Oceanologia, 67 (4)/2025, 67411
Polish Academy of Sciences
Institute of Oceanology

https://doi.org/10.5697/RXWV1889

Does mesh size matter? Influence of mesh size on estimation of meiofauna abundance, biomass and on size spectra

Barbara Górska[1,*], Katarzyna Grzelak[1], Bodil A. Bluhm[2], Silvia Hess[3], Maria Włodarska-Kowalczuk[1]

Abstract
For muddy-bottom meiofauna analyses, samples are typically sieved on 32 μm sieves for animal extraction. However, some studies use a 63 μm sieve to reduce fine sediment overload. Such variation in sieving protocols hampers comparisons across studies. We quantified and compared the effects of mesh size (63 versus 32 μm) on meiofauna abundance, biomass, community composition, and size spectra in muddy sediments. Between 8 and 21% of individuals (mostly nematodes) were missed in the 63 μm mesh-based analyses (compared to 32 μm). However, the larger mesh size did not affect biomass estimations or the construction of size spectra. For muddy sediments, a 63 μm sieve can be used interchangeably with a 32 μm sieve for meiofauna biomass estimation.

Keywords
Meiofauna; Biodiversity; Processing methods; Size spectra

[1] *Institute of Oceanology Polish Academy of Sciences, ul. Powstańców Warszawy 55, 81–712 Sopot, Poland*
[2] *UiT The Arctic University of Norway, PO Box 6050 Stakkevollan, N–9037 Tromsø, Norway*
[2] *University of Oslo, PO Box 1047 Blindern, NO–0316 Oslo, Norway*
***Correspondence**: basia@iopan.pl (B. Górska)

Received: 29 May 2025; **revised:** 22 October 2025; **accepted**: 28 October 2025

1. Introduction

Meiobenthos is a collective term for the most diverse communities of the marine realm, including both protists and metazoans. Meiofauna is defined as all organisms which pass through an upper sieve of 500 μm mesh and are retained on a finer lower sieve, the mesh size of which is not clearly defined and depends on the type of sediment (Giere, 2009). Typically, 32 μm is used in deep-sea studies or 45/63 μm in shallow waters. Due to their high abundance and diversity, widespread distribution, rapid reproduction time, and fast metabolic rates, meiofaunal organisms play an important role in carbon cycling and the provision of energy to higher trophic levels (Zeppilli et al., 2015). These characteristics make meiofauna excellent study organisms to test ecological hypotheses and theories (Bonaglia et al., 2014; Nascimento et al., 2011).

Meiofauna biomass is rarely assessed directly, as measuring wet weight is challenging due to small organism sizes and a large range of error (Giere, 2009). However, indirect estimation of biomass is necessary for the assessment of the role of meiofauna in carbon budgets and its contribution to energy flow through ecosystems. Furthermore, biomass size spectra of meiofauna (distribution of biomass among logarithmic size classes) have led to new insights into the dynamics of these communities (Górska et al., 2020; Górska and Włodarska-Kowalczuk, 2017; Grzelak et al., 2020; Schwinghamer, 1983). Organism size has a large influence on bioturbation potential. Meiofauna bioturbation influences the degradation of organic matter and the availability of resources to higher trophic levels (Aller and Aller, 1992; Giere, 2009). Meiofauna biomass can also be used as a proxy for detecting responses of benthic communities to environmental changes. This makes understanding the patterns and drivers of meiofauna distribution and functioning highly important in the face of rapid climate change.

The wide geographic distribution of meiofauna facilitates large-scale comparisons of data from different studies. However, such a global comparison of meiofaunal data is severely hampered by the absence of a unified sieving protocol (Udalov et al., 2005). While most studies employ an upper sieve with 500 μm mesh, some researchers still use a 1000 μm sieve, leading to inconsistent macrofaunal exclusion. Even more problematic is the choice of a lower mesh size, which varies widely – from 32 μm

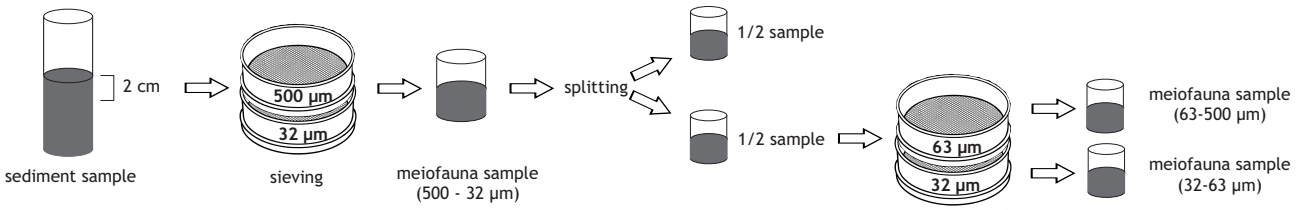

Figure 1. Schematic processing of meiofauna sample.

up to 63 μm – across different investigations. In some reviews, data obtained by sieving on >45 μm mesh size are excluded from comparative studies (e.g., Udalov et al., 2005), leading to unfortunate gaps in data coverage, despite the research effort having been undertaken in remote localities or across time series. In the muddy sediments of the deep sea, the most popular sieve used for meiofauna studies is 32 μm (Giere, 2009), but in some studies, a 63 μm sieve is still applied (e.g., Bessière et al., 2007; Charrier et al., 2023; Grove et al., 2006; Kitahashi et al., 2018; Tachibana et al., 2023). This lack of agreement on both upper and lower sieve dimensions prevents meaningful synthesis of abundance, biomass, and community composition data from different regions and makes it difficult to detect real ecological patterns rather than methodological artefacts.

Several previous studies have assessed how mesh size influences nematode recovery (e.g., Leduc et al., 2010; Soltwedel et al., 2003; Vanreusel et al., 1995) and the whole meiofauna (e.g., de Bovée et al., 1974; Elmgren, 1973); however, the latter did not estimate biomass. Remarkably, to our knowledge, no study to date has provided an equally detailed, community-wide evaluation of how variations in lower mesh sizes affect estimates of total metazoan meiofauna biomass, abundance, taxonomic composition, and size-class distributions. Our work fills this critical gap by directly comparing samples from the same muddy sediments sieved through both 32 μm and 63 μm mesh sieves – across four seasons at 189 m depth in the northeastern Barents Sea – to quantify and contrast the impacts of mesh size not only on overall abundance and biomass but also on the full spectrum of meiofaunal taxa and their size distributions.

