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Should we redefine meiofaunal organisms? The impact of mesh size on collection of meiofauna with special regard to nematodes

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Abstract Meiofaunal organisms are the predominant metazoans in benthic systems and important members of the benthic food web. They are defined by mesh size and specifically by their retention on a sieve with a 44- μm mesh size. In this study, we examined the accuracy of this standard collection method by counting the number of meiobenthic individuals, life stages and nematode species in a sample. A filter cascade consisting of five different mesh sizes (41 μm , 30 μm , 20 μm , 10 μm and 1 μm) was used to fractionate a natural freshwater meiobenthic collection, and the individuals in each fraction were then counted. In line with the current definition of meiofauna, all tardigrades, microcrustaceans, chironomids and oligochaetes were retained by the largest mesh size, whereas 9% of the rotifers were first retained on the 30- μm meshes. For nematodes, 23% were not retained on the 41- μm meshes and individuals were collected even from the 1- μm fraction. With declining mesh size, the yield of retained nematodes increased,

the age structure shifted to juveniles, evenness declined, and the species composition changed. As all of these findings were significant, this study therefore shows that the current definition of meiofauna is not sufficient to encompass the entire spectrum of meiofauna present in a sample and may result in misleading assessments of the diversity and composition of these organisms. We therefore propose that, especially for nematodes, a definition based on a smaller mesh size (at least 20 μm) is more appropriate.

Keywords Benthos · Nematodes · Diversity · Species composition · Age structure · Mesh size

Introduction

The term “meiobenthos” or “meiofauna” is well established in aquatic biology and was first used by Mare (1942) to describe the smallest metazoans that colonize sediments and other substrates of aquatic habitats (e.g., microcrustaceans, rotifers and nematodes). According to Higgins and Thiel (1988), meiobenthic organisms are those that pass through a net with a mesh size of 1000 μm and which are held back by nets of 42- μm mesh size. Giere (2009) later defined limit values for meiofauna of 500 μm and 44 μm . Through a literature search on the databases Google Scholar (last search: 17th February 2020), we

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obtained 100 studies, all of them published within the last 40 years (1980–2020), that investigated meiofaunal structure in permanent freshwater habitats while also noting the mesh size used to collect the organisms (keywords: freshwater meiofauna/meiobenthos or meiofauna/meiobenthos community + stream or lake). In 60% of these studies, meiofauna was collected with a minimum mesh size in line with that used by Giere (2009) or even smaller ($\leq 44 \mu\text{m}$), whereas many of the other studies relied on much larger (up to 100- μm) meshes (Fig. 1). Studies in which meiofauna was mentioned only casually, for example as bycatch during plankton sampling, were not taken into account, but we noted that the mesh sizes used by the respective authors were up to 250 μm .

The classification of meiofauna is not based on taxon membership but on body size and even on body form and flexibility. For example, a nematode of 1 mm body length or a soft-bodied rotifer is able to pass through a net with a mesh size of 500 μm , which is impossible for a more spherically shaped, hard bodied *Daphnia*, whose average body length is also 1 mm. However, Giere (2009) showed that the capture success of meiofauna and especially of nematodes could be greatly improved by the use of a smaller mesh size, i.e., 31 μm rather than 44 μm (e.g., for meiofauna from deep-sea environments). Previous studies had shown that juvenile nematodes (*Caenorhabditis elegans*), which have an average body length of 0.3 mm,

