy work, that, we hope, will greatly benefit the scientific community. We completed the manuscript according to the reviewers' comments as much as possible. Besides, we also provided a few modifications in the R package (fuzR), a few things in help menu, improved the fuz.plot() function, and corrected a typo in the database (+ feeding type modalities according to Reviewer 2).

Reviewer 1

A macrobenthic traits database is long over due, so credit to the authors for delivering on this.
The manuscript is very comprehensive in terms of both philosophical considerations and analyses of the data in the data base. This could be reduced. I am surprised that Bremner's work from the 2000s, the first application of the traits and fuzzy coding approach developed by Chevenet et al is not cited at all. The authors also do not provide a discussion on the need to select traits to avoid issues weighting out comes given that some traits will be biologically linked. There are also challenges around biogeographical extent - modalities developed in temperate areas may not be useful in the topics for example. Again a cautionary note/discussion would be useful.

Dear reviewer,

Many thanks for your time and feedback. Some of the comments certainly deserve some discussion useful to a wide audience.

The manuscript reaches a certain length due to the detailed terminology. Since this is mainly a data paper, a simple summary table of traits and modalities as usually encountered would have been too much superficial. There are often several ways to structure a trait by considering different sets of modalities when comparing papers. In each description that we provided, we wanted to show why the trait was built in the way it was in order to comply either with biological reality or practical considerations. Also, as there is still no such a detailed terminology in the literature, we strove to reference our documentation as best as possible based on the rich old literature of natural history. This leaves a traceability when justifying our developments (as it should be), and, possibly, inspiration for other purposes while keeping alive a valuable literature of several decades.

Bremner's works. There are at least two highly cited publications of Bremner and collaborators in the beginning of the 2000s (Bremner et al., 2003, 2006). They were not cited due to either lack of explicit reference to life-history strategy (as evolutionary convergences of adaptations) or effect trait concept as paradigmatically different. That does not detract in any way from the quality of those works; many other papers, with similar objectives, could have also been cited. There are now many reviews providing discussion and classification of all those works. However, we acknowledge that citing Bemner et al. (2003) better clarifies the historical context of the use of traits in benthic community ecology. Line 96-100, we reformulated:

"Multivariate exploration of the relationships between life-history strategies and environmental forces has been mostly investigated in freshwater and terrestrial ecology. Since Bremner et al. (2003) that marked the advent of biological trait analysis in marine benthic ecology, only a handful of studies specifically addressed the evolutionary concepts of selection and life strategy (Sutton et al., 2021; Beauchard et al., 2022; Gusha and McQuaid, 2025; Mendes et al., 2025; Bergagna et al., 2026)."

As raised and developed in the paper, functional community ecology of the marine benthos has missed an internationally coordinated agenda in which such evolutionary aspects would have represented a prominent component.

Methodological aspects. Again, this is more a data paper than a review on analytical methods. However, we consider that it is difficult to talk about the data as particular as fuzzy data without referring to methods. Separately, we tried to consider as much and as relevant as possible analytical aspects in the supplement and the appendix where the data can be handled and processed through typical multivariate ordinations. Historically, a key event was the publication of Chevenet et al. (1994) in a special issue of Freshwater Biology as mentioned in Appendix. The authors proposed a data coding method, and accordingly, Fuzzy Correspondence Analysis (FCA) as a specific modification of Multiple Correspondence Analysis (MCA; Tenenhaus and Young, 1985) for multivariate purposes. From there, if the objective remains limited to a simple examination of trait covariances along the different axes (after a careful check of the eigenvalue diagram), there is no particular trait selection required. A priori, by assuming that the set of traits is homogeneously representative of fitness or ecosystem function, species axis scores can be clustered to derive a typology of functional groups; this type of analysis, purely exploratory and deprived of trait selection, is typically called "unconstrained analysis". Our detailed terminology was also intended in this respect, accompanied with an assessment