2. Material and methods

Sediment samples were collected within the framework of the research project Nansen Legacy (The Nansen Legacy, 2025). Fieldwork took place in August (Season 1) and December (Season 2) 2019, and March (Season 3) and May (Season 4) 2021 aboard the Norwegian icebreaker r/v *Kronprins Haakon*. For the purpose of this study, sediment samples from a station at 189 m water depth in the northeastern Barents Sea (77.50°N 34.00°E) were analyzed. At this site, sediments with a predominance of silt-clay fractions (silt 63.3% and clay 24%) with an admixture of sand (12.7%) were observed. For detailed sediment information see Ricardo de Freitas et al. (2024).

Three box core replicates (BC1, BC2, BC3) of sediment were taken using a 50 × 50 cm box corer. After removal of the overlying water in the box core, one meiofauna subsample from each box core was taken using a plastic sub-core (5.5 cm diameter) which was sectioned into 1 cm layers. For the purpose of this study, the top two layers (0–1 cm and 1–2 cm) were integrated into one 0–2 cm layer. The upper 2 cm capture the majority of meiofauna individuals (Ingole et al., 2005; Sautya et al., 2021; Tong et al., 2022), and hence allowed us to answer our question comparing mesh size effectiveness. Samples were preserved with 70% ethanol and stained with Rose Bengal to ease further extraction of the meiofauna organisms from the sediment.

In the laboratory, samples were sieved on two sieves: an upper sieve with a mesh diameter of 500 μm to remove macrofauna, and a lower sieve with a mesh diameter of 32 μm (Figure 1). Sieved samples were split in half, and one half was used for meiofauna analysis. Subsequently, samples were sieved on sieves with a mesh diameter of 63 μm and 32 μm, and those two fractions were analyzed separately. All individuals of metazoan meiofauna were counted and identified to higher taxa under a stereoscope.

Differences in univariate (abundance; based on Euclidean distances of abundance data) and multivariate (composition; Bray-Curtis similarity of square-root transformed taxa abundance data) meiofauna characteristics between sieve fractions (32–500 μm and 63–500 μm) and sampling season were tested using a two-way PERMANOVA model design with the factors: Sieve (fixed) and Season (fixed). The calculation of Pseudo-F and p values was based on 9999 permutations of the residuals under a reduced model. PERMANOVA tests were performed in PERMANOVA+ software (Anderson, 2005).

From one subsample (BC1), all individuals were photographed with a camera connected to a stereomicroscope in order to estimate their biomass. For each specimen, the maximum length and width were measured using the digital image analysis tool of Leica Application Suite v 4.2. Nematode lengths and widths were measured using a semi-automated image analysis method (Mazurkiewicz et al., 2016). Nematode biovolume (V [μm^3]) was calculated by using an equation for the volume of a cylinder: $V = r^2L/10^6$, where r [μm] is the radius (width/2) and L [μm] is the nematode length (Mazurkiewicz et al., 2016).

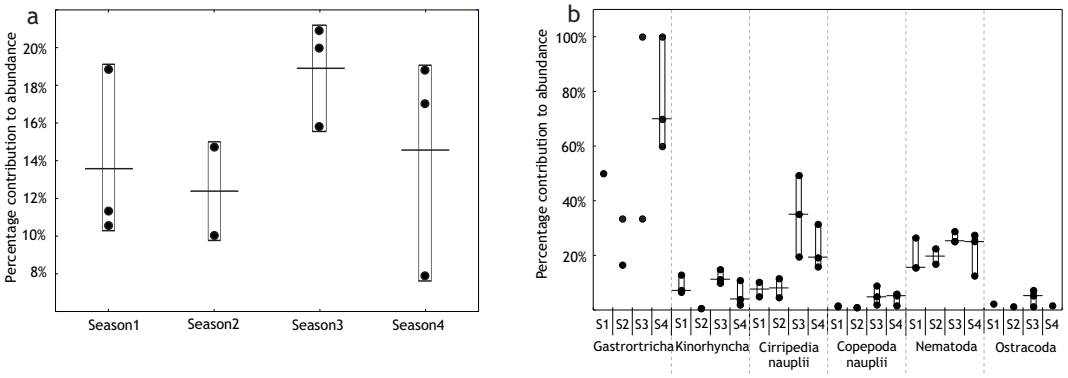

Figure 2. Percentage contribution of total meiofauna which passed 63 μm relative to total abundance (i.e. estimate based on 32–500 μm fraction). Min-max and mean from three subsamples are presented (a). Percentage contribution of six taxa, which passed 63 μm relative to abundance of those taxa in 32–500 μm fraction (b). Min-max and mean from three subsamples are presented. For seasons in which presented taxa occurred in only one or two subsamples, mean values were not calculated. (S1 – Season1, S2 – Season2, S3 – Season3, S4 – Season4).

For all other meiofauna taxa, biovolumes (V) were calculated by applying Feller and Warwick's (1988) formula: $V = LW^2c$, where L is the length, W is the width and c is the taxon-specific coefficient. The wet weight (WW) and dry weight (DW) were calculated using the following equations: $WW = 1.13V$; $DW = 0.25WW$ (Feller and Warwick, 1988).

Each individual was classified into a $\log_2$ size class based on its DW [μg]. For example, class 0 includes all organisms for which $DW \geq 1$ and <2 μg (i.e., $\geq 2^0$ μg and $< 2^1$ μg). Abundance and biomass size spectra were constructed by plotting abundance or DW in each size class against the $\log_2$-transformed class mid-point. The differences in the distribution of the biomass among size classes between sieve fractions in four seasons were tested using a nonparametric, two-sample Kolmogorov-Smirnov test.

3. Results

3.1 Mesh size effects on abundance estimates

Mean total meiofauna abundance (i.e., summed abundance from samples sieved on 32 and 63 μm sieves) in the 0–2 cm layer was 1592 ind. 10 cm^{-2} (Table S1). Nematodes constituted 61% of all individuals, followed by Harpacticoida (13%), Copepoda nauplii (12%), and Kinorhyncha (7%). Twelve other taxa contributed the remaining 7%.