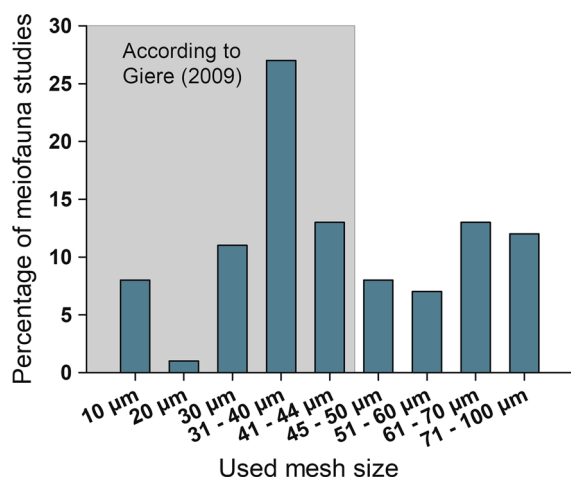


Fig. 1 Percentage distribution of the mesh sizes used in studies ($n = 100$) on the composition of the meiofauna communities from the period 1980–2020

are not retained by nets with a mesh size of 35 μm (Kreuzinger-Janik et al. 2019; Ptatscheck et al. 2015) or even by those with 5- μm meshes (Kreuzinger-Janik et al. 2019). According to Strayer (1985), the chosen mesh size has a strong influence on the results of meiofaunal examinations.

Meiobenthic organisms are an inherent component of all aquatic habitats. They are present in soft and hard substrates of freshwaters, including lakes, streams, cave waters and groundwater as well as in marine habitats (Beier and Traunspurger 2001; Bergtold and Traunspurger 2004; Hakenkamp et al. 1994; Heip et al. 1985; Muschiol et al. 2015; Peters and Traunspurger 2005; Traunspurger 2000; Traunspurger et al. 2012). Even temporary water bodies are colonized by numerous meiobenthic taxa within just a few days (Devetter 2004; Ptatscheck and Traunspurger 2014; Zotz and Traunspurger 2016). In streams, lakes and marine environments, up to 82%, 92% and 99% of metazoans are represented by meiofauna (Gerlach 1971; Majdi et al. 2017; Nalepa and Quigley 1983; Robertson et al. 2000; Schmid-Araya et al. 2002; Tod and Schmid-Araya 2009; Traunspurger et al. 2019).

Rotifers (in freshwater), copepods (in marine environments) and nematodes are usually dominating within meiofauna, but also other microcrustaceans, small annelids as well as tardigrades and chironomid larvae are frequent and diverse meiobenthic representatives (Giere 2009; Majdi et al. 2017; Reiss and Schmid-Araya 2008; Stead et al. 2003; Traunspurger et al. 2012). For example, in a sample obtained from the periphyton of different lakes and containing over 1300 meiobenthic organisms per cm^2 , Schroeder et al. (2012a) found mostly rotifers (26%) and nematodes (58%), with the latter represented by 48 species (Schroeder et al. 2012b). In the study by Beier and Traunspurger (2003a, b), 71 and 113 nematode species were identified in $\sim 100 \text{ cm}^3$ of sediment (26- cm^2 sediment area) obtained from two streams during the course of the year. In the sediment of Lake Königssee, 116 species were detected (Traunspurger 1996a, b), and in Lake Obersee a 3-year study yielded 152 nematode species (Michiels and Traunspurger 2004; 2005).

The ecosystem function of meiofauna is often greatly underestimated, as the contributions of these organisms to trophic interactions, nutrient cycling and food web are important (Hakenkamp and Morin 2000;

Majdi et al. 2017; Majdi and Traunspurger 2015; Schmid-Araya and Schmid 2000). In lotic and lentic environments, meiofauna account for up to 50% of total secondary production (Bergtold and Traunspurger 2005; Reiss and Schmid-Araya 2010; Stead et al. 2005). Furthermore, meiofauna can serve as a reliable indicator of environmental pollution (Beier and Traunspurger 2001; Höss et al. 2011; Zeppilli et al. 2015). All these investigations benefit from a correct assessment of abundance of meiofauna organisms.

