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Review Paper

Examining the diet of meiofauna: a critical review of methodologies

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Abstract Meiofaunal organisms are diverse, and so is their diet comprising bacteria, fungi, micro-algae, flagellates, ciliates, and other meiofauna. Studies have inferred diet from correlative evidences, observations of feeding or gut contents. Incubation experiments have also helped to link meiofauna's role to microbially mediated ecosystem processes, reporting in most cases beneficial effects on microbial activity. Nevertheless, our knowledge of meiofauna's trophic ecology still lags far behind that of other aquatic fauna (i.e. zooplankton, macroinvertebrates, vertebrates), probably because the small-size and the cryptic nature of the meiofauna becomes an issue when it comes to detect their isotopic or lipid composition. Here, we provide a critical review of diverse methodologies used while examining meiofaunal diets. Observation of feeding, incubation experiments, gut content analyses, calorimetry, stable isotopic and fatty acid analyses are very helpful and some modifications of standard materials and methods can help reduce the time-consuming sorting of individuals. Other analytic tools used by microbial ecologists like compound-specific stable isotopic analysis, DNA-stable isotopic probing, confocal laser scanning microscopy, coherent anti-stokes Raman spectrometry and nanoscale secondary ion mass spectrometry have the potential to unravel hidden trophic channels between meiofauna and microbes.

Keywords Meiobenthos · Food web · Gut content · Microscopy · Mass spectrometry · Spectroscopy

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Introduction

Elton (1927) formulated nearly all principles on which modern ecological theory is based, and described complex animal communities as interconnected food chains that form food webs. He further outlined that smaller animals are more abundant than larger ones to represent the "pyramids" ordered in increasing organismal size so that material flows through the community from small to larger organisms. Recently, those two facets of trophic ecology (i.e. predator–prey interactions and energy flows) have attracted more

attention within the fast-growing field of ecological research: Trophic ecology emerged as a promising ground in an attempt to merge complex concepts such as natural selection, ecological networks, ecological stoichiometry and ecosystem metabolism (see Garvey & Whiles, 2017). This trend has been fostered by considerable improvements and developments in methods to observe feeding interactions and quantify the assimilation and transfer of organic matter (Majdi et al., 2018).

Nevertheless, meiofaunal communities are composed of inconspicuous assemblages of microscopic animals needing advanced taxonomical expertise and specific methodologies to examine their feeding interactions. This creates regional biases and knowledge shortfalls especially concerning species taxonomy (*i.e.* Linnean shortfall), abundance/biomass patterns (*i.e.* Prestonian shortfall), functional traits (*i.e.* Raunkiaeran shortfall) and feeding interactions (*i.e.* Eltonian shortfall) (see e.g. Fontaneto et al., 2012; Hortal et al., 2015). Although current research grants do not really promote thorough taxonomic works on species level, technological improvements of microscopy- and molecular-based techniques may reduce costs and/or offer alternatives to unravel large-scale diversity of species and their morpho-functional traits (Fonseca et al., 2018; Neury-Ormanni et al., 2019; Schenck & Fontaneto, 2019). Missing data about the functional traits and feeding interactions of the meiofauna will persist but there are some empirical research that highlight the role of meiofaunal-sized animals within the functioning of ecosystems (e.g. in Freshwater ecosystems: Schmid-Araya et al. 2002a, b, 2016; Majdi et al., 2012b; Majdi & Traunspurger, 2017. Marine ecosystems: Nascimento et al., 2012; Bonaglia et al., 2014; Braeckman et al., 2018. Soil ecosystems: Pausch et al., 2016; Maboreke et al., 2018).

Here, we review the experimental approaches and analytical tools useful to study feeding interactions and energy fluxes of the metazoan meiofauna. Further, we summarize the limitations of these methods, their advantages, and their potential while assessing meiofaunal diets. Although we mainly aim to highlight methodologies adapted to freshwater samples, we propose application examples from freshwater, marine and soil environments because (a) of the scarcity of examples from the freshwater only, and (b) most methodologies can be used across different habitat types.

Indirect evidences

Correlative evidences of trophic linkages

Many meiofaunal studies are primarily descriptive, reporting spatial and/or temporal variations of abundances. Reviewing 93 studies dealing with the trophic ecology of freshwater nematodes, Majdi & Traunspurger (2015) found that 42% of the studies suggested the existence of a trophic linkage through correlative evidences. For instance, several studies have found positive correlations between Chlorophyll-*a* concentration and the abundance of meiofauna in epilithic biofilms, suggesting a trophic linkage (Peters & Traunspurger, 2005; Esser, 2006; Gaudes et al., 2006; Vidakovic et al., 2011; Majdi et al., 2012a; Schroeder et al., 2012; Weitere et al., 2018). However, field patterns are not necessarily conclusive about trophic interactions and energy flows because correlations between species can be obscured by many factors (e.g. successional state of the assemblages, constraints of the abiotic environment). Furthermore, another problem with inferring trophic interactions from community structure correlatives is that the approach is sensitive to the Linnean shortfall, a shortfall that often characterizes meiofaunal and microbial datasets. For example, the meiofauna is often loosely determined to the phylum-level, while microbial communities are estimated through raw counts or biomarkers. Sometimes, one meiofaunal phylum is described up to genus- or species-level (often nematodes), but studies examining the spatiotemporal dynamics of all meiofaunal species in a freshwater habitat are very rare (but see Reiss & Schmid-Araya, 2008). Moreover, it is also rare that microbial biomass, or any other microbial biomarkers are measured together with the abundance and biomass of meiofauna. Hence, inferring trophic interactions from correlations in the community structure is also sensitive to the Prestonian shortfall (but see Traunspurger et al., 2012).

Provided that coherent reference databases are available, molecular-based methodologies may dramatically improve the identification of meiofaunal assemblages from field samples and thus overcome the

Linnean shortfall, and in some cases, the Prestonian shortfall when semi-quantitative or quantitative methodologies are used (see e.g. Schenck & Fontaneto, 2019). Molecular-based methodologies may provide a more detailed account of species' occurrences in field samples, and thus may be helpful to suggest the most probable trophic interactions. For example, the detection of consistent associations between meiofaunal species or between meiofaunal species and microbial species may indicate potential trophic or symbiotic associations. Following this approach, Rzeznik-Orignac et al. (2018) recently observed associations between bacteria and nematodes in deep-sea canyons. They reported significant correspondences between microbial communities associated to different ecosystem functions and some species of bacterivorous nematodes (e.g. Nitrospirales bacteria correlated with *Daptonema* spp., *Deltaproteobacteria* with *Dorylaimopsis* spp., sulphate-reducing bacteria with *Terschellingia* spp.). Correlative evidences may ideally be merged with other lines of evidences such as morphology of the buccal cavity, stable isotopic signatures or composition of the microbiome to confirm trophic linkages (Derycke et al., 2016; Vecchi et al., 2018).

Trait-based inferences

Species' biological traits help describing biodiversity by focusing on functional features instead of taxa (Gravel et al., 2016). In turn, the data entailed on matrices of biological traits are used to infer the ecological functions carried out by a community of species. Indeed, the usefulness of trait-based inferences depends upon the accuracy of biological-traits matrices available (Jardim et al., 2016). Some biological traits need empirical knowledge on species behavior and life history, and thus they often missed meiofaunal-sized organisms because their autecological data are difficult to measure in the field, but can be examined using laboratory populations (e.g. Fueser et al., 2018; Majdi et al., 2019). There are, however, three ways to overcome the Raunkiaeran shortfall:

(1) It is possible to fill sparse trait databases using models that consider the mechanisms causing missing data (e.g. Rubin, 1976). Imputation models considering species' phylogenetic information seem to be the most relevant because related species have more probabilities to share common traits (Guénard et al., 2013; Jardim et al., 2016). Nevertheless, it is important to consider the pattern of missing data and then to use appropriate modelling methods in order to reduce potential misinterpretations when using imputed trait databases only (Jardim et al., 2016).

(2) Complex databases of traits can be developed from literature and from microscopic observations of meiofaunal-sized organisms (Ristau et al., 2015; Neury-Ormanni et al., 2019) by classifying species based on a large set of morphological, behavioral, life-history and feeding traits (e.g. body size and shape, characteristics of the feeding apparatus and of locomotory organs, reproduction mode). When combined to estimates of standing stocks, one can infer the ecological role of the community whenever one can find correlations between the prevalence of specific traits and the trophic status of an ecosystem (e.g. lake eutrophication, see Ristau et al., 2015) or the magnitude of an ecosystem process like primary production (Neury-Ormanni et al., 2019). Developing standardized measurement protocols leading to coherent databases of traits is a challenging task for disparate species assemblages such as the meiofauna, but there are now extensive repositories of traits including some meiofaunal species (e.g. Degen & Faulwetter, 2019). Furthermore, advances in cell-sorting methodologies and image treatment automatization have the potential to foster the inclusion of meiofauna in trait-based ecology by providing a high-throughput of morphological data from a known community (e.g. Kydd et al., 2018).