Individuals which passed the 63 μm sieve and were retained on the 32 μm sieve constituted 8 to 21% of all individuals in the samples (Figure 2a). The highest proportion of individuals that passed 63 μm was observed in Season 3 (16 to 21%) and the lowest in Season 2 (10–15%), but differences were not statistically significant (PERMANOVA, $p > 0.05$). Among the individuals that passed through the 63 μm sieve, 7 out of 16 taxa were present. Nematodes were the most numerous, followed by Cirripedia nauplii, Copepoda nauplii, and Kinorhyncha. Among nematodes, 12 to 29% of individuals passed the 63 μm sieve (Figure 2b), while among Cirripedia nauplii, the range was from 5 to 49%, and among Copepoda nauplii from 1 to 9% (Figure 2b). The highest proportion of individuals passing the 63 μm sieve was observed among Gastrotricha, ranging from 33 to 100%. There were no significant seasonal differences in the percentage contribution of individuals passing the 63 μm sieve for each taxon relative to their total abundance in the 32–500 μm fraction (PERMANOVA, $p < 0.05$).

Mean abundance in the 32–500 μm fraction varied between 1010 ± 321 ind. 10 cm^{-2} (mean $\pm$ SD) in Season 1 and 2029 ± 242 ind. 10 cm^{-2} in Season 3 (Figure 3). The corresponding values in the 63–500 μm fraction were 868 ± 258 ind. 10 cm^{-2} and 1649 ± 236 ind. 10 cm^{-2}, respectively; thus, relying solely on the 63–500 μm fraction reduced abundance by approximately 14% in Season 1 and 19% in Season 3 relative to the full 32–500 μm community. Nevertheless, a two-way PERMANOVA did not indicate a significant effect of sieve size on total abundance ($p > 0.05$), while significant seasonal differences were confirmed ($p < 0.05$; Table 1).

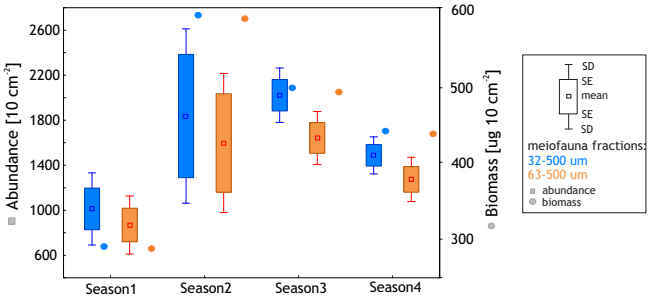

Figure 3. Total meiofauna abundance and biomass in the two size fractions (32–500 μm and 63–500 μm) in all seasons.

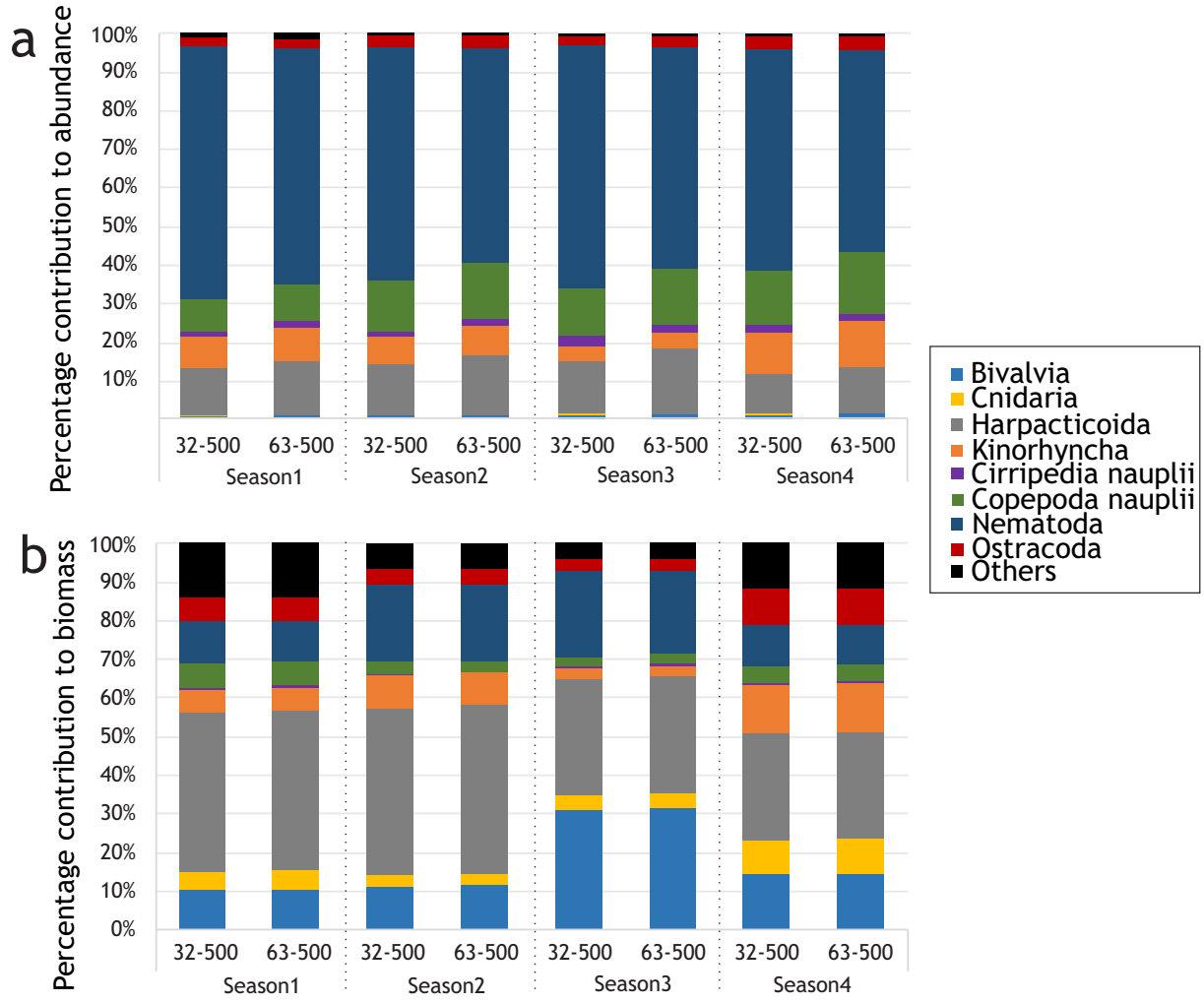

Figure 4. Percentage contribution of different taxa to abundance (a) and biomass (b) in four seasons in different sieve fractions. Other – other Crustacea, Gastrotricha, Halacariidae, Loricifera, Ophiuroidea, Polychaeta, Priapulida larvae, Rotifera.