Our methodologically based study examined the freshwater meiofaunal organisms retained by sieving. Specifically, we asked whether, regardless of the extraction method and sampled habitat, all extracted taxa and life stages of this group could be completely retained by sieving according to the prescribed size limits? The results validated the recommendation of Giere (2009) that meiofauna and especially nematodes could be more completely collected by the use of a 31- μm mesh. Therefore, a suspension containing a natural meiofaunal community was filtered using a five-stage filter cascade employing mesh sizes of 41 μm , 30 μm , 20 μm , 10 μm and 1 μm . We expected that (H1) larger organisms, including chironomids, oligochaetes and hard bodied taxa such as microcrustaceans, would be retained by the 41- μm mesh, whereas (H2) soft-bodied rotifers and especially nematodes, with their long, slender shapes, would partially pass through. We then focused on nematodes, the most abundant meiobenthic group, and hypothesized that (H3) the current definition of meiofauna is insufficient to reflect the real composition of nematode communities in a sample because it results in the omission of juvenile stages and possibly even some species.

Materials and methods

Meiofaunal organisms were extracted from the streambed of the Furlbach, a sandy headwater-stream (predominant grain size < 250 μm) with a low detritus content, and the littoral sediment of the Sandforther See (Lake Sandforther), a quarry pond with fine sandy and muddy sediment (predominant grain size < 250 μm). Both water bodies are located in North Rhine–Westphalia, Germany, and were chosen because their high meiofaunal density and high

diversity of nematodes are well established. Sampling was conducted in February 2019 during a single day. Shovels were used to transfer the top 10 cm of the sediments into buckets, which were then filled with habitat water. After the samples had been mixed by hand, the supernatants were decanted through a sieve with a mesh size of 10 μm and a diameter of \varnothing 14.2 cm (polyamide fabric). Most of the sand particles remained in the bucket. Additionally, submerged moss was collected along the watercourse of the Furlbach, thoroughly rinsed with tap water and filtered (10 μm mesh size, \varnothing 14.2 cm, polyamide fabric). All retained components from the sediments of the two habitats and the Furlbach moss were pooled ($n = 1$), preserved in formaldehyde (final concentration: 4%) and stained with rose Bengal. For this study, \sim 900 ml of concentrated sediment, organic matter and the contained organisms were used. Meiofauna were extracted from the remaining sediment and organic particles by density centrifugation (LudoxTM50, Sigma–Aldrich, Munich, Germany; 1.14 g ml⁻¹) according to Pfannkuche and Thiel (1988), using a six-fold quantity of Ludox. The resulting suspension was divided into ten 40-ml replicates. These were filtered through a cascade of five polyamide sieves of decreasing mesh size: 41 μm (\varnothing 6.4 cm), 30 μm (\varnothing 6.4 cm), 20 μm (\varnothing 6.4 cm), 10 μm (\varnothing 14.2 cm) and 1 μm (\varnothing 18.8 cm) (open mesh area: 31%, 20%, 14%, 4%, 1%). The sieves were carefully flushed with 600 ml (41- μm sieve) or 200 ml (30- to 1- μm sieves) of tap water from a beaker. The filtering process was accelerated by lightly tapping the sieve frames, but not by stirring or the use of a water jet. Only in the case of the 1- μm sieves did we touch the underside of the mesh, gently dislodging trapped material using circular movements made with our fingers. After each use, the sieves were cleaned in an ultrasonic bath (30 min, 35 kHz). Each fraction was thoroughly washed from the sieve with tap water from a wash bottle and placed in gridded Petri dishes. All meiofauna were counted under a Leica L2 stereomicroscope (40 \times magnification). 100 nematodes per sample and per sieve were prepared using the methods of Seinhorst (1959, 1962). When the number of nematodes was less than 100, all individuals were prepared. Nematodes were identified to the species level based on Leica Dialux microscopy observations (1250 \times magnification) according to the criteria of Andr assy (2005, 2007, 2009), Loof et al.

(1999, 2001) and references herein and classified into juvenile and adult individuals.

Data analysis

It was assumed that all organisms retained by a sieve with a particular mesh size would be retained by all sieves with smaller mesh sizes. Thus, for the data analysis, cumulative organism and species numbers determined from the respective sieve and from all larger mesh sizes were used to evaluate the efficiencies of the five sieves (cumulative fractionation).