(3) Another way to reduce the Raunkiaeran shortfall is to focus on a subset of traits in a relatively ubiquitous and numerically dominant group of the meiofauna like nematodes. As a preeminent functional feature of nematodes, the feeding type (i.e. a quantitative trait considering the size, morphology and anatomical structures of the digestive tract and of the mouth cavity) may give insights about diet (Yeates et al., 1993). This simplification has been widely used to counterbalance the lack of other species-level information on feeding behavior. For instance, nematologists have developed coherent feeding-type classifications for terrestrial, marine and freshwater nematodes (see Wieser, 1953; Yeates et al., 1993; Traunspurger, 1997). In the case of meiofauna where hundreds of species with similar feeding types may coexist in small patches, it is however questionable whether feeding-type classifications alone can really

help to better understand the diet spectrum and its resource dependence (Schmid & Schmid-Araya, 2002). Furthermore, experiments with bacterivorous nematodes suggest that species expected to occupy the same trophic niches do not really seem that redundant (De Mesel et al., 2004, 2006; dos Santos et al., 2009; Gingold et al., 2013; Gansfort et al., 2018). Also, some meiofauna possess suction-feeding stylets (e.g. tardigrades, dorylaimid nematodes, water mites), protruding pharynges (some catenulid microturbellarians) or mandibles and ligula (e.g. tanypod chironomids) enabling them to feed on a wide range of prey. In those cases, feeding type (and body size) may not always conform to patterns of trophic positioning. Nevertheless, it is conceivable that feeding-type structure may help to infer the most probable interactions occurring in a community: Recently, Sieriebriennikov et al. (2014) used the functional diversity of nematodes as a useful tool for the diagnoses of soil food webs. Also, Traunspurger et al. (2019) found a correspondence between the abundance of nematodes with large mouth cavities and the trophic state of lakes. However, we recommend that inferences using feeding types should be carried out cautiously or should also include direct measures of diet such as stable isotopes (Estifanos et al., 2013) and gut content analyses (Kazemi-Dinan et al., 2014).

Measuring trophic interactions and their consequences

Observation of feeding

The most straightforward and oldest approach to study feeding interactions relies undoubtedly in observations of the feeding of living animals (Giere, 2019). For meiofaunal-sized organisms, most observations need to be performed under a microscope in the laboratory, thereby introducing inevitable bias in comparison to field observations of the feeding behavior of large animals. Nonetheless, laboratory observations also allow to measure feeding responses under standardized conditions and thus, to test the effects of variables such as temperature, water velocity or food type, on feeding rates. A classical example of laboratory observation of feeding is the study of Duncan et al. (1974), producing one of the few experimental measures of bacterial-grazing rates by the free-living freshwater nematode *Plectus palustris* de Man, 1880. In their study, Duncan et al. (1974) used a mixture of observations under the microscope (counting pumping rates of the oesophageal bulb) with measures of ^{14}C assimilation through the consumption of radio-labelled bacteria. They estimated a mean grazing rate of 5000 cells min^{-1} and a gut-filling time in the range between 3 and 10 min. They concluded that *P. palustris* females could daily consume on average 650% of their body weight, which was similar to the 1000% found for the pelagic rotifer *Brachionus plicatilis* Müller, 1786 by Doohan (1973). Later, Moens & Vincx (1997) successfully observed the feeding of many species of free-living marine nematodes using an inverted microscope and agar spot plates with tiny patches of plant-detritus or sediment. They were able to observe the consumption of food items (such as detritus, bacteria, diatoms, protozoa, other nematodes and meiofauna), confirming that only a few species were confined to a narrow diet (e.g. only bacteria). In freshwater, biofilms were grown directly in micro-flow chambers and observed live under a microscope, Esser (2006) estimated the individual grazing rates of one chromadorid nematode as 93 chlorophytes and 58 diatoms per day. Food-choice (*aka* cafeteria) experiments have been carried out successfully with meiofauna allowing to examine food-selectivity under various constraints as well as the role of volatile organic compounds operating as attractors towards a given food patch (Höckelmann et al., 2004; Weber & Traunspurger, 2013; Wilden et al., 2019). Furthermore, video-microscopy can be successfully applied in micro-flow chambers to continuously monitor behavior and grazing events (Weitere et al., 2018). Other recent developments in microscopic imaging have the potential to reveal directly the movements of animals within sediment columns (i.e. X-ray microtomography: Johnson et al., 2004) or the effects of micro-grazers on the 3-dimensional structure of microbial aggregates (i.e. confocal laser scanning microscopy: Neu & Lawrence, 2015).

Incubation and food clearance experiments

Incubation experiments are popular among meiobenthologists, because meiofaunal groups are generally well-suited for experimental work: From sandy/silty habitats, some groups can be easily retrieved (e.g. within a sediment core) and obtained in large numbers

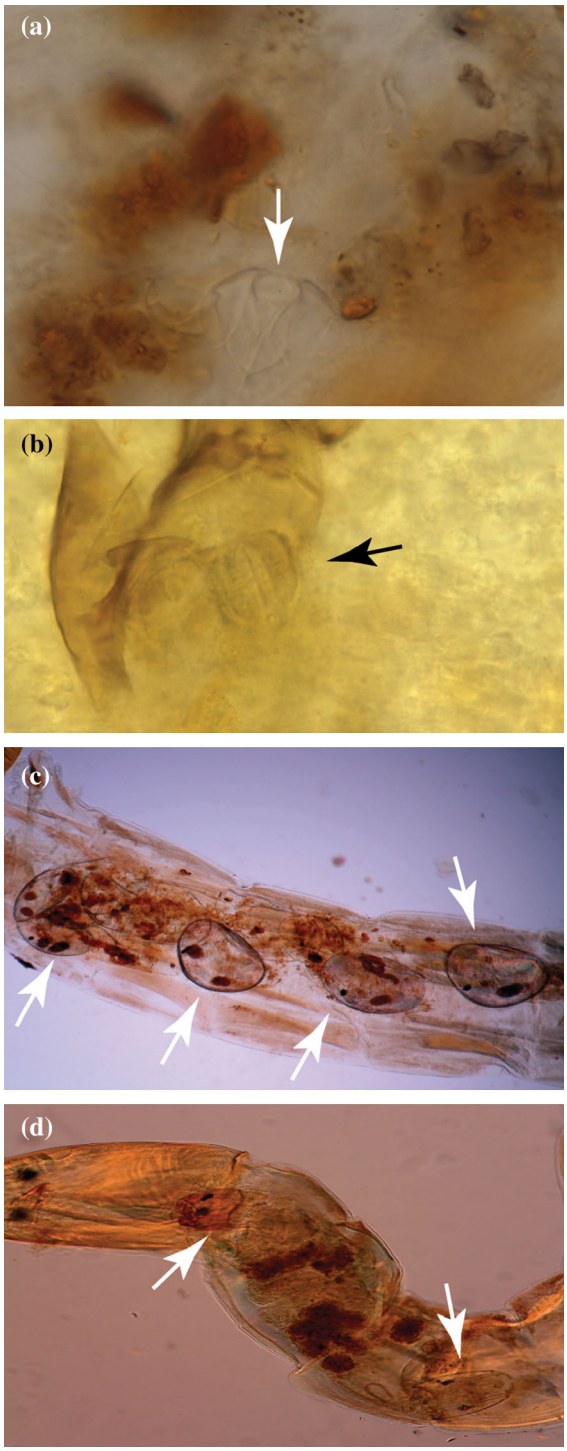
and directly exposed to different experimental treatments in the laboratory (e.g. Bell, 1988; Hägerbäumer et al., 2015). Another advantage of incubations is a relatively low degree of invasiveness, and the possibility to measure assemblage- to ecosystem-level effects, thus, determining meiofaunal feeding in rather realistic context of multispecies interactions. Various enclosure/exclosure experiments have been designed to examine the effects of the presence of meiofauna on microbial abundances and processes: (a) static or flow-through sediment cores of different sizes (e.g. Borchardt & Bott, 1995; Traunspurger et al., 1997; Nascimento et al., 2012; Bonaglia et al., 2014; Liu et al., 2017); (b) flow-through chambers of various sizes (e.g. Perlmutter & Meyer, 1991; Esser, 2006; Kathol et al., 2009), and (c) full-grown microbial biofilms exposed to different meiofaunal abundances (Mathieu et al., 2007; Peters et al., 2007; Liu et al., 2015; D'Hondt et al., 2018). Other experiments have measured prey disappearance as a function of prey number to examine the shape of predator–prey functional responses using turbellarians, oligochaetes, chironomids, tardigrades, nematodes or copepods as predators and algae, ciliates or nematodes as prey (e.g. Taylor, 1980; Goldfinch & Carman, 2000; Mohr & Adrian, 2000; Bergtold et al., 2005; De Troch et al., 2005; Hohberg & Traunspurger, 2005; Muschiol et al., 2008; Reiss & Schmid-Araya, 2011; Ptatscheck et al., 2015; 2017; Kreuzinger-Janik et al., 2018, 2019).