of affinity for response or effect. In the case of environment-trait correlative analysis, “constrained analyses” take place. Nowadays, after a long series of papers, the RLQ/Fourth-corner combination has represented the most robust and unbiased way to proceed (Dolédec et al., 1996; Legendre et al., 1997; Dray and Legendre, 2008; ter Braak et al., 2012; Dray et al., 2014; Peres-Neto et al., 2027). Additional papers can be found regarding the univariate context, especially niche modelling. Note that a derived version, the double constrained Correspondence Analysis, can compete with RLQ (dc-CA; ter Braak et al., 2018). The origin of RLQ can be found in Co-Inertia Analysis (2 matrices; Dolédec and Chessel, 1994), later extended to 3 matrices (Dolédec et al., 1996). Dray et al. (2003) provided a review on the concept of co-inertia; compared to RDA, co-inertia can tolerate more collinear predictors while RDA remains unstable in such a case. However, when correlating environmental variables with a set of traits, both R and Q ordinations should exhibit similar gradients in order to ensure a significant pattern. A given set of traits exhibit a certain multidimensionality, and adding or removing a trait, depending of its correlations with the other traits, can substantially alter the multidimensionality of table Q. Therefore, trait selection should take place regarding table Q as well as table R To our knowledge, there is still no standard procedure through RLQ.

In summary, under constrained analysis through co-inertia (RLQ), there is no limit to the numbers of environmental or trait variables. In practice, and theoretically, selection (e.g., environmental filtering) should limit specific sets of correlated R and Q variables. We think that analyses should be processed with careful ordinations and different combinations of R and Q variables should be separately tested before considering results as definitive. In our North Sea case study (supplement), we do not use all the traits. Also, we simplified some of them for which the initial format lead to non-significant outcomes (while showing the usefulness of our R functions). So, we added some text in the supplement to explain the subtleties inherent to RLQ. Page 25, after the first paragraph of section S5:

“In a more analytical context, this case study illustrates the complexity of applications combining the Fourthcorner and RLQ analyses (Dray et al., 2014). In its traditional use, RLQ relates environmental variables (table R) with biological traits (table Q) through species distributions (table L). Importantly, a significant R-Q pattern implies that R variables form gradients that match species distribution gradients, themselves corresponding to trait modality distributions along matching species gradients (Dolédec et al. 1996). In this application example, not all combinations of R and Q variables may lead to a significant RLQ pattern. Therefore, the user is encouraged to run the procedure with different combinations of R and Q variables to apprehend the need for deep data exploration before considering definitive RLQ outcomes. Besides, double constrained Correspondence Analysis, more recently developed (dc-CA; ter Braak et al. 2018, ter Braak and van Rossum 2025), may offer a better technical alternative if the dataset meets certain conditions. In cases of more sampling stations than environmental variables or more species than trait modalities, the modelling nature of dc-CA enables R and Q variable selection according to standard procedures in regression analysis (ter Braak and van Rossum 2025). However, the use of fuzzy traits implies a high number of Q variables as correlated predictors of table L in dc-CA, in which case RLQ may better perform (Dray et al. 2003, ter Braak et al. 2018).”

There are also challenges around biogeographical extent - modalities developed in temperate areas may not be useful in the topics for example.

What do you mean exactly? While Spalding et al. (2007) provided biogeographic ecoregions within biogeographic provinces, we limited species inventory at the province level due to insufficient information at the ecoregion level. However, as mentioned in the text, we compiled this information as broad thermal niche from tropical to polar realms remains of potential interest.

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Reviewer 2

I commend the authors on such a detailed compilation of trait data for a global set of benthic species. The authors have provided detailed descriptions for each trait and modality, building on the work of others, which is extremely helpful to end users. All traits are also accompanied by the source reference to enable end users to easily revisit the originating information. I have not repeated the previous reviewers comment except for the length of the manuscript which could be reduced in certain sections (see comment below). I have several other comments which are presented below:

How are ‘unknown’ traits dealt with in the DB and are these clearly distinguishable from ‘no affinity’. Has it been clearly signposted where traits are fully backed up by the literature and where they have been assigned based on congeneric information or expert knowledge. The fact that each trait has a reference which helps, but it would enable the end users to have confidence in the data if this was clear e.g. Clare et al used a scoring system from 0-3 to indicate confidence in assessments.

Following on from this, It would be good to have an understanding of how many species have full trait records (from original sources) of the 41 traits included in the DB – as per Tyler et al 2014 Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology.