The evenness (E_{var}) of the nematode community was calculated according to Smith and Wilson (1996).

Data with a confirmed normal distribution (Kolmogorov–Smirnov test) and homogeneity of variance (Levene test) were subjected to ANOVA and Tukey post hoc tests to compare the five fractions with respect to the percentage of juvenile nematodes, nematode species number and evenness. These tests were performed using Sigmaplot (version 12; SYSTAT Software, San Jose, California).

Differences in the nematode species composition of the five fractions were investigated using an analysis of similarity (ANOSIM). The resulting R -values (0–1) revealed differences in the nematode species composition in the fractions obtained with the five mesh sizes. R -values near 0 indicate no separation, while larger R -values suggest separation between groups. In addition, the percentage dissimilarity between the fractions was determined using an analysis of similarity percentages (SIMPER). Nematode composition was clustered using non-metric multi-dimensional scaling (nMDS). All techniques were based on a Bray–Curtis similarity using untransformed data. The analyses were carried out using the Primer 5 (PRIMER-E Ltd., 2001) software package.

Results

The mean number of organisms (10 replicates) obtained from the five different sieves was 13,944.7 (± 2224.0 , SD). While rotifers ($82.9\% \pm 2.9\%$, mean \pm SD) and nematodes ($14.4\% \pm 2.4\%$, mean \pm SD) dominated, other typical meiobenthic taxa, such as microcrustaceans and oligochaetes, were also present (Table 1).

Tardigrades, microcrustaceans, chironomids and oligochaetes were completely retained by the 41- μ m meshes. In the case of rotifers, 9.2% (± 3.2 , SD) passed through but were completely retained on the 30- μ m meshes. The only meiofaunal taxon collected from all five sieves was nematodes: 77.0% ($\pm 6.1\%$, SD) were trapped on the 41- μ m mesh, 85.4% ($\pm 4.3\%$, SD) on 30- μ m mesh, 90.4% ($\pm 3.1\%$, SD) on 20- μ m mesh, 97.1% ($\pm 3.1\%$, SD) on 10- μ m mesh. 2.9% ($\pm 3.0\%$, SD) passed through the 10- μ m mesh and were retained by the 1- μ m mesh (Table 1).

4202 of the nematodes retained on the five sieves could be assigned to 75 species. The dominant species were *Eumonhystera vulgaris* ($49.5\% \pm 1.7\%$, SD) and *Eumonhystera pseudobulbosa* ($13.1\% \pm 1.6\%$). All other species were detected at $< 4.0\%$. Sixteen species, including the predominant taxa, were found in every replicate, while 20 species were collected from only one replicate. The total nematode composition of the sample is listed in Table S1.

With decreasing mesh size, the number of collected nematode species increased from an average of 26.4 (41 μ m) to 35.5 species (1 μ m) (Table 2). The differences between the number of species collected on the 41- μ m sieve and all sieves with smaller mesh sizes were significant (Tukey test, all tested pairs: $p < 0.001$) (Table 3). By contrast, the evenness decreased with decreasing mesh size, with significant differences between all fractions with the exception of those derived from the 10- μ m and 1- μ m meshes (Tukey test, all tested pairs: $p < 0.01$) (Table 3). An analysis of the age distribution of the nematodes in the different fractions revealed a significant increase in the number of juveniles retained on the smaller meshes (Table 2). Thus, whereas on sieves with a 41- μ m mesh size, juveniles accounted for 56.5% ($\pm 4.4\%$, SD) of the collected nematodes, on the 1- μ m meshes the percentage increased to 81.3% ($\pm 2.6\%$). With the exception of the 10- μ m and 1- μ m meshes, the differences between all fractions were significant (Tukey test, all tested pairs: $p < 0.05$) (Table 3).