Incubation experiments have unravelled interesting facets of meiofauna–microbe interactions such as the apparent stimulation of bacterial (or algal) activity and nutrient/organic matter cycling with increasing meiofaunal densities (Traunspurger et al., 1997; Mathieu et al., 2007; Nascimento et al., 2012; Bonaglia et al., 2014; Liu et al., 2015, 2017; D'Hondt et al., 2018). Based on the above results, it is necessary to examine whether enhanced microbial activity may be due to either: (a) micro-bioturbation of meiofauna increasing the porosity of microbial mats to nutrients and light, (b) grazing pressure that optimizes growth rates of microbial populations or (c) a combination of both. Some studies also point out the indirect role of meiofaunal secretions products (mucus trails, faecal pellets or gut flora), stimulating microbial growth locally (Riemann & Helmke, 2002; Moens et al., 2005; De Troch et al., 2010; Hubas et al., 2010; Cnudde et al., 2011; Gaudes et al., 2013).

Gut content analysis

Gut content analysis (GCA) is a practice to characterize individual diet and to draw species-interaction networks. While GCA is commonly used for macroinvertebrates and fishes, very few studies have examined gut contents of meiofauna to infer its diet and position in food webs (but see e.g. Schmid-Araya & Schmid, 1995; Schmid & Schmid-Araya, 1997). A possible rationale might be the severe difficulties for non taxonomic experts to detect specific remains of meiofaunal organisms such as trophies of rotifers (e.g. Figure 1a, b), pharinges and claws of tardigrades, scales and spines of gastrotrichs, chaetae of small oligochaetes, pharinges and stylets of microturbellarians, mouth-parts of chironomids.

Nevertheless, GCA proves especially useful to document the (a) dietary composition and predator–prey relationships (Schmid & Schmid-Araya, 1997), (b) food web topology (Schmid-Araya et al., 2002a, 2016) and (c) patterns of food web connectance (Schmid-Araya et al., 2002b). GCA also offers the possibility to assess prey size or developmental stage giving more detailed information on diet (Fig. 1). For instance, using GCA, Schmid & Schmid-Araya (1997) found that three species of stream predatory tanypods fed on numerous different meiofaunal prey (41 benthic rotifer species and 23 chironomid species, see e.g. Figure 1). The predatory tanypods switched diet from rotifers in early instars to chironomids and diverse other meio- and macrofaunal taxa in later instars, so growing tanypods expanded their upper size thresholds but continued to include smaller prey species in their diet. These larval tanypods consumed on average 1.32 prey individuals per predator type and prey consumption varied with sediment depth layer with higher prey consumption in the upper 20 cm of the streambed. GCA has also revealed that lotic food webs contain a high proportion of species (60–80% of total community) in the meiofaunal size range and many of these species belonged to the intermediate category (species with both prey and predator) improving the food web completeness (Schmid-Araya et al. 2002a, b, 2016). However, discrepancies in the taxonomic distinctness of the approach are inevitable since the assessment of diet is only based on prey items hard enough to persist in guts: Soft-bodied prey or tissues being poorly recognizable or quickly digested can be underestimated. Also, GCA



◀**Fig. 1** Illustrative examples of various items found (rotifers, ostracods and chironomids) in gut contents of meio- and macrofaunal consumers (Photos Schmid & Schmid-Araya). **a** *Dicranophorus luetkeni* (Bergendal, 1892) (Rotifera) trophy found in guts of Tanypodinae (Chironomidae- Diptera) larvae. **b** Bdelloidea trophy found in the gut of the caddisfly *Plectrocnemia conspersa* (Curtis, 1834) (Trichoptera). **c** A series of ostracods eaten by the larvae of *Macropelopia* sp. (Tanypodinae, Chironomidae- Diptera). **d** The gut content of a tanypod chironomid larva that had eaten an orthocladinae larva and a tanypod chironomid

represents a snapshot of diet, and thus, it should be highly replicated to provide more robust conclusions about diet spectrum.

It is possible to improve GCA using biomarkers in order to highlight hardly recognizable or minor food items present in the guts of meiobenthic animals. For example, the auto-fluorescence of ingested chlorophyll or carotenoid pigments can be detected in the guts of rotifers under a confocal laser scanning microscope (Mialet et al., 2013). Additionally, ingested biomarker pigments can be extracted from guts and quantified using HPLC to assess diet at population scales or in relation to the temporal availability of algae in the habitat (Buffan-Dubau et al., 1996; Buffan-Dubau & Carman, 2000; Majdi et al., 2012c).

The genetic techniques of polymerase chain reaction (PCR)-amplification of DNA may also contribute substantially to unravel certain trophic relations particularly on soft-bodied meiofauna. Prey DNA can be amplified from digestive systems, faecal pellets or whole organisms mostly of large-sized invertebrates where barcodes are available (King et al., 2008). In some cases under controlled laboratory conditions, it was possible to detect from copepods and from their faecal pellets: (a) a model alga offered to filter-feeding copepods (Nejstgaard et al., 2003) or (b) copepod prey given to carnivorous copepods (Vestheim et al., 2005). As another example, laboratory and field experiments by Heidemann et al. (2011) found that the so-called 'detritivorous' gamasid and oribatid mites carried out predation and scavenging on nematodes in soils. Also, PCR-based approaches were successfully applied to highlight the diet of soft-bodied meiofaunal predators such as marine microturbellarians (Maghsoud et al., 2014) and the extension of the method can open up a vast venue for trophic analyses. The next challenge has been the development of real-time quantitative PCR (qPCR) already demonstrated by Nejstgaard et al. (2008) in marine zooplankton. They found that a

target gene of phytoplankton varied with growth phase while developing a qPCR assay to target gene fragments to estimate copepod feeding. Their field studies using gut contents derived from qPCRs, gut pigment and direct microscopy (GCA) demonstrated a semi-quantitative relationship. However, absolute estimates of gut content based on qPCRs were lower than expected, probably due to the digestion of prey-species' nucleic acids. Moreover, by sequencing the microbial 16S rRNA gene, Derycke et al. (2016) confirmed the existence of species-specific microbiomes of three cryptic species of the nematode *Litoditis marina* (Bastian, 1865) Sudhaus, 2011. More strikingly, Derycke et al. (2016) found that the food offered to these cryptic species affected their microbiomes, illustrating different feeding behavior between the cryptic species. These molecular approaches to highlight diet are far from being common practice for meiofauna and many disadvantages persist. Among the downsides of these methods are (a) risks of contamination, (b) the potential bias by different DNA degradation dynamics during digestion for quantitative assessment, (c) DNA extraction protocols can strongly affect comparison of results and (d) potential uncertainties while disentangling ingested microbes from the resident gut microbiome, parasites or symbionts.

Detecting energy fluxes and assimilation

Measuring nutritional status and metabolism

Body mass indices, life-history traits related to fitness (e.g. development rate, survival, reproduction success) as well as elemental composition and energy storage have long been used by ecologists to infer the nutritional status of individuals, or to evaluate the nutritional quality of a food source (e.g. Jakob et al., 1996; Raubenheimer et al., 2009). Although these approaches may be sensible to other triggers than food (e.g. temperature, light, ontogeny), they have been used extensively in meiofaunal research under standardized conditions to document community- or population-level responses to (a) nutrient enrichment (Ristau et al., 2012; Gaudes et al., 2013), (b) determinations of optimal food concentrations for population growth (e.g. Schiemer et al., 1980; Robertson & Salt, 1981; Muschiol & Traunspurger, 2007; Schroeder et al., 2010; Weber & Traunspurger, 2013). It is also possible to evaluate the nutritional status and the metabolism through measuring the protein content/composition of animals. For this purpose, matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF MS) can generate protein mass spectra from small individual specimen (e.g. harpacticoid copepods as little as 350 µm length) or even from copepod body parts (Rossel & Martínez Arbizu, 2018). Besides, protein composition can be used to perform chemo-taxonomy, i.e. link specific protein fingerprints to species identity (Rossel & Martínez Arbizu, 2018, 2019). Another way to collect information on the nutritional status of meiofauna is to combine measures of life-history traits at the individual-level (e.g. using hanging-drop cultures) with the determination of lipid contents in single nematode individuals using coherent anti-stokes Raman spectroscopy (CARS) (Fueser et al., 2018). This approach is well-suited for translucent, meiofaunal-sized organisms unravelling the three-dimensional distribution of lipid droplets across tissues.