In the 32–500 μm fraction, among 16 taxa, nematodes constituted 55 to 74% of total abundance, followed by Harpacticoida (9 to 16%), Copepoda nauplii (8 to 16%), and Kinorhyncha (3 to 11%; Figure 4a). Rotifera was the only taxon which was found exclusively in the finer fraction (32–62 μm). In the 63–500 μm fraction, among 15 taxa, nematodes were also the most numerous (47 to 57% of total abundance), followed by Harpacticoida (12 to 19%), Copepoda nauplii (7 to 16%), and Kinorhyncha (3 to 12%). Community composition did not differ between sieve fractions (PERMANOVA, $p > 0.05$; Table 1).

Table 1. Results of two-way PERMANOVA test for differences in univariate meiofauna characteristic (abundance) and multivariate characteristic (composition – Bray-Curtis similarities of square-root transformed data of taxa abundances in samples) for two factors: Season and Sieve mesh size. PsF – PERMANOVA pseudo F, CV – component of variation. Significant effects: $^{*}p < 0.05$, $^{**}p < 0.001$.

Source	df	Abundance		Composition	
		PsF	CV	PsF	CV
Season	3	7.72*	1.5×105	7.42**	95.02
Sieve	1	2.64	18511	0.93	−0.54
Season × Sieve	3	0.12	−38593	negative	−30.94
Residuals	14		1.2×10^5		80.73

3.2 Mesh size effects on biomass estimates

The body sizes of a total of 8,818 meiofauna individuals were measured. The smallest specimen (Cirripedia nauplius) was just 43 μm long, while the largest (a nematode) reached 6904 μm. Organisms that passed through the 63 μm sieve accounted for only 0.8–1.1% of the total meiofauna biomass. Among nematodes, the mean individual weight in the <63 μm fraction was 0.01 μg, compared to 0.08 μg in the 63–500 μm fraction. Similarly, Ki-

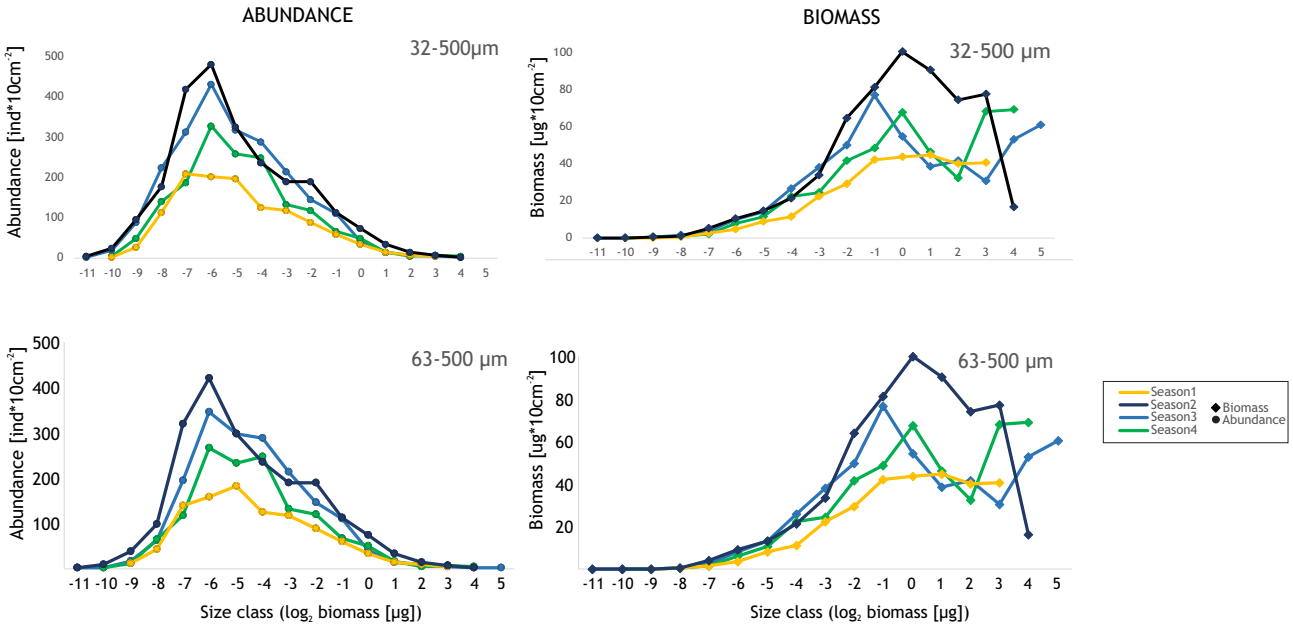

Figure 5. Meiofauna abundance and biomass size spectra based on data obtained using sieves: 32–500 μm and 63–500 μm.

norhyncha and Cirripedia nauplii that were retained on the 63 μm sieve weighed on average 0.32 μg and 0.10 μg, respectively, substantially more than their counterparts in the 32–500 μm fraction (0.03 μg and 0.04 μg, respectively). Total biomass in the 32–500 μm fraction ranged from 290 μg 10 cm^{-2} in Season 1 to 590 μg 10 cm^{-2} in Season 2 (Figure 3). In both sieve fractions (32–500 μm and 63–500 μm), Harpacticoida dominated total biomass (constituting 28 to 44% of total biomass), followed by nematodes (11 to 22%), Bivalvia (10 to 31%), and Kinorhyncha (3 to 13%; Figure 4b).

3.3 Abundance and biomass size spectra

Individual meiofauna biomass across all four seasons and both sieve fractions spanned 17 logarithmic size classes (from −11 to 5), ranging from 6.1×10^{-4} to 35.9 μg. Neither biomass nor the abundance distribution among size classes differed significantly between the 32–500 μm and 63–500 μm fractions (Kolmogorov-Smirnov test, $p > 0.05$). There were also no seasonal differences in abundance and biomass distribution among size classes (Kolmogorov-Smirnov test, $p > 0.05$).

