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MEIOFAUNA IN FRESHWATER ECOSYSTEMS

Review Paper

An overview of meiofaunal and nematode distribution patterns in lake ecosystems differing in their trophic state

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Abstract In the benthos of lakes, habitat size and structure as well as oxygen or resource availability can affect species distribution at local scales. By contrast, there is little knowledge about the mechanisms that determine the structure of benthic communities at larger scales. Here, we compiled data from the literature (23 studies monitoring 129 sites from 75 lakes located in central and northern Europe) to search for broad patterns in abundance, biomass, and community structure linked to lake trophic state (oligo-, meso-, or eutrophic), habitat features (hard vs. soft substrates), and water depth (littoral vs. profundal). The benthic meiofauna appeared much more abundant in the periphyton, and biomass was lower in oligotrophic lakes. Focusing on free-living nematodes, community structure differed markedly in hard vs soft substrates. Further, nematodes were especially dominant in profundal zones, where their diversity was significantly influenced by lake trophic state. In profundal zones of eutrophic lakes, nematode assemblages were less diverse and dominated by larger, mostly omnivorous or predacious taxa.

Keywords Biodiversity · Distribution · Invertebrates · Eutrophication · Biofilm · Profundal · Littoral · Lakes

Introduction

Lentic meiofauna (sensu Rundle et al., 2002) is very diverse and presents high spatial and temporal variability (Strayer, 1985; Tinson & Laybourn-Parry, 1986; Traunspurger, 1996a, b; Bergtold & Traunspurger, 2004; Michiels & Traunspurger, 2004, 2005; Schroeder et al., 2012b). This heterogeneous distribution is influenced by various factors such as carbon content in food, timing of algal bloom deposition, and daily vertical migration of micro-crustaceans through the water column (e.g., Nalepa & Quigley, 1985; Tinson & Laybourn-Parry, 1986; Goedkoop & Johnson, 1996). Large-scale responses to food availability may be estimated based on correlations of animal standing stocks with lake trophic state. This approach is particularly useful when direct evidences of resource utilization are lacking, as is often the case with minute benthic meiofaunal organisms (see Majdi

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et al., *this issue*). Generally, studies of lake trophic state and the effects of eutrophication have overlooked the meiofauna, focusing on the responses and patterns of benthic macroinvertebrate communities, especially in the littoral zones of lakes (e.g., Brodersen et al., 1998; Poikane et al., 2016).

However, several studies have highlighted the integral role of meiofauna in freshwater food webs (e.g., Schmid-Araya et al., 2002; Bergtold & Traunspurger, 2005; Kathol et al., 2011; Majdi et al., 2017; Weber et al., 2018), hence the structure of benthic meiofaunal communities may represent a useful bioindicator of lake trophic state (Ristau & Traunspurger, 2011; Schroeder et al., 2012a, b; Kazemi-Dinan et al., 2014). For example, comparing three lakes with different trophic status (oligo-, meso- and eutrophic), Schroeder et al. (2012b) found the highest meiofaunal abundances in the mesotrophic lake. Kurashov (2002) compared meio- and macrobenthic production in lakes differing in their trophic state and showed that meiofauna production was highest in the littoral of eutrophic lakes and was twice as high as the production of benthic macroinvertebrates in the shallow zone of a mesotrophic lake.

In terms of diversity, a peak of species richness, or at least that of benthic macroinvertebrates (e.g., Brodersen et al., 1998) and zooplankton (e.g., Dodson, 1992; Jeppesen et al., 2000; Barnett & Beisner, 2007), has generally been observed in oligotrophic or mesotrophic lakes. For example, by monitoring plankton communities in 18 lakes in Canada that differed in their phosphorus availability, Barnett & Beisner (2007) determined a strong negative correlation between lake trophic state and the functional (mostly trophic) diversity of crustacean zooplankton. According to those authors, the greater heterogeneity of phytoplankton (less dominated by cyanobacteria) under the most oligotrophic conditions increased the number of trophic niches available for the establishment of more diverse zooplankton communities. The existence of similar mechanisms has rarely been investigated for the benthic meiofauna, although Ristau & Traunspurger (2011) also found more nematode species and a higher diversity of feeding types in the sediments of oligo- and mesotrophic lakes in comparison to eutrophic lakes.

Many studies have demonstrated that micro-habitat features are important drivers of meiofaunal community structure (see Giere, 2009 and references therein). At the scale of meiofaunal organisms, the texture of a sediment grain, the presence of microbial colonies, and interstitial pore size are crucial features that shape the ability of individuals to access resources or escape stressors. The fact that meiofauna is systematically overlooked by limnologists is surprising, because these tiny organisms can reach considerable abundances, especially in some typical substrate–water interface habitats like the periphyton (or biofilm) coating hard substrates in the littoral zones of lakes. This was demonstrated by Schroeder et al. (2012b), finding up to 13 million individuals per m^2 in the periphyton coating the stones of Lake Erken (Sweden). The high abundance therein was mostly the result of the remarkable abundance of an algivorous nematode species, *Punctodora ratzeburgensis* (Linstow, 1876) (see in Schroeder et al., 2012a). Other studies have reported consistent positive correlations between periphytic biomass (or chlorophyll concentrations) and the abundance of meiofauna (e.g., Peters & Traunspurger, 2005; Gaudes et al., 2006; Bogut et al., 2009; Majdi et al., 2012a; Kazemi-Dinan et al., 2014; Neury-Ormanni et al., 2016). This suggests a strong trophic link between primary producers and the periphyton-dwelling meiofauna. This also suggests that the periphyton itself is a complex landscape and food web comprising meiofaunal grazers, filter feeders, as well as predators (Weitere et al., 2018).