Dear reviewer,

Many thanks for your time and feedback. Your comments relevantly raised some points that deserve some explanations and justifications. Indeed, the manuscript need some additional text to clarify the content of the database.

We should mention in section 4, third paragraph, that there is currently no missing data in the database. As indicated in that section, when facing missing information, it was completed mostly at the genus level. Sometimes, we referred to higher taxonomic level in books of general biology regarding qualitative and phylogenetically conserved traits (e.g., offspring type or development). Importantly, the compilation was intended to provide a global database as complete and exhaustive as possible. Unfortunately, the use of related taxa to complete information not available at the species level has not been noted. The coding of Clare et al. (2022), attributing higher score for species-level information, remains only informative. In analytical context, it is ambiguous since a low score can be by chance as good as bad (e.g., “bad” when score attributed from genus or higher level in case of characters highly conserved within the clade). Besides, as

we show in Appendix A, this 0-3 scoring does not significantly differ from a random scoring when investigating species-trait patterns.

The MacroTraits compilation started based on a species pool documented as part of some North Sea projects (Dutch waters), and was progressively extended to other parts of the world (from 2013 onward). The search for information was carried out phylum by phylum, class by class, or order by order. Within each of those higher levels, the search was carried out species by species, especially when the documentation of a species was also mentioning information on sister species or genus; hence, more than an entire year could be needed for completing a single phylum. Within-higher level search was often finalised with review papers or books documenting either part or complete biology of groups of species. When no species with substantial amount of information could not be found in the literature, the search was continued within another phylum.

Google scholar was often the starting point for documenting a species (for which the existence of a minimum amount of information was known). In general, life-history traits represent the bottleneck for a complete documentation given the huge work they require to be identified/quantified (e.g., fecundity, offspring size, development duration). However, when such information was available, all the other traits could also be documented, except sometimes life span and maturity. These traits can be studied either in case of commercial fisheries (in many edible crustaceans and clams) or due to remarkable growth pattern. In this respect, there are still many boreal/Arctic species such as in bivalves or echinoderms for which the information is limited to growth given their peculiar long life span; as well, many corals from cold to warm waters. Those species were excluded from the compilation since we wanted an exhaustive documentation that reliably enables data analyses.

Tyler et al. (2014), a reference we unfairly forgot, provided a very informative work; we will add this reference, very worth to be considered, especially in introduction. Based on existing data bases, Tyler et al. (2014) assessed the availability of trait information in fish and invertebrate taxa encountered in UK waters. Numbers of documented invertebrate species appear lower than what is documented in MacroTraits. However, the authors do not report total numbers of references in databases or per species. Also, and very importantly, we do not know whether there was an intended exhaustive documentation behind each species in the used databases. Projects such as FishBase or SeaLifeBase were initially intended to be comprehensive in taxonomic coverage, not exhaustive in documenting every published trait observation. For information, there are 8 references per species on average in MacroTraits when excluding the first trait (Biome). In the European northwestern shelf (biogeographic province 2) that includes most UK waters, 589 species are documented based on 2418 sources, 9 +/- 3 sources per species (mean +/- SD). This might be a consequence of considering primarily original bibliographical sources while avoiding existing databases as much as possible as mentioned in the text. In this respect, MacroTraits can be considered as an independent work (see the very limited number of records derived from websites).

Finally, while the amount of information in MacroTraits can be surprising, in fact, several traits related to reproduction and development had never received substantial interest in published data sets. In contrast, several other traits, especially those related to dwelling mode (e.g., sea floor affinity, motility, mobility), a very limited number of sources are enough to document many species (very often, a drawing tells more than a text). By the end, more than the amount of information in MacroTraits, the most surprising may be the large absence of North American applied studies on benthic functional community ecology in the literature given the substantial numbers of species from the Atlantic and Pacific American provinces already documented...

Epitoky is not mentioned as a method of reproduction – this needs to be considered.