The nMDS plot (Fig. 2) clearly showed the clustering of the nematode species composition of the five fractions. In particular, the nematodes from the 41 μ m meshes were separated from the other groups, while the 10- μ m and 1- μ m fractions overlapped each other. These results were supported by the ANOSIM (Table 4), which showed no differences in nematode species composition between the fractions from the

Table 1 Initial composition (density in the entire sample and percentage) of the investigated meiofaunal organisms and their cumulative fractionation on sieves with five different mesh sizes

	Taxon	Initial density	Percentage	Percentage of organisms on the sieves				
				41 μm	30 μm	20 μm	10 μm	1 μm
The mean of ten replicates is shown, with the SD in parentheses	Nematodes	1994.2 (\pm 291.8)	14.42 (\pm 2.39)	77.0 (\pm 6.1)	85.4 (\pm 4.3)	90.4 (\pm 3.1)	97.1 (\pm 3.0)	100.0 (\pm 0.0)
	Rotifers	11585.1 (\pm 2142.7)	82.88 (\pm 2.94)	90.8 (\pm 3.2)	100 (\pm 0.0)	–	–	–
	Tardigrades	3.9 (\pm 3.7)	0.03 (\pm 0.03)	100.0 (\pm 0.0)	–	–	–	–
	Copepods/nauplii	36.1 (\pm 6.4)	0.27 (\pm 0.07)	100.0 (\pm 0.0)	–	–	–	–
	Ostracods	4.3 (\pm 2.8)	0.03 (\pm 0.02)	100.0 (\pm 0.0)	–	–	–	–
	Cladocerans	4.6 (\pm 2.6)	0.03 (\pm 0.02)	100.0 (\pm 0.0)	–	–	–	–
	Chironomids	55.7 (\pm 15.6)	0.41 (\pm 0.15)	100.0 (\pm 0.0)	–	–	–	–
	Oligochaetes	260.8 (\pm 69.5)	1.93 (\pm 0.66)	100.0 (\pm 0.0)	–	–	–	–
	Total	13,944.7 (\pm 2,224.0)	100 (\pm 0.00)	–	–	–	–	–

Table 2 Cumulative nematode species number, evenness and percentage of juveniles collected from the five sieves differing in their mesh size

Mesh size	Species number	Percentage juveniles	Evenness
41 μm	26.4 (\pm 3.4)	56.5 (\pm 4.4)	0.59 (\pm 0.03)
30 μm	32.1 (\pm 3.5)	69.0 (\pm 3.0)	0.47 (\pm 0.03)
20 μm	33.6 (\pm 3.0)	74.3 (\pm 4.1)	0.41 (\pm 0.03)
10 μm	35.2 (\pm 2.4)	79.3 (\pm 3.3)	0.36 (\pm 0.02)
1 μm	35.5 (\pm 2.5)	81.3 (\pm 2.6)	0.35 (\pm 0.03)

Mean ($n = 10$) and SD (in parenthesis)

10- μm and 1- μm meshes ($R = 0.008$, $p > 0.5$), but significant separation between those from all other meshes, in which the R -values ranged between 0.7 and 1 ($p < 0.001$).

With increasing differences between the mesh sizes, the dissimilarities between the composition of

the retained nematode species increased as well. Thus, the largest dissimilarity (65.6%) was that between the 41- μm and 1- μm fractions (Table 4). A comparison of adjacent mesh sizes showed a dissimilarity of 42.2% between the 41- μm and 30- μm sieves but smaller values ($< 30\%$) for all other adjacent sieve pairs.

The dissimilarities between all tested pairs were mainly caused by the abundances of *E. vulgaris*, *E. pseudobulbosa* and *Rhabdolaimus terrestris*, whose contributions were between 36 and 56%.

Discussion

Our study demonstrates that the mesh size commonly used for the collection of meiofauna does not result in the isolation of the entire community. Accordingly, the current definition of meiofauna, based on the mesh size used to obtain these organisms, does not accurately portray the whole meiofaunal community nor does it allow statements on species composition and diversity of nematodes and thus on the ecological relevance of this group.