The profundal zone of deep lakes is characterized by a constant temperature and absence of light, such that conditions are more stable than in the littoral or the littori-profundal zone (Silver et al., 2002; Traunspurger et al., 2012), but benthic consumers in the profundal are higly dependent on the input of sedimenting phytodetritus and other particulate organic matter from the pelagic. Limnologists have always been curious about the “bottom fauna” of freshwater lakes but again, the ecology of benthic macroinvertebrates was much more studied than that of the meiofauna (but see, e.g., Goedkoop & Johnson, 1996; Traunspurger, 1996b; Bergtold & Traunspurger, 2004, 2005). Profundal meiofauna can assimilate sedimenting algal blooms at a rate comparable to that of benthic macroinvertebrates and bacteria (Goedkoop & Johnsson 1996). We may thus expect some general patterns, for example, lake trophic state may influence the diversity and functional structure of profundal meiofaunal communities, because greater algal blooms in eutrophic lakes may allow longer trophic chains in the profundal characterized by the existence of larger, predacious taxa as observed by Särkkä (1993, 1996).

In this study, we used meiofauna as a model community in a literature-based analysis aimed at determining how the abundance, biomass, and structure of meiofaunal communities respond to lake trophic state (oligo-, meso- or eutrophic), habitat features (hard vs. soft substrates), and water depth (littoral vs. profundal). Although we expect high variability, we may also detect some broad patterns (e.g., higher meiofaunal abundances in hard substrates, lower meiofaunal biomass in oligotrophic lakes). Focusing on nematode assemblages, we further expect to detect relationships between nematode diversity and lake trophic state and/or with habitat features.

Methods

Literature search

The initial literature search was based on the broad keywords (meiofauna OR meiobenthos AND freshwater OR lake OR reservoir) and was performed using the software *publish or perish* (Harzing, 2007) with the literature databases Google Scholar® and ISI Web of Science®, which yielded 510 and 427 studies, respectively. The last literature search was performed on November 26, 2018. Studies were screened to confirm that they dealt with meiofaunal organisms in lentic freshwater ecosystems (lakes or reservoirs); studies reporting meiofauna in very small water bodies (< 1 Ha, e.g., ponds) were excluded from the analysis. We also cross-checked the literature list with studies cited in the books of Rundle et al. (2002) and Eyualem-Abebe et al. (2006).

First screening yielded a list of 88 studies, we then categorized the water bodies according (1) to their trophic status (oligo-, meso-, eutrophic), (2) to the habitat (hard or soft substrates) and depth (littoral or profundal) of the sampling, and (3) to the methodology used (sampling device, mesh size used for sieving). To facilitate comparisons, we considered only studies reporting accurately the characteristics of the sampling site and using a mesh size < 50 µm. Since nematodes are usually a dominant meiofaunal group and one of the phylum the most commonly identified to genus or species level in the literature, we prioritized studies reporting genus- or species-level analysis of nematode assemblages. This constrained the final list of studies included in our literature analysis to 23 (see Table S1 in supplementary material).

Site characteristics, methodology used, and data extraction

From the 23 selected studies, meiofaunal communities from 75 lakes were available. The lakes differed in size (from 1 to 59 200 Ha) and were mostly distributed in central and northern Europe. Some lakes were sampled several times or at different locations, resulting in 129 average site values. Eutrophic conditions were represented by 41 sites, mesotrophic conditions by 37 sites, and oligotrophic conditions by 51 sites (Table S1). Ninety-three sites were identified as soft substrates (sediments), 36 as hard substrates (periphyton on artificial substrates, stones, or macrophyte stems), and 24 sites were situated in the profundal zone.

Sediment samples were typically collected using corers, and periphyton samples using brush samplers, most studies used mesh sizes between 30 and 45 µm (Table S1). Fauna was extracted from sediments using quantitative flotation methods (e.g., Ludox flotation), whereas the periphyton was either directly processed without extraction or also extracted using flotation methods. In most cases, the samples were stained, preserved in 4% formaldehyde, counted, and mounted on slides for species identification.

In the included studies, we searched for mean abundances (standardized as individuals (ind.) 10 cm^{-2}) and biomass (µg Wet Weight 10 cm^{-2}, using a dry:wet ratio of 0.25 for conversion, whenever necessary). Most studies reported the abundances of nematode genera (Table S2). We also compiled data on nematode species richness (S), Shannon's diversity (H), and feeding-type composition (deposit feeders, epistrate feeders, suction feeders, and chewers; after the classification of Traunspurger 1997a).

Statistical analyses

Information on nematode feeding types was synthesized by calculating the index of trophic diversity (ITD), defined by Heip et al. (1985) as $\mathrm{ITD} = 1 - (\Sigma\theta^2)$, where θ is the relative contribution of each of the four feeding types. Thus, ITD = 0.75 if all four feeding types contribute 25% each (balanced trophic diversity), and 0 if only one feeding type makes up 100% of the community (unbalanced trophic diversity). General lineal models (GLMs) of the negative-binomial family were used to test for correlations between abundance, biomass, diversity, and lake trophic state (oligo-, meso-, or eutrophic), habitat features (hard vs. soft substrates), and water depth (littoral vs. profundal), and their interactions. The effect of lake trophic state on nematode community structure was tested by partitioning the sums of squares of Bray–Curtis distances using a permutational analysis of variance (PERMANOVA, 9999 permutations, 'adonis' function) after Anderson (2001). The multivariate homogeneity of group dispersion was initially checked using PERMDISP2 (Anderson, 2006), a multivariate analogue of Levene's test. Non-metric multidimensional scaling (nMDS) based on Hellinger-transformed abundance data and Bray–Curtis distances was used to ordinate sites and genera scores in a bi-dimensional space ('metaMDS' function). The significance of genus-site group associations was tested in a multilevel pattern analysis ('multipatt' function, 9999 permutations; Cáceres & Legendre, 2009) using the nematode genera dataset. All statistical analysis were performed with R (R Development Core Team, 2018), using the packages *vegan* and *indicspecies*.

Results

Abundance and biomass

Overall, abundance and biomass values reported in the literature varied considerably (Table 1). Nevertheless, the abundance of meiofauna was significantly lower in soft (usually < 1000 ind. 10 cm^{-2}; Fig. 1A) compared to hard substrates (GLM, $t = -2.94$, $P = 0.004$). In the soft substrates of the littoral zones of lakes, meiofaunal biomass was significantly lower in oligotrophic lakes (Fig. 1B) compared to eutrophic lakes (GLM, $t = -2.65$, $P = 0.013$).