Lucas & Watson (2002) defined animal metabolism as the collective processes of anabolism and catabolism. As heterotrophs, animals achieve biosynthesis (anabolism) at the expense of energy from organic matter that is consumed and degraded (catabolism). In aerobic organisms, measurement of the rate of oxygen consumption gives a measure of the energy expenditure in the normal processes of the body and the metabolic rate per unit body weight of the intensity of its metabolism (Duncan & Klekowski, 1975). In direct calorimetry, the amount of heat produced by the animal itself is measured. Recently, Ruiz et al. (2018) used multichannel isothermal micro-calorimeters to estimate in real-time the metabolic rates of cladocerans as heat flow while offering stoichiometrically balanced or unbalanced algal food. Ruiz et al. (2018) observed that, to maintain their stoichiometric homeostasis, the animals fed stoichimetrically unbalanced food showed higher metabolic rates at the expense of growth. This experiment also demonstrated that real-time micro-calorimetry was a powerful technique to obtain precise measures of metabolic rates at the scale of meiofaunal individuals.

Indirect calorimetry involves the measurement of oxygen uptake (i.e. respirometry), which has long been the conventional approach to measure the metabolism of meiofaunal-sized invertebrates (e.g.

Schiemer & Duncan, 1974; Schiemer, 1982; Herman & Vranken, 1988). However, in comparison to direct calorimetry, indirect measures of metabolism like respirometry can lead to under-estimations of metabolism (e.g. Walsberg & Hoffman, 2005; Burnett & Grobe, 2013), as respirometry only measures aerobic heat production while calorimetry measures the sum of aerobic and anaerobic catabolism. Moreover, respirometry does not consider the storage of CO_2 as bicarbonates and biochemical synthesis in the cells of tissues, and closed respirometers can produce further biases as concentrations of gases change during closure time (Malte et al., 2016).

Bulk stable isotopic analysis

The stable isotope composition of carbon and nitrogen in bulk tissues is one of the most popular method using trophic tracers (Majdi et al., 2018). In the case of the meiofauna, marine studies considering stable isotopic analysis (SIA) have flourished over the last two decades (Giere, 2019). Meiofaunal SIA have only been reported recently in freshwaters (e.g. Majdi et al., 2012b; Estifanos et al. 2013; Schmid-Araya et al., 2016; Majdi & Traunspurger, 2017). Since stable isotopic composition is based on the result of the assimilation of a diet over relatively long periods, stable isotopes (and other assimilation tracers) have the immense advantage of quantifying fluxes of biomass over meaningful periods of time. However, a general disadvantage of assimilation tracers is that the presence of a tracer does not only reflect resource consumption but it also depicts the pathway from the resource to consumer's tissues (e.g. selective digestion). Another major limitation of SIA while assessing the diet of meiofaunal assemblages is the sensitivity of the conventional elemental analyser-stable isotope mass ratio spectrometers (EA-IRMS), which may force to sort and clean a large number of individuals (Fig. 2). Indeed, this step is time-consuming and needs taxonomic expertise, but great numbers of living specimen can be retrieved from the field which may drastically reduce sorting-time (see e.g. migration/extraction procedures described in Wu et al., 2019). Moreover, the sample-size limitation can be overcome by reducing the volume of EA-IRMS columns after Carman & Fry (2002) as used for freshwater meiofauna by Schmid-Araya et al. (2016). Less helium is required to transport gaseous samples from the EA to the IRMS, thus samples are less diluted during transport, and detection limit can be reduced to 2 µgC (Carman & Fry, 2002); but it is also important to reduce potential sources of contaminations by using smaller tin cups (Carman & Fry, 2002). Langel & Dickmans (2014) also describe improvements of the conventional EA-IRMS (termed µEA-IRMS) leading to detection limits as low as 1 µgC and 0.6 µgN. Further use of the µEA-IRMS revealed stable isotopic signatures of soil nematodes at unprecedented genus and/or family levels, as few as fifteen nematode individuals being sufficient to get a reliable signal (Melody et al., 2016).

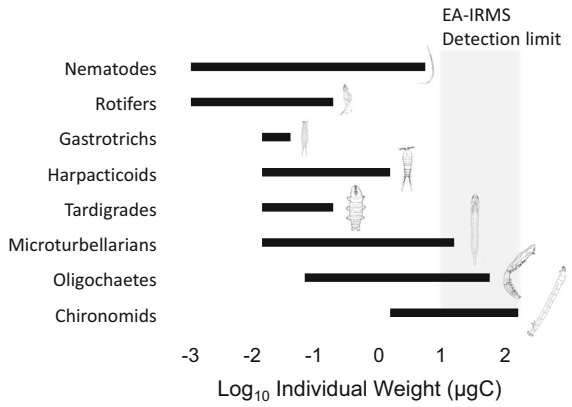


Fig. 2 Range of individual body masses in a meiofaunal community dwelling sandy streams (after Majdi et al., 2016), and compatibility with the detection limits of conventional EA-IRMS platforms

SIA and its improvements have the potential to provide quantitative estimates of elemental fluxes between different trophic levels of a food web at a relatively low-cost and effort. Nevertheless, SIA cannot assess the number of links in a food web for which direct observations, such as GCA or in conjunction with other approaches are better suited. It is possible (and probably advisable) to combine complementary approaches like SIA and food-choice experiments (Moens et al., 2013), or SIA and GCA to document the two facets of meiofauna's trophic ecology (interactions and energy flow). For example, combining SIA with GCA, Schmid-Araya et al. (2016) showed that between 28 and 44.2% of the top consumers (having prey but no predators) were meiofaunal species. Consequently, it was assumed that (a) small-bodied taxa do not only occur low in the food webs, and (b) trophic positions do not necessarily

increase with body size (Schmid-Araya et al., 2016; Majdi & Traunspurger, 2017).

Recently, meiobenthologists have used SIA to explore particular trophic connection between chemoautotrophic bacteria and some marine nematodes or harpacticoid copepods, showing strongly depleted $\delta^{13}C$ signatures typical for methane- or sulphur-oxidizing bacteria (Van Gaever et al., 2009; Vafeiadou et al., 2014; Cnudde et al., 2015). This trophic connection has not been investigated for freshwater meiofauna, although freshwater macroinvertebrates (those dwelling in back-water pools, hyporheic zones or soft sediments in lakes), may assimilate substantial amounts of methane-derived C (e.g. Kohzu et al., 2004; Deines et al., 2007b). It is also not clear whether meiofauna uses chemotrophic-derived C by consuming bacteria or by hosting symbiotic chemoautotrophs, an issue that may be examined using approaches described below.

Stable isotopic probing and compound-specific stable isotopic analysis

Injections of small quantities of isotopically enriched sources can be applied to trace C or N pathways throughout the consumer network (referred to as stable isotope probing; SIP). These studies follow a time-course of the added tracer and have proven powerful to document microbial involvement in biogeochemical processes and to quantify trophic transfers from bacteria or micro-algae to consumers (e.g. Middelburg et al. 2000; Radajewski et al., 2000; Witte et al., 2003; Crotty et al., 2012; Majdi et al., 2012b). ^{13}C-enriched sodium bicarbonate has been used to label photosynthetic products and the excess ^{13}C can be tracked through time in meiofaunal consumers to quantify "green" trophodynamics (Middelburg et al., 2000; Majdi et al., 2012b; Estifanos et al., 2013). ^{13}C-enriched glucose can be added to trace the "brown" pathways and the consumption of heterotrophic bacteria by meiofauna (e.g. Van Oevelen et al., 2006).

High-resolution imaging secondary ion mass spectroscopy (SIMS) can be combined with SIP to localize ^{13}C enrichments at the cellular level (ca. 50 nm), thereby ruling out sample-size limitations in conventional EA-IRMS. Thus, there are new opportunities to study feeding selectivity, resource routing and processing in tissues, and intraspecific variability in feeding at the scale of the meiofauna (Musat et al., 2016). For instance, using this approach, Volland et al. (2018) demonstrated that the epidermis of a colonial ciliate coated with thiotrophic symbiotic bacteria processed rapidly the ^{13}C-bicarbonate in the presence of H_2S. The ciliate host then assimilated labelled organic carbon compounds within 25 min or through phagocytosis of ectosymbiotic bacteria over longer periods of time.