Consistent with the long-standing definition of meiofauna and in accordance with hypothesis (H1),

Table 3 Results of the analysis of variance (ANOVA) and post hoc Tukey test of differences in the cumulative number of nematode species, evenness and the percentage of juveniles determined from the five sieves with different mesh sizes

		Species number	Percentage juveniles	Evenness
ANOVA	<i>df</i>	4.00	4.00	4.00
	<i>F</i>	15.28	79.26	131.60
	<i>p</i>	< 0.001	< 0.001	< 0.001
Post hoc	41 µm vs. 30 µm	***	***	***
	41 µm vs. 20 µm	***	***	***
	41 µm vs. 10 µm	***	***	***
	41 µm vs. 1 µm	***	***	***
	30 µm vs. 20 µm	n.s.	*	***
	30 µm vs. 10 µm	n.s.	***	***
	30 µm vs. 1 µm	n.s.	***	***
	20 µm vs. 10 µm	n.s.	*	**
	20 µm vs. 1 µm	n.s.	***	***
10 µm vs. 1 µm	n.s.	n.s.	n.s.	

df degrees of freedom, *n.s.* not significant, **p* < 0.05, ***p* < 0.01, ****p* < 0.001

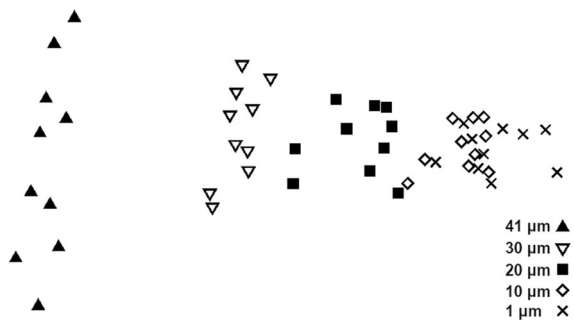


Fig. 2 nMDS plot (stress 0.07) of cumulative nematode species composition in the fractions obtained from sieves differing in their mesh size. The Bray–Curtis similarity was calculated without transformation

microcrustaceans, tardigrades, chironomids and oligochaetes were retained by the 41-µm sieve. However, for the two most dominant taxa this was not the case, as 9% of rotifers passed through this sieve and nematodes were not completely retained even by the 10-µm sieve (H2). Our results are in line with those of Hummon (1981), who was able to show that nematodes and rotifers were not retained by a 37-µm sieve, while microcrustaceans and insect larvae did not pass through an even larger mesh (62 µm). In our study, nematodes comprised 14% of the meiofaunal community, but in other investigations (Beier and Traunspurger 2001, 2003c; Reiss and Schmid-Araya 2008; Schroeder et al. 2012a) values of more than 90% were recorded. As shown in Table 1, a 23% loss of the predominant taxon would be considerable.

Table 4 Comparisons of the cumulative nematode species composition determined in the fractions from the five mesh sizes

Mesh size	41 µm	30 µm	20 µm	10 µm
30 µm	0.993*** (42.2)			
20 µm	1.000*** (53.1)	0.735*** (24.9)		
10 µm	1.000*** (62.7)	0.999*** (36.6)	0.712*** (22.6)	
1 µm	1.000*** (65.6)	1.000*** (40.8)	0.881*** (26.9)	0.008 ^{n.s.} (14.5)

The *R*-values resulting from the ANOSIM and the percentage dissimilarity based on the Bray–Curtis analysis (in parentheses) are shown

n.s. not significant, ****p* < 0.001

Between mesh sizes (global *R* = 0.731***)