Community structure

Nematodes were the numerically dominant group of the meiofauna (Table 1). Hence, nematode abundance was also significantly lower in soft compared to hard substrates (Fig. 2A; GLM, $t = -3.00$, $P = 0.003$), and it was also significantly lower in profundal compared to littoral zones (Fig. 2B; GLM, $t = -4.59$, $P < 0.001$). Despite the very high abundances attained by nematodes in the periphyton of some eutrophic lakes, the only significant effect of trophic state was a crossed interaction with profundal (GLM, $t = 3.12$, $P = 0.002$): Nematode abundances being significantly higher in oligotrophic lakes, but only in the profundal zone (Fig. 2A). Rotifers were the second most abundant group but their contribution to overall biomass was fairly minor (Table 1), and no significant trend was detected. The abundance of micro-crustaceans (comprising harpacticoid copepods, ostracods, and cladocers) was also extremely variable. Generally, these organisms represented $\leq 20\%$ of the numerical stocks. Nevertheless, micro-crustaceans and oligochaetes accounted for a large share of meiofaunal biomass (Table 1), but no significant trend was detected.

Taxonomic and functional diversity of nematode assemblages

We examined the effects of substrate, depth, and trophic state on nematode species richness, Shannon's diversity, and trophic diversity (Table 2). The number of nematode species in the sediment was, on average, twice as high as in the periphyton (Table 2; Fig. 3A; GLM, $t = 2.20$, $P = 0.029$). Nematode species richness in littoral sediment was remarkably high, as shown by the clear differences between littoral and profundal zones (Table 2; Fig. 3B; GLM, $t = -6.21$, $P < 0.001$). Trophic status had an effect on species richness through a crossed interaction with water depth (GLM, $t = 2.57$, $P = 0.01$); namely, species richness was higher in oligotrophic lakes but this relationship was significant only in the profundal zone (on average, 20.4 species in the oligotrophic vs. 6.7 in the eutrophic profundal; Table 2). Shannon's diversity index was also lower in the profundal zone of eutrophic lakes (Fig. 3C,D; GLM, $t = -2.24$, $P = 0.027$). The index of trophic diversity (ITD) was also very low in the profundal zone of eutrophic lakes (Fig. 3F; GLM, $t = 4.08$, $P < 0.001$) indicating pretty uneven distribution of feeding types (Fig. 3E, F). This result can probably be attributed to the very high proportion of chewers (up to 63% on average, Table 2)

Table 1 Composition, abundances, and biomass of the permanent meiobenthos in the littoral zones of a selection of lakes

Standing stocks	Hard substrates (periphyton, epiphyton)						Soft substrates (fine sand, mud)					
	Eutrophic		Mesotrophic		Oligotrophic		Eutrophic		Mesotrophic		Oligotrophic	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Biomass (µg wet weight 10 cm^{-2})												
Nematodes	800.0		920.0		400.0		1040.3	1659.5	539.9	357.2	182.9	196.7
Crustaceans	1680.0		1480.0		600.0		789.3	906.3	470.0	263.0	432.2	330.4
Rotifers	200.0		400.0		120.0		25.8	33.4	14.0	2.8	5.0	5.8
Tardigrades	120.0		40.0		40.0		1.3				55.4	70.5
Oligochaetes	800.0		920.0		80.0		1701.0	1991.6	750.0	347.9	554.5	518.9
Abundance (individuals 10 cm^{-2})												
Nematodes	955.0	1051.6	672.7	624.4	710.8	536.2	212.5	323.4	116.3	87.1	254.9	392.8
Crustaceans	154.0	135.7	110.1	120.3	84.7	81.9	25.1	39.3	22.7	23.3	101.7	160.2
Rotifers	304.7	220.0	285.0	329.9	234.3	240.6	186.8	261.3	41.8	20.4	166.2	239.6
Tardigrades	280.0		230.0		20.0		17.1	23.6	7.1	9.0	205.2	408.5
Oligochaetes	70.0		240.0		30.0		48.7	95.4	25.3	27.4	33.1	35.3

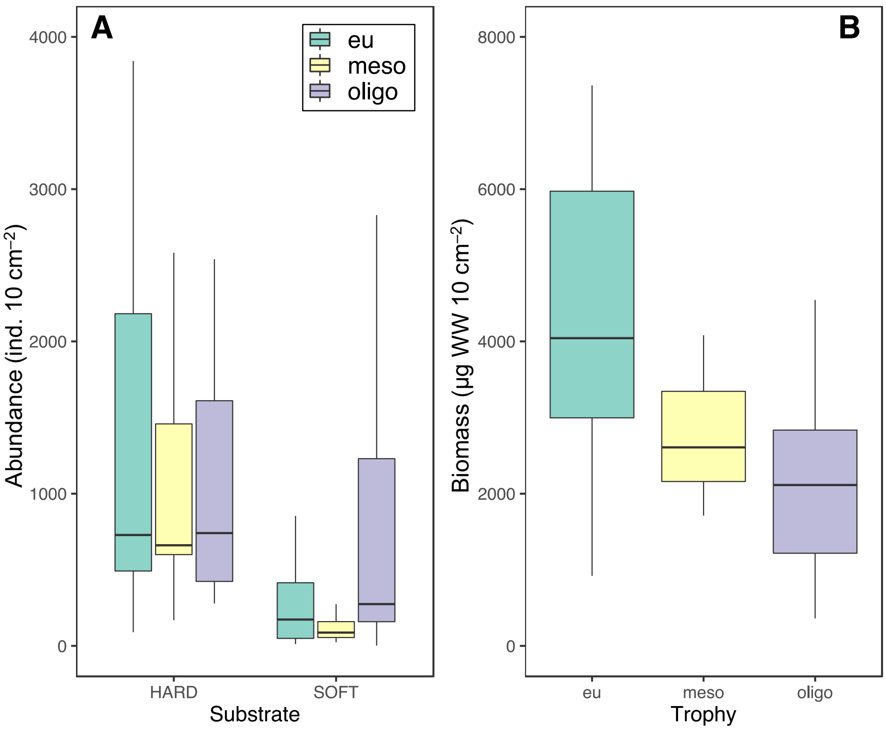

Fig. 1 Total **A** Abundance and **B** biomass of the meiobenthos in a selection of lakes. Values are the medians; the boxes and whiskers show the interquartile intervals. eu: eutrophic lakes, meso: mesotrophic lakes, oligo: oligotrophic lakes

found in the profundal zone of eutrophic lakes. The ITD was also generally higher in sediments than in the periphyton (Table 2, Fig. 3E; GLM, $t = 2.91$, $P = 0.003$), attributable to a higher proportion of deposit feeders in the latter (Table 2, Fig. 4; GLM, $t = 2.05$, $P = 0.04$). In oligotrophic lakes, the proportion of deposit feeders in soft substrates was higher (GLM, $t = -3.11$, $P = 0.002$), whereas the proportion