Compound-specific isotopic analysis (CSIA) determines the isotopic ratios of specific proteins, metabolites, fatty acids, or amino acids and is widely applied by microbial ecologists in combination with SIP to overcome sample-size and taxonomic limitations they also face (Jehmlich et al., 2016; Lueders et al., 2016; Wegener et al., 2016). The amino-acid CSIA received great attention; Coupled with SIP, ribosomal RNA or DNA have been used as integrative tracers. The amplification and barcoding of sequences that have assimilated the ^{13}C or ^{15}N-tracer allows the identification of species that have assimilated the labelled resource (more details reading e.g. Neufeld et al., 2007). The approach is promising to trace specific functional guilds of microbes (e.g. methanotrophic bacteria) and their fate as prey for consumers (Lueders et al. 2004). Moreover, CSIA of poly-unsaturated fatty acids (PUFAs) has also been used together with SIP to reduce errors prone to unpredictable trophic enrichment factors and intermolecular variability of isotopic signatures within the same food source (Bec et al., 2011). Deines et al. (2007a) incubated lake sediment cores with ^{13}C-labelled CH_4 and added chironomid larvae. After exposure, chironomids were starved and PUFAs profiles demonstrated the pathway of CH_4 to chironomids via consumption of *Methylobacter*.

Fatty acids

Since four decades, poly-unsaturated fatty acids (PUFAs) have proved useful to trace fluxes and nutritional quality of food. The relevance of PUFAs as trophic biomarkers relies on specific values of their ratios found in resources and/or in producers (e.g. 16:1ω7/16:0 for diatoms). These are then transferred to the consumers' tissues and can be detected assuming that consumers do not synthesize PUFAs de novo. The fact that some PUFAs can only be acquired by feeding on specific sources underlies the critical importance of (sometimes minor) food items for the

Table 1 Summary of methodological approaches to examine meiofaunal trophic interactions

Method	Sample requirements	Field and routines	Limitations	Advantages	Potential improvements and advices
Correlative evidences of trophic linkages	Variable, but usually quantitative subsamples may contain > 200 individuals to provide correct estimations of density	Known volume/area of substrate, quantitative extraction (e.g. Ludox), counting, sorting, taxonomic identification, body-size measures, or bulk extraction of DNA and PCR	Environmental "noise", sample extraction and counting is time-consuming, sensitive to Linnean shortfall	Well-defined sampling methodologies, the most commonly used approach to infer meiofaunal species' diet, allometric conversion of body size to estimate biomass or production	Consider molecular-based methodologies. Works well in combination with other lines of evidences such as abundances/ biomass patterns, functional traits, isotopic composition, composition of the microbiome
Trait-based inferences	Sampling/ observation is not necessarily needed, can use data from literature or modelling approaches	Can include species-level observation of mobility, morphometrics, feeding preferences, measures of life-history traits using laboratory populations	Some feeding traits do not conform to assumed diet (e.g. stylet-bearing species can either prey on microbes or switch to macroscopic prey through ecto/endo-parasitism). Omnivory widespread in meiofaunal organisms	Relatively inexpensive matrices of traits can be developed based on the taxonomic literature, or specimen repositories on slides in museums. Trait-based matrices are useful to complement already acquired descriptive field data	Implementation models may be used to fill sparse datasets using phylogenetic information. Traits databases should be designed as open-repositories to foster inclusion of meiofaunal species' traits by other researchers. Feeding types of ubiquitous taxa may be used as proxy, in case very few information exists for most of the community.
Observation of feeding	Usually sample size should meet standard sample-size and replication used in behavioral research	Observations of living animals under the microscope in the laboratory. Can be complemented with measures of pumping rate frequency, carbon assimilation, prey encounter and predation events	May be time-consuming. Disconnected from field conditions. Concern a subset of species tolerant to culture conditions. Relatively difficult to expand conclusions to natural populations and to community-level mechanisms	May highlight the nature and magnitude of feeding interactions as well as other behavioral responses (e.g. attraction) under laboratory-controlled conditions. May be used at individual-level to investigate intraspecific competition	Video-microscopy to monitor more behavioral events over longer time periods. X-ray microtomography to unravel movements in semi-natural sediment columns. Real-time CLSM to unravel meiofauna activity in biofilms

Table 1 continued

Method	Sample requirements	Field and routines	Limitations	Advantages	Potential improvements and advices
Incubation and food clearance experiments	Microcosms (e.g. cores, dishes) monitored over relevant periods of time depending on the research question	Various: Static or flow-through sediment microcosms. Microbial biofilms grown on slides or micro-flow chambers. Agar-based media to favour observation and live counts	Sampling and counting may be time-consuming. May also be disconnected from field conditions in case assemblages used in experiments are over-simplified	May mimic field conditions with possibility to control variables such as temperature, light, food quantity and quality. Measures of community to ecosystem-level responses. Measures of prey handling time and functional response curves	Useful to link meiofaunal feeding and activities to broader community structure and ecosystem processes (e.g. micro-bioturbation and other indirect effects)
Gut content analysis	From 1 to > 500 individuals (for pigment extraction method)	Mounting translucent specimen on slides and observing the presence of prey remains in guts, or fluorescence under CLSM. Extracting pigments from pooled individuals, measures using HPLC. PCR-amplification of target prey DNA	Time-consuming, requiring expert taxonomic skills. Difficulties to detect/identify soft prey remains in guts. Snapshot of ingestion only. DNA gut content analysis can be affected by general downsides of molecular approaches and by genetic signatures of the microbiome	Very useful to detail diet (identity and size of prey), and thus compare food web topologies, and potentially ontogenetic shifts in diet. Works well with field samples	Improvement using biomarkers (like pigments or DNA) to measure the ingestion of poorly recognizable prey items
Nutritional status and metabolism	From individual to population-level measures	Population growth rate in laboratory cultures, measuring biomarkers of metabolism, respirometry, micro-calorimetry	Sensible to other triggers than food. May be disconnected from field conditions (standard measures). Respirometry underestimates metabolism	From individual to population-level responses to nutrient enrichment, food quality. Depending on the design (hanging-drop cultures and micro-calorimetry can be used to perform single specimen measures)	Micro-calorimetry may be used to measure real-time metabolism in response to various stimuli. Hanging-drop cultures may be used to provide accurate measures of growth rate and fertility. CARS can be used to unravel the distribution of lipid reserves through the body. MALDI-TOF–MS can give protein fingerprints

Table 1 continued

Method	Sample requirements	Field and routines	Limitations	Advantages	Potential improvements and advices
Bulk stable isotopic analysis	Sort 1 to > 500 individuals (depending on size and methodology used)	Quantitative extraction of animals from field or laboratory samples. Food sources should be sampled as well	Sensible to selective digestion and to a lack of isotopic discrimination between sources. Sorting enough individuals to meet conventional EA-IRMS detection limits is tedious and time-consuming (i.e. potentially quite sensitive to the Linnean shortfall)	Relatively cheap. Very popular method in trophic ecology. Measures assimilation and elemental fluxes. Works well with field samples	The volume of EA-IRMS columns can be reduced to reduce detection limits
Stable isotopic Probing	Sort 1 to > 500 individuals (depending on size and methodology used to measure label uptake)	Quantitative extraction of animals from field or laboratory samples. Food sources should be sampled as well	May be expensive depending on the quantities of label needed	Quantifies a trophic transfer from a source to consumers through time (pulse-chase experiments). Less sensitive to lack of isotopic discrimination between sources	Can be coupled to SIMS to localize label uptake in tissues (but expensive). Targeting some specific isotopically enriched compounds (like DNA or fatty acids) helps to overcome sample-size and taxonomic limitations as well (but expensive and complex protocols)
Fatty acids	Sort 1 to > 500 individuals (depending on size and methodology used)	Quantitative extraction of animals from field or laboratory samples	Sorting enough individuals to meet conventional GC–MS detection limits may be time-consuming. For smallest meiofauna (e.g. rotifers) should use mass extraction of laboratory-cultured populations	May help to underline the selective use of minor, high-quality food sources. May help to unravel *de novo* synthesis of PUFAs by meiofaunal organisms	Detection limits can be reduced by using GC-FID instead of GC–MS. Or DTD-GCxGC-TOF–MS to reduce co-elution of closely related PUFAs

PCR polymerase chain reaction, *CLSM* confocal laser scanning microscope, *HPLC* high-performance liquid chromatograph, *CARS* coherent anti-Stokes Raman spectroscope, *EA-IRMS* elemental analyser coupled to isotope ratio mass spectrometer, *MALDI-TOF MS* matrix-assisted laser desorption/ionization time-of-flight mass spectrometer, *SIMS* secondary ion mass spectrometer. *GC–MS* gas chromatograph coupled to mass spectrometer, *GC-FID* gas chromatograph coupled to flame ionization detector, *DTD-GCxGC-TOF–MS* direct thermal desorption comprehensive two-dimensional GC coupled to time-of-flight mass spectrometer

development of animals, and thereby introduces the concept of nutritional quality. Although the use of PUFAs is popular in aquatic ecology (Arts et al., 2009), few studies have measured fatty acid profiles in meiofaunal-sized organisms (but see e.g. Caramujo et al., 2008; Leduc & Probert, 2009; Guilini et al.,