Epitoky (reproductive transformation in some annelid polychaetes during reproduction, prior to fertilisation). This is a prominent feature in the organism biology of marine worms. In MacroTraits, we aimed to document traits that could express response or effect as much as independently of taxonomy, i.e., translating processes through a coding relatively common to relatively distant taxa (e.g., among phyla). Does epitoky express a distinct reproductive mode that clearly contributes to growth, survival and reproduction across phyla? In epitoky, the reproductive individuals actively swim in the water column and simultaneously shed their gametes to optmise fertilisation success. In fact, “reproductive mode” does not exist in MacroTraits. Rather, there is a trait “Fertilisation” that accounts for the result of epitoky: how the reproductive products are spread; in the case of epitoky, this is the modality “Broadcasting”. The reviewer’s remark is quite important as this refers to how building a trait. If epitoky would have been considered as a separate modality of a given trait, this would have induced a taxonomic effect as epitoky is specifically encountered within the class Polychaeta. A certain trait simplification is sometimes needed when exploring possible evolutionary convergences (life-history strategies as functional similarities among distant clades). While epitoky may improve fertilisation rate, many characteristics of the resulting products are shared by many species from other phyla: in most cases, pelagic egg/larval development (albeit not always following epitoky) with associated vulnerability and development time with a certain degree of dispersal in the water column. Of course, phylogenetic constraints cannot be fully avoided: for instance, there is no benthic amphipod species with a pelagic development, and although the release of adult miniatures (after internal

incubation) is also found in some mollusks and echinoderms, this reproductive aspect is mainly represented in Peracarida (mainly Amphipoda, Cumacea, Isopoda and Mysida).

Nevertheless, we added some text related to epitoky in the terminology and explain how it can be expressed with our trait modalities (lines 482-487):

"Also, epitoky, as reproductive transformation in some annelid, was not considered as a separate modality to avoid a taxonomic effect as epitoky is specifically encountered within the class Polychaeta. Under epitoky, the reproductive individuals actively swim in the water column and simultaneously shed their gametes to optmise fertilisation success (Clark, 1961). In MacroTraits, this can be identified by the combination of the modalities swimmer (partly for motility), broadcasting (fertilisation) of pelagic egg/larva (offspring type) and development in the water column (offspring development; albeit not always following epitoky)."

Besides, this does not mean that epitoky is not a relevant modality within a trait that would express reproductive modes. This can be relevantly implemented in a trait data set more specific to Polychaetes such as Polytraits (Faulwetter et al., 2014), and that would enable more specific explorations of eco-evolutionary patterns.

The authors mention the differences in life span of a species from Arctic and temperate waters and the use of fuzzy coding to account for differences. However, if someone was using this trait DB only with Arctic data, the fuzzy coding (consideration of all geographical zones and hence different lifespans) would not enable a reliable assessment (underestimate). This would be the same for size as it is well document that the same species will be larger in arctic environments than in temperate or tropical. How does the DB accommodate for these geographical differences? On p31 of the Supplement this is again stated: "Some species with a wide geographic distribution have variable scores for lifespan and age at maturity. They must be adjusted to the local populations" – how will they be adjusted? Manually by the user ? or is there specific code to do this within the R package. This needs to be clear to the users.

This problem concerns the very few quantitative traits that are quantitative. Probably life span and age at maturity are the most concerns given the substantial work needed to quantify those traits for a single population. Nevertheless, among the documented species, we think that a very few number of species distributed over a large latitudinal range exhibit this particularity. We completed the text accordingly. At least, this remark is highly relevant to improve the R package in a future version with additional functions that could provide more details regarding species bibliography. We completed the text accordingly lines 1062-1063.

Section 5.4 Historical considerations needs further work if to be retained as there is no discussion on this as per the other sections and feels slightly out of place. Perhaps this can include some statistics on traits within the literature e.g. how many species in the DB have complete traits (excluding expert judgement)

We think that section 5.4 (historical considerations) was better placed before 5.3 (correlation pattern), just after section 5.2 (spatial representativeness). This more harmoniously places time just after space; then, Figure 8 became Figure 7.

We completed Figure 7 with three other figures: (a) initial figure; (b) cumulative number of species documented per trait over time for the Western World (European and North American provinces; 1126 species); (c) the same for the species not present in the Western World (767 species); in (b) and (c), an additional curve represents the number of species based on earliest publication year; (d) time between the first and the last publication against first publication year. While our trait documentation does not include the overall literature of the considered species, we can assume that a part of the sources is a random subset of the existing literature (e.g., when several publications report the same information). In this respect, publication years cannot be considered biased towards the earliest or latest years.