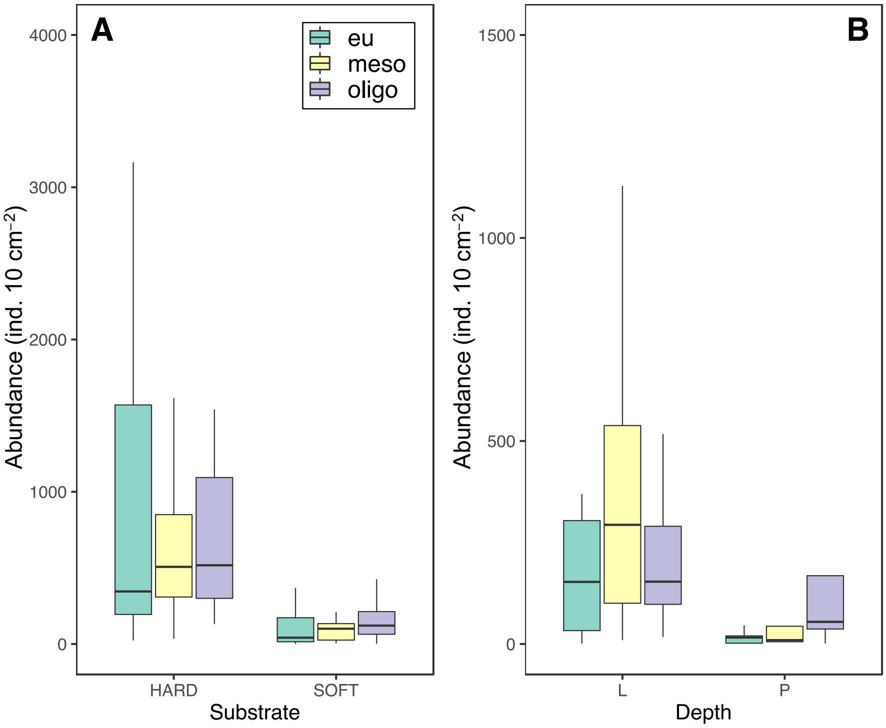

Fig. 2 Abundance of nematodes in a selection of lakes differing in their trophic state. Nematode densities are shown across **A** substrates and **B** depth zones (L: littoral, P: profundal). Values are the medians; the boxes and whiskers show the interquartile intervals. eu: eutrophic lakes, meso: mesotrophic lakes, oligo: oligotrophic lakes

of chewers (i.e., larger omnivores and predators) was lower regardless of the substrate (GLM, $t = 2.89$, $P = 0.004$; Fig. 4).

We also observed a negative correlation between the proportions of deposit feeders vs. chewers ($F_{1,106} = 63$, adj-$R^2 = 0.37$, $P < 0.001$; Fig. 5). The proportion of epistrate feeders, by contrast, was variable (Table 2) without showing any clear pattern (Fig. 4). Suction feeders were rarely found and there was no significant trend in their distribution.

Distribution of nematode genera

Bray–Curtis distances were homogeneously distributed across trophic status and substrate types (PERMDISP2, for trophy: $F_{2,127} = 14.78$, $P = 0.58$; for substrate $F_{1,128} = 2.31$, $P = 0.13$), but not between littoral and profundal ($P < 0.001$), probably due to the smaller number of samples in the profundal. Thus, the homogeneous multivariate distribution of distances-to-centroids allowed to use a PERMANOVA only with trophic status and substrate as factors. Both trophic status and substrate had a significant effect on the structure of nematode genera ($\text{PERMANOVA}_{\text{trophy}}$, $F_{2,127} = 8.98$, $P < 0.001$; $\text{PERMANOVA}_{\text{substrate}}$, $F_{1,128} = 27.32$, $P < 0.001$). The nMDS allowed distinguishing the genera most associated with a specific trophic status or substrate (genera close to centroids) (Fig. 6).

A multilevel pattern analysis identified five genera significantly associated with hard substrates, *Crocodorylaimus*, *Chromadorina*, *Rhabdolaimus*, *Punctodora*, and *Epidorylaimus* (group-stat > 0.59, $P < 0.001$), and four genera significantly associated with soft substrates, *Monhystera*, *Ethmolaimus*, *Ironus*, and *Theristus* (group-stat > 0.44, $P < 0.011$). When considering trophic state as factor, genera associated with a specific trophic state condition were less distinct, but still, the genus *Prismatolaimus* appeared significantly associated with oligotrophic lakes (group-stat $= 0.57$, $P = 0.012$), the genera *Chromadorina* and *Punctodora* were significantly associated with mesotrophic lakes (group-stat > 0.53, $P < 0.03$), and the genera *Dorylaimus* and *Tobrilus* were significantly associated with eutrophic lakes (group-stat > 0.63, $P < 0.005$).