2013; Braeckman et al. 2015; Wu et al., 2019). Indeed, the conventional gas chromatographs coupled to mass spectrometers (GC–MS) displays sample-size limitations as for EA-IRMS. Nevertheless it is possible to overcome sample-size limitations using comprehensive two-dimensional GC (*aka* GC x GC). The main advantage is that closely related molecules migrate over 2-dimensions and are thus better separated than with unidimensional GC, which also enable to detect smaller quantities. Akoto et al. (2008) describe a set-up (Direct thermal desorption-GCxGC-time-of-flight mass spectrometer) and a protocol compatible with meiofauna samples. Another way to reduce sample-size requirement is to couple GC to flame ionization detectors (FID) instead of MS (Hordijk et al., 1990; Boschker et al., 2001; Caramujo et al., 2008). Using GC-FID, Caramujo et al. (2008) were able to track PUFAs from a cyanobacteria or diatom diet to the tissues of an harpacticoid copepod using samples of 50–150 mature females. Copepods fed cyanobacteria showed reduced fatty acid content when compared to copepods fed with diatoms. Interestingly, copepod-fed cyanobacteria showed longer-chain PUFAs suggesting the existence of a mechanism by which fatty acids from a poor diet become elongated and desaturated by the freshwater harpacticoid. Rotifers and nematodes are also known to synthesize certain essential PUFAs de novo (Rothstein & Götz, 1968; Lubzens et al., 1985; Watts & Browse, 1999). More research is needed to determine which species can synthesize PUFAs de novo, and under what conditions (Bell & Tocher, 2009). If de novo synthesis is confirmed and widespread in meiofaunal organisms, it certainly has considerable implications for the way we should conceptualize sources of essential PUFAs in aquatic ecosystems.

Conclusion

Although mounting evidences support that meiofauna produce substantial amount of biomass and are thus important intermediaries in energetic transfers between freshwater biota, meiofaunal trophic relationships have long been, and still remain, a black box to freshwater ecologists. The most probable reasons for this gap of knowledge come from the cryptic nature of the meiofauna, the necessity to have a taxonomic expertise not usually found in all laboratories, and the fact that the minute size of most meiofauna makes difficult to meet the detection limits of some analytical platforms such as elemental analyzers or mass spectrometers. The latter drawback might be alleviated through methodological improvements and here we review the different methods compatible with the study of meiofauna's trophic ecology, their requirements, routines, limitations and advantages (summarized in Table 1). It appears that many conventional methods can bring valuable information on diet specificity and ingestion rates (e.g. gut content analysis, observation of feeding, incubation experiments) with slight modifications of standard protocols. Elemental composition, stable isotopes and fatty acids can bring valuable information on assimilation and energy fluxes at the scale of the meiofauna provided minor modifications e.g. reducing the volume of combustion columns in EA-IRMS devices, or coupling gas-chromatographs to flame ionization detectors instead of mass spectrometers. The rapid development of microscopy, micro-spectroscopy and molecular-based techniques in the field of microbial ecology also opens interesting opportunities to study the interactions between microbes and meiofauna, and, as an example, those techniques could be used to better understand methane-based feeding channels in lotic and lentic systems.

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References

Akoto, L., F. Stellaard, H. Irth, R. J. J. Vreuls & R. Pel, 2008. Improved fatty acid detection in micro-algae and aquatic meiofauna species using direct thermal desorption interface combined with comprehensive gas chromatography-time-of-flight mass spectrometry. Journal of Chromatography A 1186: 254–261.

Arts, M. T., M. T. Brett & M. Kainz, 2009. Lipids in Aquatic Ecosystems. Springer, New York.

Bec, A., M.-E. Perga, A. Koussoroplis, G. Bardoux, C. Desvilettes, G. Bourdier & A. Mariotti, 2011. Assessing the reliability of fatty acid–specific stable isotope analysis for trophic studies. Methods in Ecology and Evolution 2: 651–659.

Bell, M. V. & D. R. Tocher, 2009. Biosynthesis of Polyunsaturated Fatty Acids in Aquatic Ecosystems: General

Pathways and New Directions Lipids in Aquatic Ecosystems. Springer, New York: 211–236.
Bell, S. S., 1988. Experimental techniques. In Higgins, R. P. & H. Thiel (eds), Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, DC: 169–180.
Bergtold, M., V. Gunther & W. Traunspurger, 2005. Is there competition among ciliates and nematodes? Freshwater Biology 50: 1351–1359.
Bonaglia, S., F. J. A. Nascimento & M. Bartoli, 2014. Meiofauna increases bacterial denitrification in marine sediments. Nature Communications 5: 5133.
Borchardt, M. A. & T. L. Bott, 1995. Meiofaunal grazing of bacteria and algae in a Piedmont stream. Journal of the North American Benthological Society 14: 278–298.
Boschker, H. T. S., W. De Graaf, M. Köster, L.-A. Meyer-Reil & T. E. Cappenberg, 2001. Bacterial populations and processes involved in acetate and propionate consumption in anoxic brackish sediment. FEMS Microbiology Ecology 35: 97–103.
Braeckman, U., P. Provoost, K. Sabbe, K. Soetaert, J. J. Middelburg, M. Vincx & J. Vanaverbeke, 2015. Temporal dynamics in a shallow coastal benthic food web: insights from fatty acid biomarkers and their stable isotopes. Marine Environmental Research 108: 55–68.
Braeckman, U., F. Janssen, G. Lavik, M. Elvert, H. Marchant, C. Buckner, C. Bienhold & F. Wenzhöfer, 2018. Carbon and nitrogen turnover in the Arctic deep sea: in situ benthic community response to diatom and coccolithophorid phytodetritus. Biogeosciences 15: 6537–6557.
Buffan-Dubau, E. & K. R. Carman, 2000. Diel feeding behavior of meiofauna and their relationships with microalgal resources. Limnology and Oceanography 45: 381–395.
Buffan-Dubau, E., R. de Wit & J. Castel, 1996. Feeding selectivity of the harpacticoid copepod *Canuella perplexa* in benthic muddy environments demonstrated by HPLC analyses of chlorin and carotenoid pigments. Marine Ecology Progress Series 137: 71–82.
Burnett, C. M. L. & J. L. Grobe, 2013. Direct calorimetry identifies deficiencies in respirometry for the determination of resting metabolic rate in C57Bl/6 and FVB mice. American Journal of Physiology 305: 916–924.
Caramujo, M. J., H. T. Boschker & W. Admiraal, 2008. Fatty acid profiles of algae mark the development and composition of harpacticoid copepods. Freshwater Biology 53: 77.
Carman, K. R. & B. Fry, 2002. Small-sample methods for δ13C and δ15 N analysis of the diets of marsh meiofaunal species using natural-abundance and tracer-addition isotope techniques. Marine Ecology Progress Series 240: 85–92.
Cnudde, C., A. Willems, K. Van Hoorde, W. Vyverman, T. Moens & M. De Troch, 2011. Effect of food preservation on the grazing behavior and on the gut flora of the harpacticoid copepod Paramphiascella fulvofasciata. Journal of Experimental Marine Biology and Ecology 407: 63–69.
Cnudde, C., T. Moens, E. Werbrouck, G. Lepoint, D. Van Gansbeke & M. De Troch, 2015. Trophodynamics of estuarine intertidal harpacticoid copepods based on stable isotope composition and fatty acid profiles. Marine Ecology Progress Series 524: 225–239.
Crotty, F. V., S. M. Adl, R. P. Blackshaw & P. J. Murray, 2012. Using stable isotopes to differentiate trophic feeding channels within soil food webs. Journal of Eukaryotic Microbiology 59: 520–526.
Degen, R. & S. Faulwetter, 2019. The arctic traits database—a repository of arctic benthic invertebrate traits. Earth System Science Data 11: 301–322.
De Mesel, I., S. Derycke, T. Moens, K. Van der Gucht, M. Vincx & J. Swings, 2004. Top-down impact of bacterivorous nematodes on the bacterial community structure: a microcosm study. Environmental Microbiology 6: 733–744.
De Mesel, I., S. Derycke, J. Swings, M. Vincx & T. Moens, 2006. Role of nematodes in decomposition processes: does within-trophic group diversity matter? Marine Ecology Progress Series 321: 157–166.
De Troch, M., M. B. Steinarsdottir, V. Chepurnov & E. Olafsson, 2005. Grazing on diatoms by harpacticoid copepods: species-specific density-dependent uptake and microbial gardening. Aquatic Microbial Ecology 39: 135–144.
De Troch, M., C. Cnudde, A. Willems, T. Moens & A. Vanreusel, 2010. Bacterial colonization on fecal pellets of harpacticoid copepods and on their diatom food. Microbial Ecology 60: 581–591.
Deines, P., P. L. Bodelier & G. Eller, 2007a. Methane-derived carbon flows through methane-oxidizing bacteria to higher trophic levels in aquatic systems. Environmental Microbiology 9: 1126–1134.
Deines, P., J. Grey, H.-H. Richnow & G. Eller, 2007b. Linking larval chironomids to methane: seasonal variation of the microbial methane cycle and chironomid δ13C. Aquatic Microbial Ecology 46: 273–282.
Derycke, S., N. De Meester, A. Rigaux, S. Creer, H. Bik, W. K. Thomas & T. Moens, 2016. Coexisting cryptic species of the *Litoditis marina* complex (Nematoda) show differential resource use and have distinct microbiomes with high intraspecific variability. Molecular Ecology 25: 2093–2110.
D'Hondt, A.-S., W. Stock, L. Blommaert, T. Moens & K. Sabbe, 2018. Nematodes stimulate biomass accumulation in a multispecies diatom biofilm. Marine Environmental Research 140: 78–89.
Doohan, M., 1973. An energy budget for adult Brachionus plicatilis Muller (Rotatoria). Oecologia 13: 351–362.
dos Santos, G. A., S. Derycke, V. G. Genevois, L. C. Coelho, M. T. Correia & T. Moens, 2009. Interactions among bacterial-feeding nematode species at different levels of food availability. Marine Biology 156: 629–640.
Duncan, A., & R. Z. Klekowski, 1975. Parameters of an energy budget. In Grodziński, W., Klekowski, R. Z., & A. Duncan (eds), Methods for Ecological Bioenergetics. IBP Handbook 24, Blackwell Scientific Publishing, Oxford, UK: 97–147.
Duncan, A., F. Schiemer & R. Z. Klekowski, 1974. A preliminary study of feeding rates on bacterial food by adult females of a benthic nematode, Plectus palustris De Man 1880. Polish Archives of Hydrobiology 21: 249–255.
Elton, C. S., 1927. Animal Ecology. The Macmillan Company, London.