Peaks of abundance occurred between size classes −6 and −5 and were highest in Season 2 and lowest in Season 1 (Figure 5). The range of size classes was the narrowest in Season 1 (from −9 to 3) and the widest in Season 3 (from −11 to 5). The peak of the highest biomass in Season 3 occurred in the −1 size class, whereas in Season 2 and Season 4 it shifted to class 0. In Season 1, no peak of biomass was observed as biomass was evenly distributed among size classes from −1 to 3 (from 40.2 to 44.7 μg 10 cm^{-2}). The overall highest peak of biomass was recorded in Season 2 (100.3 μg 10 cm^{-2}).

4. Discussion

The 32 μm mesh sieve is the standard for extracting meiofauna from muddy sediments (Giere, 2009). However, sieving on such a fine mesh greatly increases the amount of fine sediment particles retained in the sample, making the subsequent processing more time-consuming. Small grains/particles obscure tiny meiofaunal organisms and complicate their detection and extraction (Figure 6). The use of the centrifugation method (i.e., sediment centrifugation with Ludox followed by sieving of the supernatant; Vanreusel et al., 2000) partly resolves the problem of the high amount of small sediment particles in the sample. However, washing samples for centrifugation is significantly more labor-intensive when using a fine mesh sieve, and considerable amounts of lighter sediment particles still remain in the sample. To accelerate sample processing and reduce costs, many researchers use a coarser 63 μm sieve instead (Leduc et al., 2010). Unfortunately, these varying protocols, whether using 32 μm or 63 μm as the lower sieve, complicate direct comparisons among studies (Udalov et al., 2005).

In our investigation, we directly compared the extraction efficiency between the 32 μm and 63 μm sieves and found that 8–21% of all meiofaunal individuals passed through the 63 μm mesh and were retained on the finer 32 μm sieve. Thus, the coarser sieve both streamlines processing and captures the vast majority of the community, striking a practical balance between efficiency and com-

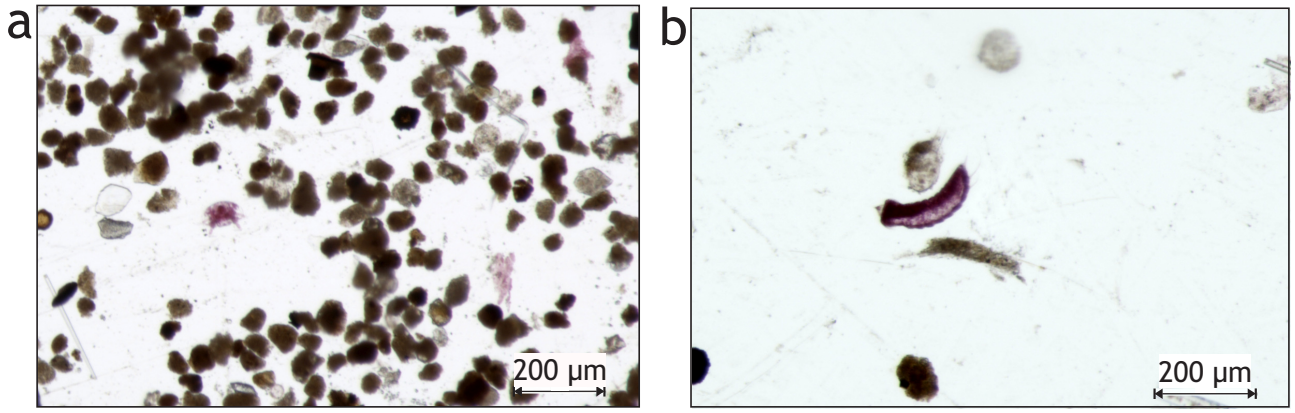

Figure 6. Stereomicroscope images of samples sieved through 32 μm (a) and 63 μm (b) sieves.

prehensiveness. Biomass estimates were barely affected by the use of the coarser mesh size.

4.1 Mesh size effects on abundance estimates

There are few studies comparing the proportions of meiofauna retained on different mesh sizes. Soltwedel et al. (2003) observed that the 32–63 μm fraction constituted 30–38% of all meiofauna individuals (i.e., those retained on a 32 μm sieve) in the Molloy Deep, Fram Strait in the Arctic (5561 m). Similarly, Schewe and Soltwedel (1999) reported that the 32–63 μm fraction accounted for 24 to 40% of meiobenthos in the deep central Arctic Ocean. In comparison to our results, the substantially higher proportion of the 32–63 μm fraction in these studies could be explained by the much greater water depths at which their samples were collected (5560 m and 864–4187 m, respectively). A higher proportion of smaller organisms with increasing water depth is a widely observed phenomenon (e.g., Danovaro et al., 2002; Schewe and Soltwedel, 1999; Zeng et al., 2017). Moreover, in both studies, the unicellular Foraminifera were included, whereas our study focused exclusively on metazoans. Including Foraminifera could increase the proportion of the 32–63 μm fraction.

Nematodes are the dominant taxon in metazoan meiofauna globally, often accounting for 80–95% of total abundance (Giere, 2009), which explains why many studies focus exclusively on this group (Baguley et al., 2004). In our material, 12 to 29% of nematodes passed through the 63 μm sieve. Comparable proportions were reported from abyssal NE Atlantic sites (22–26%; Vanreusel et al., 1995), the Fram Strait (24.5%; Soltwedel et al., 2003), and central Arctic Ocean sediments (20%; Schewe and Soltwedel, 1999). By contrast, Leduc et al. (2010) observed unexpectedly high proportions of small nematodes – 41% in the 0–5 cm layer and 51% in the 0–1 cm layer – on the highly productive Chatham Rise (near New Zealand; 1250 m depth). The environmental drivers shaping nematode body size along productivity or depth gradients remain poorly understood: some authors report smaller average sizes in deeper or less productive regions (e.g., Brown et al., 2001; Górska and Włodarska-Kowalczuk, 2017; Grzelak et al., 2020), whereas others detect no consistent relationship between the proportion of small-sized nematodes and such gradients (e.g., Schewe and Soltwedel, 1999; Vanreusel et al., 1995). These studies indicate that a combination of ecological and methodological factors may influence the observed patterns.