Table 2 Proportion of feeding types (DF: deposit feeders, EF: epistrate feeders, C: chewers, SF: suction feeders), index of trophic diversity (ITD), species richness (S), and Shannon's diversity (H) of the nematode communities found on different substrates in a selection of eutrophic, mesotrophic, and oligotrophic lakes

Nematode community index	Littoral hard substrates						Littoral soft substrates						Profundal soft substrates					
	Eutrophic		Mesotrophic		Oligotrophic		Eutrophic		Mesotrophic		Oligotrophic		Eutrophic		Mesotrophic		Oligotrophic	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Feeding type (%)																		
DF	51.0	30.1	63.3	26.6	60.6	17.2	33.3	17.5	33.1	23.3	54.2	20.3	25.1	27.1	54.5	19.1	44.7	24.9
EF	32.3	31.1	21.0	26.7	22.6	16.2	15.2	14.1	31.2	21.0	20.0	15.7	13.0	13.4	25.0		18.3	10.1
C	7.9	6.2	3.7	5.5	0.2	0.6	34.1	15.3	26.7	14.7	17.1	13.0	63.4	31.1	21.0	7.1	36.1	12.6
SF	8.7	6.3	12.1	13.5	16.6	8.2	17.0	16.7	6.6	5.4	8.6	9.6					1.2	1.1
Diversity index																		
ITD	0.4	0.1	0.4	0.2	0.5	0.1	0.6	0.1	0.6	0.1	0.5	0.1	0.3	0.2	0.6	0.1	0.6	0.1
S	21.1	10.7	14.6	7.1	17.9	5.9	35.5	31.0	37.9	15.5	46.1	20.1	6.7	5.0	11.5	1.9	20.4	15.3
H	2.1	0.6	2.1	0.6	2.1	0.5	1.7	0.5	2.5	0.4	2.1	0.6	1.2	0.7	2.1	0.1	2.4	0.2

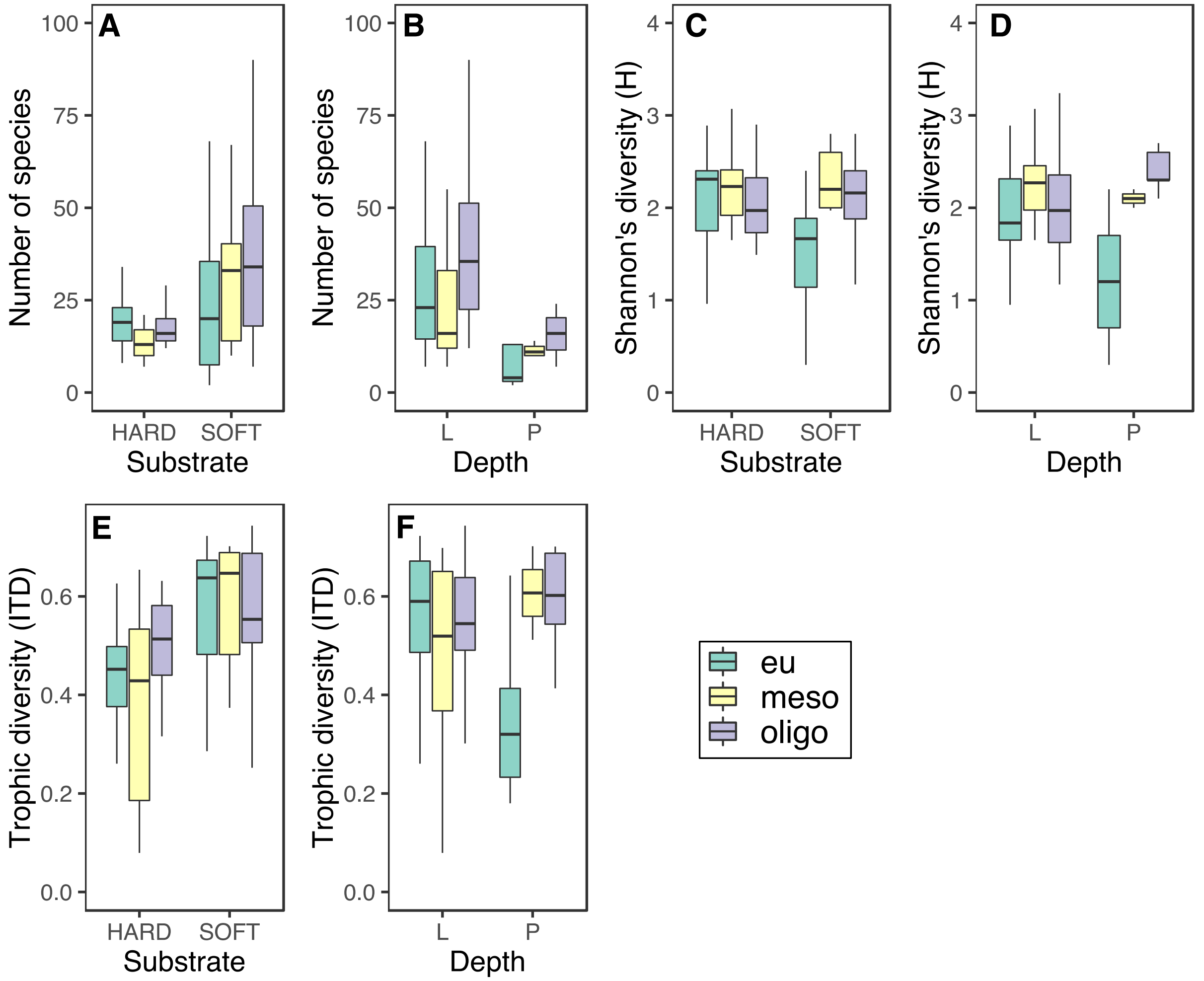

Fig. 3 **A**, **B** Species richness, **C**, **D** Shannon's diversity, and **E**, **F** index of trophic diversity of nematodes in a selection of lakes differing in their trophic state. The data are presented with respect to substrate and depth zone (L: littoral, P: profundal). Values are the medians; the boxes and whiskers show the interquartile intervals. eu: eutrophic lakes, meso: mesotrophic lakes, oligo: oligotrophic lakes