Esser, M., 2006. Long-term dynamics of microbial biofilm communities of the river Rhine. PhD Thesis, Universität zu Köln, Germany.

Estifanos, T. K., W. Traunspurger & L. Peters, 2013. Selective feeding in nematodes: a stable isotope analysis of bacteria and algae as food sources for free-living nematodes. Nematology 15: 1–13.

Fonseca, G., D. Fontaneto & M. Di Domenico, 2018. Adressing biodiversity shortfalls in meiofauna. Journal of Experimental Marine Biology and Ecology 502: 26–38.

Fontaneto, D., A. M. Barbosa, H. Segers & M. Pautasso, 2012. The 'rotiferologist' effect and other global correlates of species richness in monogonont rotifers. Ecography 35: 174–182.

Fueser, H., N. Majdi, A. Haegerbaeumer, C. Pilger, H. Hachmeister, P. Greife, T. Huser & W. Traunspurger, 2018. Analyzing life-history traits and lipid storage using CARS microscopy for assessing effects of copper on the fitness of *Caenorhabditis elegans*. Ecotoxicology and Environmental Safety 156: 255–262.

Gansfort, B., J. Uthoff & W. Traunspurger, 2018. Interactions among competing nematode species affect population growth rates. Oecologia 187: 75–84.

Garvey, J. E. & M. R. Whiles, 2017. Trophic Ecology. CRC Press, Boca Raton.

Gaudes, A., I. Muñoz & T. Moens, 2013. Bottom-up effects on freshwater bacterivorous nematode populations: a microcosm approach. Hydrobiologia 707: 159–172.

Gaudes, A., S. Sabater, E. Vilalta & I. Muñoz, 2006. The nematode community in cyanobacterial biofilms in the river Llobregat, Spain. Nematology 8: 909–919.

Giere, O., 2019. Future trend lines in ecological meiobenthos research. In Giere, O. (ed.), Perspectives in Meiobenthology. Springer, New York: 37–49.

Gingold, R., T. Moens & A. Rocha-Olivares, 2013. Assessing the response of nematode communities to climate change-driven warming: a microcosm experiment. PLoS ONE 8: e66653.

Goldfinch, A. C. & K. R. Carman, 2000. Chironomid grazing on benthic microalgae in a Louisiana salt marsh. Estuaries 23: 536–547.

Gravel, D., C. Albouy & W. Thuiller, 2016. The meaning of functional trait composition of food webs for ecosystem functioning. Philosophical Transactions of the Royal Society B: Biological Sciences 371: 20150268.

Guénard, G., P. Legendre & P. Peres-Neto, 2013. Phylogenetic eigenvector maps: a framework to model and predict species traits. Methods in Ecology and Evolution 4: 1120–1131.

Guilini, K., G. Veit-Koehler, M. De Troch, D. Van Gansbeke & A. Vanreusel, 2013. Latitudinal and temporal variability in the community structure and fatty acid composition of deep-sea nematodes in the Southern Ocean. Progress in Oceanography 110: 80–92.

Hägerbäumer, A., S. Höss, P. Heininger & W. Traunspurger, 2015. Experimental studies with nematodes in ecotoxicology: an overview. Journal of Nematology 47: 1–11.

Heidemann, K., S. Scheu, L. Ruess & M. Maraun, 2011. Molecular detection of nematode predation and scavenging in oribatid mites: laboratory and field experiments. Soil Biology and Biochemistry 43: 2229–2236.

Herman, P. M. J. & G. Vranken, 1988. Studies of the life-history and energetics of marine and brackish-water nematodes. II. Production, respiration and food uptake by Monhystera disjuncta. Oecologia 77: 457–463.

Höckelmann, C., T. Moens & F. Jüttner, 2004. Odor compounds from cyanobacterial biofilms acting as attractants and repellents for free-living nematodes. Limnology and Oceanography 49: 1809–1819.

Hohberg, K. & W. Traunspurger, 2005. Predator-prey interaction in soil food web: functional response, size-dependent foraging efficiency, and the influence of soil texture. Biology and Fertility of Soils 41: 419–427.

Hordijk, C. A., I. Burgers, G. J. Phylipsen & T. E. Cappenberg, 1990. Trace determination of lower volatile fatty acids in sediments by gas chromatography with chemically bonded FFAP columns. Journal of Chromatography A 511: 317–323.

Hortal, J., F. de Bello, J. A. F. Diniz-Filho, T. M. Lewinsohn, J. M. Lobo & R. J. Ladle, 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. Annual Reviews of Ecology Evolution and Systematics 46: 523–549.

Hubas, C., C. Sachidhanandam, H. Rybarczyk, H. V. Lubarsky, A. Rigaux, T. Moens & D. M. Paterson, 2010. Bacterivorous nematodes stimulate microbial growth and exopolymer production in marine sediment microcosms. Marine Ecology Progress Series 419: 85–94.

Jakob, E. M., S. D. Marshall & G. W. Uetz, 1996. Estimating fitness: a comparison of body condition indices. Oikos 77: 61–67.

Jardim, L., L. M. Bini, J. A. F. Diniz-Filho & F. Villalobos, 2016. Challenging the Raunkiaeran shortfall and the consequences of using imputed databases. BioRxiv. https://doi.org/10.1101/081778.

Jehmlich, N., C. Vogt, V. Lünsmann, H. H. Richnow & M. von Bergen, 2016. Protein-SIP in environmental studies. Current Opinion in Biotechnology 41: 26–33.

Johnson, S. N., D. B. Read & P. J. Gregory, 2004. Tracking larval insect movement within soil using high resolution X-ray microtomography. Ecological Entomology 29: 117–122.

Kathol, M., H. Norf, H. Arndt & M. Weitere, 2009. Effects of temperature increase on the grazing of planktonic bacteria by biofilm-dwelling consumers. Aquatic Microbial Ecology 55: 65–79.

Kazemi-Dinan, A., F. Schroeder, L. Peters, N. Majdi & W. Traunspurger, 2014. The effect of trophic state and depth on periphytic nematode communities in lakes. Limnologica 44: 49–57.

King, R. A., D. S. Read, M. Traugott & W. O. C. Symondson, 2008. Molecular analysis of predation: a review of best practice for DNA-based approaches. Molecular Ecology 17: 947–963.

Kohzu, A., C. Kato, T. Iwata, D. Kishi, M. Murakami, S. Nakano & E. Wada, 2004. Stream food web fueled by methane-derived carbon. Aquatic Microbial Ecology 36: 189–194.

Kreuzinger-Janik, B., S. Kruscha, N. Majdi & W. Traunspurger, 2018. Flatworms like it round: nematode consumption by Planaria torva (Müller 1774) and Polycelis tenuis (Iijima 1884). Hydrobiologia 819: 231–242.

Kreuzinger-Janik, B., H. Brüchner-Hüttemann & W. Traunspurger, 2019. Effect of prey size and structural complexity on the functional response in a nematode-nematode system. Scientific Reports 9: 5696.

Kydd, J., H. Rajakaruna, E. Briski & S. Bailey, 2018. Examination of a high resolution laser optical plankton counter and FlowCAM for measuring plankton concentration and size. Journal of Sea Research 133: 2–10.