4.2 Mesh size effects on biomass estimates

Mesh size effects on biomass estimates were minimal; only 0.8 to 1.1% of the biomass of metazoan meiofauna passed through the 63 μm sieve. To our knowledge, no other studies have compared total meiofauna biomass retained on 32 μm and 63 μm sieves. The only existing comparison, conducted by Leduc et al. (2010), focused exclusively on nematodes and showed that nematode biomass estimated from samples sieved on a 32 μm sieve was only 5% higher than that estimated from a 63 μm sieve. We emphasize the importance of methodology in obtaining such estimates: in our study, all meiofauna individuals were measured, and biomass was calculated based on published equations on body dimensions. Accurate measurements of each individual require high-quality images where the entire organism is clearly visible and not obscured by sediment particles. Samples sieved on the 32 μm sieve contained considerably more fine particles than those sieved on the 63 μm sieve (Figure 6), which significantly increased the time needed for image acquisition and measurement of individuals. The negligible differences in biomass between samples sieved on different mesh sizes, combined with the substantial time savings achieved when using the 63 μm sieve, suggest that this coarser mesh is more efficient for meiofauna biomass estimation.

As nematodes are usually the dominant taxon in terms of abundance, meiofauna biomass estimations are often based solely on this group, with nematode biomass commonly assumed to represent the entire metazoan meiofauna biomass (e.g., Hughes and Gage, 2004; Tseitlin et

al., 2001). In the present study, however, we analyzed all taxonomic groups to obtain true biomass estimated for the total metazoan meiofauna and found that nematodes constituted only 11 to 22% of the total biomass. In the few earlier studies that also calculated biomass for all taxa, the estimates of the nematode proportion varied widely. In some cases, nematodes were found to dominate, comprising 50 to 90% of the total meiofauna biomass (Giere, 2009), with similarly high ranges reported by several authors, e.g., 42–78% on Chatham Rise (Berkenbusch et al., 2011), 41–62% in Svalbard fjord (Kotwicki et al., 2004), or 34–58% in the Aegean Sea (Lampadariou and Eleftheriou, 2018). In contrast, other studies have reported values more comparable to our findings. For example, Tietjen (1992) observed that in the deep sea, the relative contribution of nematodes to total meiofauna biomass ranged between 13 to 65%. Similarly, Danovaro et al. (1995) found that nematodes constituted only 14% of the total meiofauna biomass in the Mediterranean Sea, while Gooday et al. (1996) reported contributions of 19–24% in the Porcupine Seabight. These substantial differences in the relative contribution of nematodes to total metazoan meiofauna biomass highlight the need for caution when extrapolating nematode biomass to represent the entire community. Such extrapolations may be particularly misleading in environments where other taxa contribute significantly to total biomass or where community composition varies greatly. Therefore, when precise estimation of community biomass is required, e.g., for secondary production estimations or assessments of the role of meiofauna in carbon budgets, it is highly important to include all meiofaunal taxonomic groups or at least large taxa (i.e., Harpacticoida, Ostracoda) in biomass estimations. Comprehensive, taxon-inclusive approaches provide a more accurate and ecologically meaningful insight into meiofaunal community functioning.

4.3 Size spectra

Size is an easily measurable trait of animals that can be an effective and powerful tool for ecological comparisons across different assemblages (Peters, 1983). The size-based approach focuses on the distribution of biomass among community members, sorted into logarithmic intervals based on a measure of organism size, such as body mass, length, or equivalent spherical diameter (Sheldon et al., 1972). Biomass size spectra of communities have proven to be an efficient descriptor of ecosystem functioning, particularly with respect to productivity and energy flow. As patterns in benthic size spectra are increasingly explored in marine ecosystems, it is important to compare biomass distributions among size classes across different studies and geographical regions.

In the present study, we did not observe any significant differences in biomass or abundance distribution among size classes between the two meiofauna fractions (32–500 μm and 63–500 μm). Specifically, both fractions exhibited an identical range of size classes (from -11 to 5 size class) and showed the same positions of abundance and biomass peaks. This consistency suggests that, despite differences in mesh size, the overall structure of the size spectra remains robust. These findings are consistent with earlier observations by Tseitlin et al. (2001), who compared the logarithmic distribution of nematode volume among samples sieved on different mesh sizes and reported no significant differences between 32 and 63 μm sieves. We conclude that the 'sieving method' for size fractionation is imprecise. The finer sieve retains long and thin animals, such as nematodes, while the coarser sieve may retain small animals whose dimensions are extended through protruding body parts, such as harpacticoids, causing them to remain on the coarser sieve. Furthermore, the distribution of organisms among sieves depends not only on body size but also on the grain size composition of the sediment and the amount of detritus particles, which animals can attach to and, as a result, be retained on the coarser sieve.

5. Recommendations

Our comparison of meiofauna extraction efficiency between two sieves with a mesh diameter of 32 and 63 μm showed that the 32–500 μm fraction yielded approximately 8–21% higher abundance estimates than the 63–500 μm fraction. However, statistical tests revealed no significant differences in overall abundance and community composition between the two fractions. Likewise, the total biomass in the 32–500 μm fraction was only about 1% larger than in the 63–500 μm fraction. Therefore, we recommend including data derived from 63 μm sieving in large-scale meiofauna comparisons. In our view, results obtained with mesh sizes between 32 and 63 μm can be directly compared in a meaningful way. For muddy shelf sediments, we further recommend using a 63 μm sieve for meiofauna biomass estimation. Using a coarser sieve is more time-efficient, due to faster sample washing and a clearer view under the stereomicroscope, while at the same time, this mesh size does not substantially affect biomass estimation.

We also recommend estimating the biomass of the entire meiofauna assemblage, as nematodes do not always constitute the majority of metazoan meiofauna biomass. Their contribution may be as low as 20% of total metazoan biomass, implying large underestimation of meiofauna biomass when only nematodes are included. Analyses performed within this study indicate that abundance and biomass size spectra constructed for meiofauna data based on sieving on 32 μm and 63 μm can also be compared given there were no statistical differences in abundance or biomass distribution among size classes related to the sieve size. The range of size classes was also identical regardless of the sieve mesh size. However, because

our study was based on the materials collected on a shelf, more caution should be paid in the deep-sea studies, especially when differences occur in the lower end of the size spectrum.

Acknowledgements

This study was financially supported by project no 5226/Norway/2022/0 in the framework of Polish Ministry of Education and Science program PMW 2022–2023 and the Nansen Legacy project supported by the Research Council of Norway (project 276730).