Discussion

Responses to micro-habitat type

Overall, abundance patterns were largely influenced by nematodes confirming the numerical importance of free-living nematodes in benthic ecosystems (e.g., Pennak, 1988; Traunspurger, 2000, 2002). Nematodes could reach extremely high abundances in the periphyton growing on hard substrates (e.g., Traunspurger, 2002; Schroeder et al., 2012a), as we observed in our analysis, but other meiofaunal groups like rotifers also tended to reach remarkable abundances in the periphyton in comparison to soft substrates. Thus our results mostly stressed that meiofauna abundance was higher in hard vs. soft substrates, providing further evidence that the periphyton is a hotspot of life in lakes (Vadeboncoeur & Steinman, 2002). Potential rationales are (1) Periphyton is a productive interface ecosystem offering high-quality basal resources (e.g., diatoms) to micrograzers like nematodes and rotifers (Majdi et al., 2012b, c; Estifanos et al., 2013). (2) Within the periphyton, microbial colonies create mucilaginous, canopy-like structures, or intricated surfaces that may provide refuges for small animals against predation or hydrodynamics. (3) At least in littoral zones, periphytic filaments can be agitated by waves so that

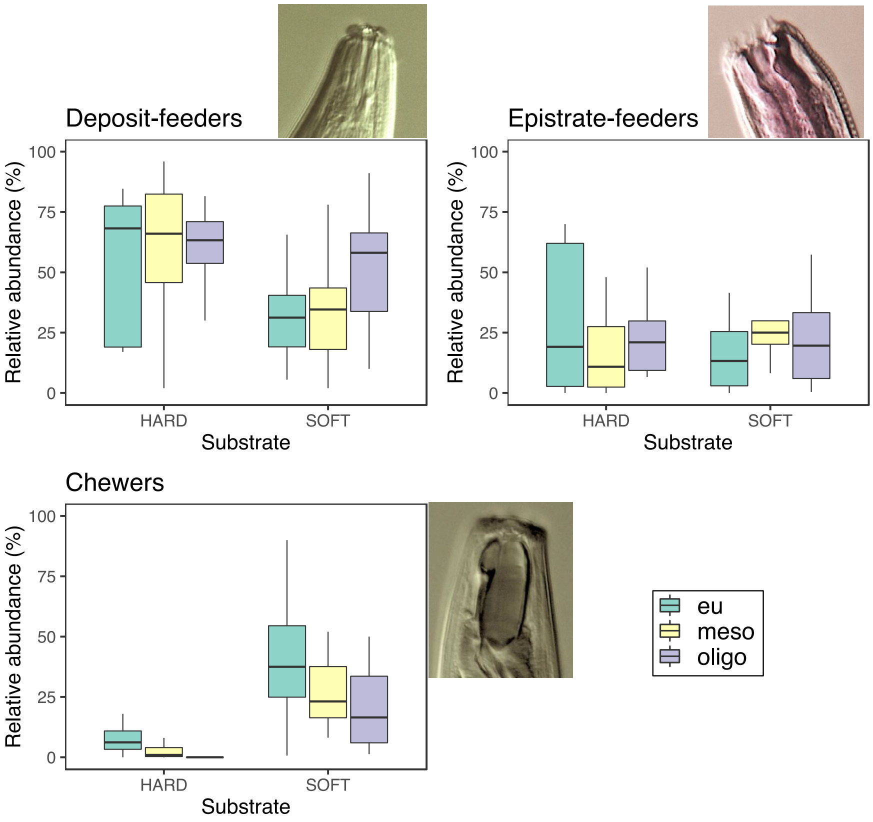

Fig. 4 Relative abundances of the main nematode feeding types across substrates in a selection of lakes differing in their trophic state. Values are the medians; the boxes and whiskers show the interquartile intervals. eu: eutrophic lakes, meso: mesotrophic lakes, oligo: oligotrophic lakes

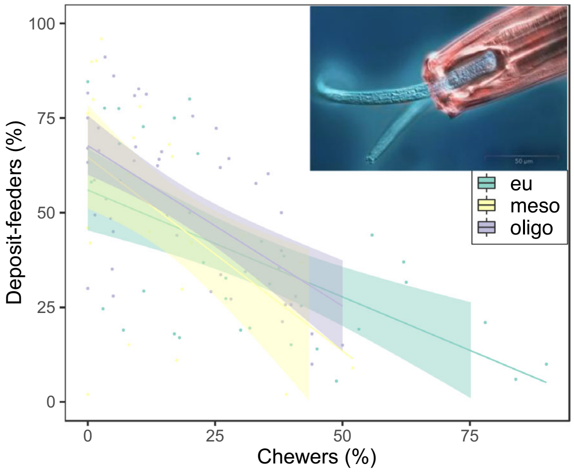

Fig. 5 Relationship between the relative abundance of deposit-feeding nematodes (bacterivores) and the relative abundance of chewers (predatory nematodes) in a selection of lakes differing in their trophic state. Lines ± 95% confidence intervals show the results of the fitted linear model. eu: eutrophic lakes, meso: mesotrophic lakes, oligo: oligotrophic lakes. The picture shows *Prionchulus* sp. feeding on *Teratocephalus* sp.

nutrient fluxes and oxygen availability gradients are probably less limiting for the fauna and flora than in muddy soft bottoms.

Indeed, because the periphyton may also be detached by excessive hydrodynamics or overgrazed by fishes and benthic macroinvertebrates, the periphytic meiofauna must be able to resist or avoid those stresses, for example, using attachment structures or sticky secretions providing resistance against wave shear stress, or by swimming out the periphyton. It has been shown that nematodes from the family Chromadoridae (to which the genera *Punctodora* and *Chromadorina* belong) secrete sticky mucus trails that they use to stay attached to hard surfaces (e.g., Meschkat, 1934; Croll & Zullini, 1972). Rotifers also possess adhesive glands and are generally good swimmers showing an epi-benthic or even a bentho-pelagic lifestyle (Ricci & Balsamo, 2000; Kathol et al., 2011), which may explain their remarkable abundances especially during the early steps of the ecological succession in the periphyton (Peters et al., 2007; Majdi et al. 2012a).