The largest differences in abundance and species composition were between the 41-µm fraction and the fractions obtained with the smaller mesh sizes, and the smallest difference between the 10-µm and 1-µm fractions (Fig. 2, Tables 3, 4). In the preparation for the actual experiment, meiofauna were sampled and subsequently processed using 10-µm sieves. Our results suggest that smaller individuals were therefore lost and if smaller mesh sizes had been used, the differences would have been even larger. However, the use of smaller mesh sizes in field or laboratory

sampling of meiofauna is impracticable because of the fast blockage of the sieves by organic material or crystallized Ludox. Furthermore, part of the juveniles of 20 species and the adults of the three dominant species (*Eumonhystera vulgaris*, *Eumonhystera pseudobulbosa*, and *Rhabdolaimus terrestris*) were not retained even by the 10- μm meshes. The minimum values reported for the body thickness of adult nematodes are 16.67 μm (*E. vulgaris*), 9.71 μm (*E. pseudobulbosa*) and 10.50 μm (*R. terrestris*) (Andrássy 2005). Thus, the latter two species and especially the juvenile stages are able to pass through the 10- μm meshes. These findings would account for the declining evenness obtained with the smaller mesh sizes. As shown by the SIMPER analysis, the three most common species were mainly responsible for the differences in nematode species composition. Because a high portion of these three species passed through the sieve with the largest mesh size, they predominated on finer meshes even though diversity and evenness declined. Thus, taken together, our results clearly show that nematodes retained by the 41- μm mesh are only partly representative of the real community within the sample (H3).

In our study, we asked whether freshwater meiofaunal organisms are retained by meshes of the recommended sizes. To answer this fundamental question, we used suspended organisms already extracted by different methods such that less substrate was contained in the samples. Additionally, only dead organisms were sieved. Both the proportion of substrate and the condition of the organisms can affect extraction by sieving. Living organisms may actively twine through the meshes or hold onto it. For example, the appendages of some rotifer taxa serve as adhesion organs, while some nematode taxa produce caudal secretions that allow adherence to the substrate (Fontaneto and de Smet 2015; Majdi and Traunspurger 2015). Furthermore, living organisms can accumulate on large particles retained by the meshes.

These conditions explain why, despite previous 10- μm sieving of the sediment with living organisms during meiofaunal collection, dead and extracted nematodes were not completely retained by meshes of the same size as used in the filter cascade. However, while Hummon (1981) filtered living meiofauna from sandy sediment, the percentage of nematodes and rotifers retained on the 37- μm sieve was very similar to that retained on the 41- μm meshes in this study.

Finally, it was beyond the scope of our study to evaluate the sieving of meiofauna as an extraction method, as our aim was to obtain a size-based definition of meiofauna.

In conclusion, our study showed that in investigations of meiofaunal communities the mesh sizes employed to collect these organisms must be smaller than those currently used to define meiofauna (44 μm), because the latter do only partly efficiently retain nematodes and rotifers. As both groups frequently predominate in benthic systems, their loss would result in an underestimation and an inaccurate representation of the community structure of meiofauna. Over the last few decades, the ecologic importance of meiofauna has been pointed out in numerous studies. However, this claim can only be made using reliable datasets. Additionally, the wide range of mesh sizes (10–100 μm) used in studies on freshwater meiofaunal communities conducted during the last 40 years (Fig. 1) make it difficult to compare the datasets, as already noted by Strayer in 1985. For example, while in our study 97.1% of the nematodes and 100% of the rotifers in the sample were collected on a 10- μm sieve, on 125- μm meshes only 20.5% and 0.7% were retained (Hummon 1981). In 20% of the studies reviewed in Fig. 1, the mesh sizes were in between 10 μm and 30 μm , indicating that, despite the increased workload (longer sieving) resulting from the use of smaller mesh sizes, such investigations are still be practicable.

Therefore, in agreement with the recommendations of Giere (2009) and Strayer (1985), we advocate that the minimum mesh size be reduced to at least 30 μm or, even 20- μm , to obtain representative and comparable populations of meiofauna, especially when the nematode community is of scientific interest.

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Authors' contributions CP, SG and WT conceived the ideas and designed the methodology. CP and SG collected the data. CP analyzed the data. CP led the writing of the manuscript, and all authors discussed the manuscript.

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Data availability After acceptance of the manuscript, data can be obtained from the author on request.

Compliance with ethical standards

Conflict of interest Nothing to declare.

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