Conflict of interest

None declared.

Supplementary material

Supplementary material associated with this article can be found here.

References

Aller, R.C., Aller, J.Y., 1992. *Meiofauna and solute transport in marine muds*. Limnol. Oceanogr. 37, 1018–1033. https://doi.org/10.4319/lo.1992.37.5.1018

Anderson, M.J., 2005. *PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance*. Department of Statistics, University of Auckland, New Zeland.

Baguley, J.G., Hyde, L.J., Montagna, P.A., 2004. *A semi-automated digital microphotographic approach to measure meiofaunal biomass*. Limnol. Oceanogr. Methods 2, 181–190. https://doi.org/10.4319/lom.2004.2.181

Berkenbusch, K., Probert, P.K., Nodder, S.D., 2011. Comparative biomass of sediment benthos across a depth transect, Chatham Rise, Southwest Pacific Ocean. Mar. Ecol. Prog. Ser. 425, 79–90. https://doi.org/10.3354/meps09014

Bessière, A., Nozais, C., Brugel, S., Demers, S., Desrosiers, G., 2007. *Metazoan meiofauna dynamics and pelagic-benthic coupling in the Southeastern Beaufort Sea, Arctic Ocean*. Polar Biol. 30, 1123–1135. https://doi.org/10.1007/s00300-007-0270-6

Bonaglia, S., Nascimento, F.J.A., Bartoli, M., Klawonn, I., Brüchert, V., 2014. *Meiofauna increases bacterial denitrification in marine sediments*. Nat. Commun. 5, 5133. https://doi.org/10.1038/ncomms6133

Brown, C.J., Lambshead, P.J.D., Smith, C.R., Hawkins, L.E., Farley, R., 2001. *Phytodetritus and the abundance and biomass of abyssal nematodes in the central, equatorial Pacific*. Deep Sea Res. Pt. I, 48, 555–565. https://doi.org/10.1016/S0967-0637(00)00049-2

Charrier, B.R., Ingels, J., Danielson, S.L., Mincks, S.L., 2023. *Infaunal community structure, diversity, and function in Pacific-Arctic shelf sediments: a comparison of meiofaunal- and macrofaunal-sized nematodes*. Mar. Ecol. Prog. Ser. 720, 95–116. https://doi.org/10.3354/meps14397

Danovaro, R., Della Croce, N., Eleftheriou, A., Fabiano, M., Papadopoulou, N., Smith, C., Tselepides, A., 1995. *Meiofauna of the deep Eastern Mediterranean Sea: distribution and abundance in relation to bacterial biomass, organic matter composition and other environmental factors*. Prog. Oceanogr. 36, 329–341.

Danovaro, R., Gambi, C., Della Croce, N., 2002. *Meiofauna hotspot in the Atacama Trench, eastern South Pacific Ocean*. Deep Sea Res. Pt. I, 49, 843–857. https://doi.org/10.1016/S0967-0637(01)00084-X

de Bovée, F., Soyer, J., Albert, P., 1974. *The importance of the mesh size for the extraction of the muddy bottom meiofauna*. Limnol. Oceanogr. 19, 350–354. https://doi.org/10.4319/lo.1974.19.2.0350

Elmgren, R., 1973. *Methods of sampling sublittoral soft bottom meiofauna*. OIKOS Suppl. 112–120.

Feller, R.J., Warwick, R.M., 1988. *Energetics*, [In:] *Introduction to the Study of Meiofauna*, Higgins, R.P., Thiel, H. (Eds.), Smithsonian Inst. Press, Washington D.C., 181–196.

Giere, O., 2009. *Meiobenthology: the microscopic motile fauna of aquatic sediments*. Springer, Berlin.

Gooday, A.J., Pfannkuche, O., Lambshead, P.J.D., 1996. *An apparent lack of response by metazoan meiofauna to phytodetritus deposition in the bathyal north-eastern Atlantic*. J. Mar. Biol. Assoc. U.K. 76, 297–310.

Górska, B., Soltwedel, T., Schewe, I., Włodarska-Kowalczuk, M., 2020. *Bathymetric trends in biomass size spectra, carbon demand, and production of Arctic benthos (76-5561 m, Fram Strait)*. Prog. Oceanogr. 186, 102370. https://doi.org/10.1016/j.pocean.2020.102370

Górska, B., Włodarska-Kowalczuk, M., 2017. *Food and disturbance effects on Arctic benthic biomass and production size spectra*. Prog. Oceanogr. 152, 50–61. https://doi.org/10.1016/j.pocean.2017.02.005

Grove, S.L., Probert, P.K., Berkenbusch, K., Nodder, S.D., 2006. *Distribution of bathyal meiofauna in the region of the Subtropical Front, Chatham Rise, south-west Pacific*. J. Exp. Mar. Biol. Ecol. 330, 342–355. https://doi.org/10.1016/j.jembe.2005.12.038

Grzelak, K., Gluchowska, M., Kędra, M., Błażewicz, M., 2020. *Nematode responses to an Arctic sea-ice regime: morphometric characteristics and biomass size spectra*. Mar. Environ. Res. 162. https://doi.org/10.1016/j.marenvres.2020.105181

Hughes, D.J., Gage, J.D., 2004. *Benthic metazoan biomass, community structure and bioturbation at three contrasting deep-water sites on the northwest European continental margin*. Prog. Oceanogr. 63, 29–55. https://doi.org/10.1016/j.pocean.2004.09.002

Ingole, B.S., Goltekar, R., Gonsalves, S., Ansari, Z.A., 2005. *Recovery of deep-sea meiofauna after artificial disturbance in the central indian basin*. Mar. Georesour. Geotec. 23, 253–266. https://doi.org/10.1080/10641190500446540

Kitahashi, T., Watanabe, H.K., Tsuchiya, M., Yamamoto, Hideyuki, Yamamoto, Hiroyuki, 2018. *A new method for acquiring images of meiobenthic images using the FlowCAM*. MethodsX 5, 1330–1335. https://doi.org/10.1016/j.mex.2018.10.012

Kotwicki, L., Szymelfenig, M., De Troch, M., Zajączkowski, M., 2004. *Distribution of meiofauna in Kongsfjorden, Spitsbergen*. Polar Biol. 27, 661–669. https://doi.org/10.1007/s00300-004-0625-1