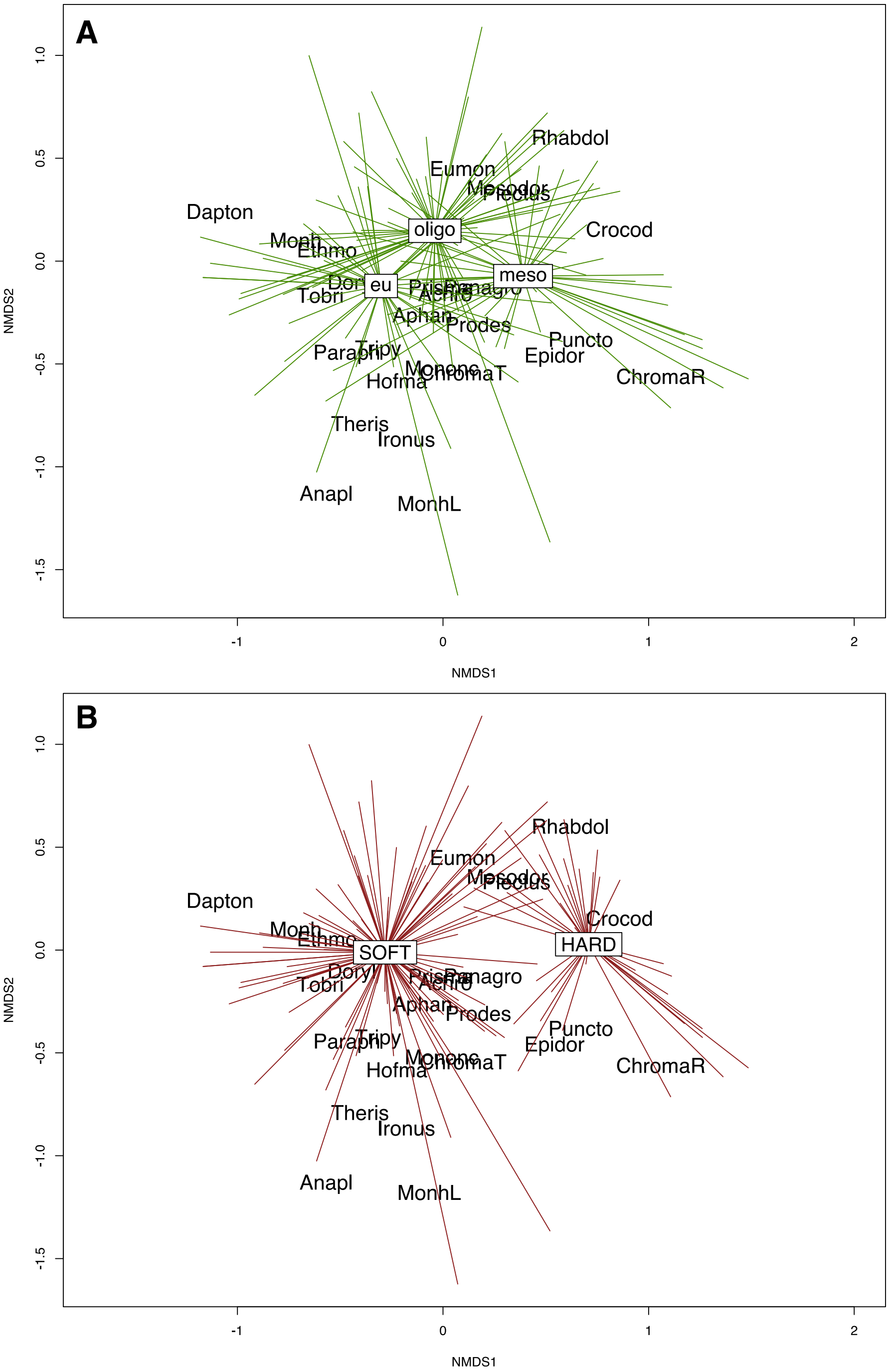

Fig. 6 Non-metric multidimensional scaling (nMDS) of the Bray–Curtis similarities of nematode genera structure across samples taken from a selection of lakes. Stress value = 0.19. Nematode genera are ordinated on the biplot; ‘spider web’ extremities show samples, and the centroids of the groups they belong. **A** Samples grouped by lake trophic status, **B** Samples grouped by habitat type. Nematode abbreviations are in Table S2

Effect of lake trophic status

One of the hypotheses often put forward in limnology to link lake trophic state with community structure is the basal productivity hypothesis (see e.g., Pimm, 2002). This hypothesis states that food chain length may be contingent upon the availability of basal resources because there are considerable losses of energy between each trophic level. In our analysis, we observed a lower biomass of meiofauna in oligotrophic lakes in comparison to eutrophic lakes. This difference was probably the result of lower prevalence of large omnivorous and predacious nematodes in oligotrophic lakes, and although it was not significant in our study, relatively large meiofaunal organisms like oligochaetes and micro-crustaceans also tended to be less abundant in oligotrophic lakes.

The determination of nematode feeding-type composition provides insights into their position in food chains (Traunspurger, 1997a; Majdi & Traunspurger, 2015). One finding of our study was the positive correlation between the proportion of larger omnivorous or predatory nematodes and lake trophic status. This was the case for both the periphyton and the sediment and this result is consistent with results of field studies (Wu et al., 2004; Ristau & Traunspurger, 2011). Similarly, in a long-term sediment microcosm experiment involving different nutrient levels, Ristau et al. (2013) found an increasing prevalence of omnivores and predators (especially *Ironus*) from meso- to eutrophic conditions. Goedkoop & Johnsson (1996) observed that phytoplankton bloom deposition is coupled to the abundances of benthic meiofauna, and Kurashov (2002) showed that the greater abundances of phyto- and bacterioplankton may help to sustain larger standing stocks of meiofauna in the sediments of eutrophic lakes. Eutrophic lakes thus offer a greater amount of resources for the meiofauna, explaining the ability of large omnivorous or predacious taxa to reach higher abundances. Large nematode species also generally show longer life spans and K-strategies so they might benefit from the stability brought by the accumulation of a greater amount of resources.