At least three main conclusions can be derived from the updated Figure 7. (1) The sharp decline in sources older than 2010 shows that we reached exhaustiveness in documenting the 1893 species (Fig. 8a). (2) As suggested in Figure 6, more species have been documented in the Western World, and earlier in higher numbers. There, a few trait documentations (motility, mobility, biome) exhibit an exponential trend due to highly informative books after 2000 (e.g., Fish and Fish, 2011; Hayward and Ryland, 2017). All other trends in (a) and (b) remain either straight or asymptotic, especially earliest publications that denote less and less species documented per year from the mid 1970's onward (Fig. 7b and 7c). In no case largest amounts of information originate from the recent period (let's say, the last 15 years). (3) The increased rate in useful information per year (Fig. 7a) was accompanied by faster publication of overall species information (Fig. 7d), within ten years or less in 2010. Therefore, the large absence of additional species after 2010, corresponding to the sharp decline in 2010 is questionable. While we cannot fully ensure that not a single species with complete trait information is missing from MacroTraits, at least we show that we are nearly close to the exhaustiveness. We concisely completed the text accordingly lines 1158-1173.

Regarding statistics on traits as often presented in data papers, we think that this is of minor importance compared to Figure 5 that tells everything. There is a likely correlation between numbers of species documented for traits and

numbers of known species per class. This tells already a lot about the most represented bio-ecological characteristics among recognised functional typologies, which are globally marked by strong phylogenetic signatures (Giangrande et al., 1973; McHugh and Rouse, 1998; Pearson, 2001). Statistics on traits and associated modalities are not deprived of interest, but they may better take place in more targeted studies, for instance why evolution results in the prominence of certain trait combinations. A myriad of meaningless statistics risk to irrelevantly burden the paper.

The discussion and conclusions are fairly long and could be considerably shorter especially as a lot of detail has gone into the main section.

If somewhere the paper appears long, this is due to section 3, the terminology. The preprint is 50 pages long, which remains in the range of what is found at ESSD. 20 pages are devoted to the terminology, not compressible without leaving critical gaps. Now, with the completion of Figure 7, the relevance of the last paragraph of the discussion, without being changed, is strengthened. The discussion (2 pages), remains in the range of what is usually found in ESSD preprints; it informs readers where and how the data can be useful (1st paragraph); why morphology was not considered (2nd paragraph); new directions with the traits by combining response and effect as an important outcome of a large part of the manuscript (3rd paragraph); limitations in taxonomic coverage, causes and perspectives (last paragraph). Nevertheless, we shortened the conclusion.

Technical comments

Line 174: Figure caption has been disassociated with the figure – should be Figure 1 and placed below the figure.

This should be arranged once the definitive manuscript would be ready.

Line 247: I would argue that most crabs are epibenthic and occasionally hyperbenthic (swimming crabs) and endobenthic when they bury.

Yes, indeed, most mobile and burrowing crabs were attributed “Epibenthic” and “Occasionally endobenthic” while “Hyperbenthic” was mostly attributed to swimming species.

Line 965 – ‘liability’ should this be ‘lability’?

Yes, “lability”.

Lines 964-984 and line 991 – consistency - reference to the shortened names of the feeding type modalities is inconsistent with the how the other traits modalities are referred to. Suggest use of full name to be consistent.

Updated with full names.

Line 1101 – ‘rebuild’ should be ‘rebuilt’

Corrected.

Lines 1147 and 1148 – use of the word ‘deducted’ – this should be ‘deduced’?

Corrected.

Supplement needs to be spell checked before publishing due to several errors

Revised.

Polytraits should be referenced- Faulwetter S, Markantonatou V, Pavloudi C, Papageorgiou N, Keklikoglou K, Chatzinikolaou E, Pafilis E, Chatzigeorgiou G, Vasileiadou K, Dailianis T, Fanini L, Koulouri P, Arvanitidis C (2014) olytraits: A database on biological traits of marine polychaetes. Biodiversity Data Journal 2: e1024. doi:10.3897/BDJ.2.e1024

Forgotten, this important reference was added.

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