Lampadariou, N., Eleftheriou, A., 2018. *Seasonal dynamics of meiofauna from the oligotrophic continental shelf of Crete (Aegean Sea, eastern Mediterranean)*. J. Exp. Mar. Biol. Ecol. 502, 91–104. https://doi.org/10.1016/j.jembe.2017.12.014

Leduc, D., Probert, P.K., Nodder, S.D., 2010. *Influence of mesh size and core penetration on estimates of deep-sea nematode abundance, biomass, and diversity*. Deep Sea Res. Pt. I, 57, 1354–1362. https://doi.org/10.1016/j.dsr.2010.06.005

Mazurkiewicz, M., Górska, B., Jankowska, E., Włodarska-Kowalczuk, M., 2016. *Assessment of nematode biomass in marine sediments: A semi-automated image analysis method*. Limnol. Oceanogr. Methods 14, 816–827. https://doi.org/10.1002/lom3.10128

Nascimento, F.J.A., Karlson, A.M.L., Näslund, J., Elmgren, R., 2011. *Diversity of larger consumers enhances interference competition effects on smaller competitors*. Oecologia 166, 337–347. https://doi.org/10.1007/s00442-010-1865-0

Peters, R., 1983. *The ecological implications of body size*. Cambridge Univ. Press, Cambridge.

Ricardo de Freitas, T., Hess, S., Renaud, P.E., Appleby, P., Alve, E., 2024. *Drivers of organic carbon distribution and accumulation in the northern Barents Sea*. Prog. Oceanogr. 225, 103286. https://doi.org/10.1016/j.pocean.2024.103286

Sautya, S., Gaikwad, S., Khokher, S., Pradhan, U.K., Chatterjee, S., Choudhury, A., Sahu, B., Attri, S., 2021. *Distribution Pattern of the Benthic Meiofaunal Community Along the Depth Gradient of the Western Indian Continental Margin, Including the OMZ and Abyssal Plain*. Front. Mar. Sci. 8, 1–17. https://doi.org/10.3389/fmars.2021.671444

Schewe, I., Soltwedel, T., 1999. *Deep-sea meiobenthos of the central Arctic Ocean: distribution patterns and size-structure under extreme oligotrophic conditions*. Vie Milieu 49, 79–92.

Schwinghamer, P., 1983. *Generating ecological hypotheses from biomass spectra using causal analysis: a benthic example*. Mar. Ecol. Prog. Ser. 13, 151–166.

Sheldon, R.W., Prakash, A., Sutcliffe, H., 1972. *The size distribution of particles in the Ocean*. Limnol. Oceanogr. 17, 327–340.

Soltwedel, T., Miljutina, M., Mokievsky, V., Thistle, D., Vopel, K., 2003. *The meiobenthos of the Molloy Deep (5 600 m), Fram Strait, Arctic Ocean*. Vie Milieu 53, 1–13.

Tachibana, K., Shimanaga, M., Langlet, D., Seike, K., Miyazaki, M., Yoshida, M., Nunoura, T., Nomaki, H., 2023. *Meiofauna in the southeastern Bering Sea: community composition and structuring environmental factors*. Front. Mar. Sci. 10, 1–11. https://doi.org/10.3389/fmars.2023.996380

The Nansen Legacy, 2025. *The Nansen Legacy Final Report*. Nansen Leg. Rep. Ser. https://doi.org/10.7557/nlrs.8041

Tietjen, J.H., 1992. *Abundance and biomass of metazoan meiobenthos in the deep sea*. [In:] *Deep-Sea Food Chains and the Global Carbon Cycle*, Rowe, G.T., Pariente, V. (Eds.), Springer, College Station, 45–62. https://doi.org/10.1007/978-94-011-2452-2_4

Tong, S.J.W., Gan, B.Q., Tan, K.S., 2022. *Community structure of deep-sea benthic metazoan meiofauna in the polymetallic nodule fields in the eastern Clarion-Clipperton Fracture Zone, Pacific Ocean*. Deep Sea Res. Pt. I, 188. https://doi.org/10.1016/j.dsr.2022.103847

Tseitlin, V.B., Mokievsky, V.O., Azovsky, A.I., Soltwedel, T., 2001. *The study of meiobenthos size structure with the sieving method (case study of the Arctic basin free-living Nematodes)*. Oceanology 41, 712–717.

Udalov, A.A., Azovsky, A.I., Mokievsky, V.O., 2005. *Depth-related pattern in nematode size: What does the depth itself really mean?* Prog. Oceanogr. 67, 1–23. https://doi.org/10.1016/j.pocean.2005.02.020

Vanreusel, A., Clough, L., Jacobsen, K., Ambrose, W., Ryheul, V., Herman, R., Vincx, M., 2000. *Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure*. Deep Sea Res. Pt. I, 47, 1855–1879. https://doi.org/10.1016/S0967-0637(00)00007-8

Vanreusel, A., Vincx, M., Bett, B.J., Rice, A.L., 1995. *Nematode biomass spectra at two abyssal sites in the NE Atlantic with a contrasting food supply*. Int. Rev. Hydrobiol. 80, 287–296.

Zeng, Q., Huang, D., Lin, R., Wang, J., 2017. *Deep-sea metazoan meiofauna from a polymetallic nodule area in the central Indian Ocean basin*. Mar. Biodivers. 48, 395–405. https://doi.org/10.1007/s12526-017-0778-0

Zeppilli, D., Sarrazin, J., Leduc, D., Arbizu, P.M., Fontaneto, D., Fontanier, C., Gooday, A.J., Kristensen, R.M., Ivanenko, V.N., Sørensen, M. V., Vanreusel, A., Thébault, J., Mea, M., Allio, N., Andro, T., Arvigo, A., Castrec, J., Danielo, M., Foulon, V., Fumeron, R., Hermabessiere, L., Hulot, V., James, T., Langonne-Augen, R., Le Bot, T., Long, M., Mahabror, D., Morel, Q., Pantalos, M., Pouplard, E., Rai-

mondeau, L., Rio-Cabello, A., Seite, S., Traisnel, G., Urvoy, K., Van Der Stegen, T., Weyand, M., Fernandes, D., 2015. *Is the meiofauna a good indicator for climate change and anthropogenic impacts?* Mar. Biodivers. 45, 505–535. https://doi.org/10.1007/s12526-015-0359-z