In terms of diversity, we observed a lower diversity of nematodes in the sediment of eutrophic lakes in comparison to oligotrophic lakes, which is also in line with the results of field studies (Wu et al., 2004; Ristau & Traunspurger, 2011). Nevertheless, we found considerable variation between lakes and we did not observe such pattern in the periphyton. The causes explaining those two observations are complex, and would probably need further investigations both through further field comparisons and laboratory experiments. Nevertheless, some rationales may be put forward: For example, a higher number of species in oligotrophic environments may be explained by (1) a greater heterogeneity of trophic niches, (2) a lower degree of competitive exclusion due to predation or to the dominance of single-resource specialists. Despite higher abundances, the nematode assemblages on hard substrates were remarkably less diverse than in soft substrates, so (3) the effects of trophic state might be less obvious in the periphyton simply because there are fewer species.

Patterns in the profundal zone

One result of our analysis was that in comparison to the littoral, the meiofauna community in the profundal showed lower abundances, and a lower diversity of nematode taxa and feeding types. Unfortunately, a comparison of hard-substrate communities between the littoral and the profundal zones of lakes was not possible because, so far, there is no study reporting meiofaunal abundances, biomasses, or diversity from profundal hard substrates. The fact that diversity was lower in the profundal in comparison to the littoral is in agreement with broad patterns in limnology, for example, $> 93\%$ of all species in large lakes are restricted to the littoral zone (Vadeboncoeur et al., 2011). The direct availability of phototrophic organisms as well as riverine inputs of organic material and greater wave disturbance regime (Witthöft-Mühlmann et al., 2006; Kreuzinger-Janik et al., 2015) are among reasons explaining why so many species of nematodes can coexist in the littoral in comparison to the profundal. In the profundal zone, nematodes are by far the most abundant metazoans (Holopainen & Paasivirta, 1977; Eyualem-Abebe et al., 2006), followed by rotifers, crustaceans, and oligochaetes. The composition and abundance of meiofauna in the profundal zone seems to be controlled by oxygen level, grain size, and water depth (e.g., Strayer, 1985; Särkkä, 1995; Traunspurger, 1996b; Silver et al., 2002; Giere, 2009). The latter complicates comparisons of the profundal communities of different lakes because the profundal zone is defined not by depth but by the absence of light. However, most studies have found a reduction in diversity with increasing depth (Särkkä, 1993; Traunspurger, 1996b; Kurashov, 2002) and studies comparing the profundal and the littoral within the same lake have generally found a lower total meiofaunal abundance in the former. Nevertheless, meiofaunal biomass, especially that of crustaceans and oligochaetes, in the profundal zone still can reach relatively high values (Särkkä & Paasivirta, 1972; Särkkä, 1995).

We found that nematode species richness was distinctly lower in the profundal than in the littoral zone. In the profundal zone, chewers are the dominant feeding type, followed by deposit feeders. The dominant genera in the profundal zone are *Tobrilus* (especially *Tobrilus gracilis* Bastian, 1865), *Eutobrilus* (mainly *Eutobrilus medius* Schneider, 1916), and *Eumonhystera* (mainly *Eumonhystera filiformis* Bastian, 1865 and *E. longicaudatula* Gerlach & Riemann, 1973) but species from the genera *Monhystera*, *Ironus*, and *Tripyla* are also typical representatives of the profundal nematode community (Traunspurger, 1996c, 1997b). The relatively stable conditions in the profundal may be thought to promote species diversity, but some parameters can strongly limit the ability of species to colonize those harsh habitats. Depending on the trophic state of the lake, variations of dissolved oxygen and sedimentation of low-quality food are a major issue for the profundal meiofauna (Särkkä, 1993, 1994, 1996; Goedkoop & Johnsson, 1996; Traunspurger et al., 2012). Because meiofaunal abundance responds to the quality and spatial distribution of organic matter (e.g., Boulton et al., 2002, Traunspurger et al., 2012), the nutrient supply is presumably of crucial importance for the distribution of meiofaunal species in the profundal zone. Recent laboratory research has shown that a wide range of biotic factors, including intra- and interspecific competition, diet switching, and predation, have the potential to affect the diversity and the structure of meiofaunal communities (e.g., Michiels & Traunspurger, 2003; Moens et al., 2006; Traunspurger et al., 2006; Hohberg & Traunspurger, 2009; Weber & Traunspurger, 2013, 2015; Weber et al., 2018; Gansfort et al., 2018). Our knowledge of the influence of those biotic factors in the field, and *a fortiori* in the profundal, is minimal and further dedicated studies would probably help to understand the drivers of species turnover in environmentally stable ecosystems like the profundal zone of lakes.

Conclusion and perspectives

Overall, our survey of the literature showed a large variability of the standing stocks and composition of the meiofauna across lakes reflecting the patchy and dynamic nature of meiofaunal assemblages as well as the fact that every lake is a unique habitat that combines many different abiotic (e.g., grain size, oxygen content, pollution) and biotic (e.g., predators, competition) factors that in turn may strongly influence community structure. For these reasons, the patterns emerging from our study should be interpreted with caution, and we encourage further research to build stronger evidences out of larger datasets, and ultimately gain a better mechanistic understanding of benthic meiofaunal communities.

Despite the considerable variability across the lakes in our study, our results suggested a link between lake trophic state and the functional structure of meiofaunal communities, as especially evidenced by the taxonomic and feeding-type composition of nematode assemblages. Micro-habitat features also had a strong effect, and communities dwelling in the periphyton on hard substrates appeared quite different from those dwelling on soft substrates. Indeed, our knowledge of the ecology of lentic meiofauna is far from being comparable to that of benthic macroinvertebrates or fishes and further studies are urgently needed to assess the relationship between small-scale biotic interactions and the larger-scale structure of communities and ecosystem functions.

Some questions meriting investigation: (1) Are periphyton-dwelling meiofauna consumed indirectly, or selected as a source of essential compounds by different types of periphyton grazers, such as fish juveniles and snails? (2) How do riparian vegetation and land-use affect the diversity of littoral meiofauna in a context of increasing anthropogenic pressure on lake shores? (3) How meiofauna dwelling on muddy substrates cope with anoxic events? (4) How far is meiofauna involved in the uptake and trophic transfer of chemo-autotrophic microbes (e.g., methanotrophic bacteria)? (5) Are meiofauna truly ubiquists and stochastically distributed so that the same species assemblages may be found worldwide in some comparable, mostly invariant biotopes, like the profundal zones of ancient lakes?

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