Langel, R. & J. Dyckmans, 2014. Combined 13C and 15 N isotope analysis on small samples using a near-conventional elemental analyzer/isotope ratio mass spectrometer setup. Rapid Communications in Mass Spectrometry 28: 1019–1022.

Leduc, D. & P. K. Probert, 2009. The effect of bacterivorous nematodes on detritus in- corporation by macrofaunal detritivores: a study using stable isotope and fatty acid analyses. Journal of Experimental Marine Biology and Ecology 371: 130–139.

Liu, Y., N. Majdi, M. Tackx, A. Dauta, M. Gérino, F. Julien & E. Buffan-Dubau, 2015. Short-term effects of nutrient enrichment on river biofilm: NO3- uptake rate and response of meiofauna. Hydrobiologia 744: 165–175.

Liu, Y., K. Dedieu, J.-M. Sánchez-Pérez, B. Montuelle, E. Buffan-Dubau, F. Julien, F. Azémar, S. Sauvage, P. Marmonier & J. Yao, 2017. Role of biodiversity in the biogeochemical processes at the water-sediment interface of macroporous river bed: an experimental approach. Ecological Engineering 103: 385–393.

Lubzens, E., A. Marko & A. Tietz, 1985. De novo synthesis of fatty acids in the rotifer, *Brachionus plicatilis*. Aquaculture 47: 27–37.

Lucas, A. & J. J. Watson, 2002. Bioenergetics of aquatic animals. CRC Press, Boca Raton: 169.

Lueders, T., B. Wagner, P. Claus & M. W. Friedrich, 2004. Stable isotope probing of rRNA and DNA reveals a dynamic methylotroph community and trophic interactions with fungi and protozoa in oxic rice field soil. Environmental Microbiology 6: 60–72.

Lueders, T., M. G. Dumont, L. Bradford & M. Manefield, 2016. RNA-stable isotope probing: from carbon flow within key microbiota to targeted transcriptomes. Current Opinion in Biotechnology 41: 83–89.

Maghsoud, H., A. Weiss, J. P. S. Smith, M. K. Litvaitis & S. R. Fegley, 2014. Diagnostic PCR can be used to illuminate meiofaunal diets and trophic relationships. Invertebrate Biology 133: 121–127.

Maboreke, H., V. Bartel, R. Seiml-Buchinger & L. Ruess, 2018. Micro-food web structure shapes rhizosphere microbial communities and growth in Oak. Diversity 10: 15.

Majdi, N. & W. Traunspurger, 2015. Free-living nematodes in the freshwater food web: a review. Journal of Nematology 47: 28–44.

Majdi, N. & W. Traunspurger, 2017. Leaf fall affects the isotopic niches of meiofauna and macrofauna in a stream food web. Food Webs 10: 5–14.

Majdi, N., B. Mialet, S. Boyer, M. Tackx, J. Leflaive, S. Boulêtreau, L. Ten-Hage, F. Julien, R. Fernandez & E. Buffan-Dubau, 2012a. The relationship between epilithic biofilm stability and its associated meiofauna under two patterns of flood disturbance. Freshwater Science 31: 38–50.

Majdi, N., M. Tackx & E. Buffan-Dubau, 2012b. Trophic positionning and microphytobenthic carbon uptake of biofilm-dwelling meiofauna in a temperate river. Freshwater Biology 57: 1180–1190.

Majdi, N., M. Tackx, W. Traunspurger & E. Buffan-Dubau, 2012c. Feeding of biofilm-dwelling nematodes examined using HPLC-analysis of gut pigment contents. Hydrobiologia 680: 219–232.

Majdi, N., I. Threis & W. Traunspurger, 2016. It's the little things that count: meiofaunal density and production in the sediment of two headwater streams: Meiofauna in Streams. Limnology and Oceanography 62: 151–163.

Majdi, N., N. Hette-Tronquart, E. Auclair, A. Bec, T. Chouvelon, B. Cognie, M. Danger, P. Decottignies, A. Dessier, C. Desvilettes, S. Dubois, C. Dupuy, C. Fritsch, C. Gaucherel, M. Hedde, F. Jabot, S. Lefebvre, M. P. Marzloff, B. Pey, N. Peyrard, T. Powolny, R. Sabbadin, E. Thébault & M.-E. Perga, 2018. There's no harm in having too much: a comprehensive toolbox of methods in trophic ecology. Food Webs 17: e00100.

Majdi, N., W. Traunspurger, H. Fueser, B. Gansfort, P. Laffaille & A. Maire, 2019. Effects of a broad range of experimental temperatures on the population growth and body-size of five species of free-living nematodes. Journal of Thermal Biology 80: 21–36.

Malte, C. L., S. Nørgaard & T. Wang, 2016. Closed system respirometry may underestimate tissue gas exchange and bias the respiratory exchange ratio (RER). Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 192: 17–27.

Mathieu, M., J. Leflaive, L. Ten-Hage, R. de Wit & E. Buffan-Dubau, 2007. Free-living nematodes affect oxygen turnover of artificial diatom biofilms. Aquatic Microbial Ecology 49: 281–291.

Melody, C., B. Griffiths, J. Dyckmans & O. Schmidt, 2016. Stable isotope analysis (δ13C and δ15 N) of soil nematodes from four feeding groups. PeerJ 4: e2372.

Mialet, B., N. Majdi, M. Tackx, F. Azémar & E. Buffan-Dubau, 2013. Selective feeding of Bdelloid rotifers in river biofilms. PLoS One 8: e75352.

Middelburg, J. J., C. Barranguet, H. T. S. Boschker, P. M. J. Herman, T. Moens & C. H. R. Heip, 2000. The fate of intertidal microphytobenthos carbon: an in situ 13C-labeling study. Limnology and Oceanography 45: 1224–1234.

Moens, T. & M. Vincx, 1997. Observations on the feeding ecology of estuarine nematodes. Journal of the Marine Biological Association of the UK 77: 211–227.

Moens, T., G. A. P. dos Santos, F. Thompson, J. Swings, V. Fonsêca-Genevois, M. Vincx & I. De Mesel, 2005. Do nematode mucus secretions affect bacterial growth? Aquatic Microbial Ecology 40: 77–83.

Moens, T., A.-M. Vafeiadou, E. De Geyter, P. Vanormelingen, K. Sabbe & M. De Troch, 2013. Diatom feeding across trophic guilds in tidal flat nematodes, and the importance of diatom cell size. Journal of Sea Research 92: 125–133.

Mohr, S. & R. Adrian, 2000. Functional responses of the rotifers Brachionus calyciflorus and Brachionus rubens feeding on armored and unarmored ciliates. Limnology and Oceanography 45: 1175–1179.

Musat, N., F. Musat, P. K. Weber & J. Pett-Ridge, 2016. Tracking microbial interactions with NanoSIMS. Current Opinion in Biotechnology 41: 114–121.

Muschiol, D. & W. Traunspurger, 2007. Life cycle and calculation of the intrinsic rate of natural increase of two bacterivorous nematodes, Panagrolaimus sp and Poikilolaimus sp from chemoautotrophic Movile Cave, Romania. Nematology 9: 271–284.

Muschiol, D., M. Markovic, I. Threis & W. Traunspurger, 2008. Predatory copepods can control nematode populations: a functional-response experiment with Eucyclops subterraneus and bacterivorous nematodes. Fundamental and Applied Limnology 172: 317–324.

Nascimento, F. J. A., J. Näslund & R. Elmgren, 2012. Meiofauna enhances organic matter mineralization in soft sediment ecosystems. Limnology and Oceanography 57: 338–346.

Nejstgaard, J. C., M. E. Frischer, C. L. Raule, R. Gruebel, K. E. Kohlberg & P. G. Verity, 2003. Molecular detection of algal prey in copepod guts and fecal pellets. Limnology and Oceanography: Methods 1: 29–38.

Nejstgaard, J. C., M. E. Frischer, P. Simonelli, C. Troedsson, M. Brakel, F. Adiyaman, A. F. Sazhin & L. F. Artigas, 2008. Quantitative PCR to estimate copepod feeding. Marine Biology 153: 565–577.

Neu, T. R. & J. R. Lawrence, 2015. Innovative techniques, sensors, and approaches for imaging biofilms at different scales. Trends in Microbiology 23: 233–242.

Neufeld, J. D., M. Wagner & J. C. Murrell, 2007. Who eats what, where and when? Isotope-labelling experiments are coming of age. The ISME Journal 1: 103.

Neury-Ormanni, J., J. Vedrenne, M. Wagner, G. Jan & S. Morin, 2019. Micro-meiofauna morphofunctional traits linked to trophic activity. Hydrobiologia. https://doi.org/10.1007/s10750-019-04120-0.

Pausch, J., S. Hofmann, A. Scharroba, Y. Kuzyakov & L. Ruess, 2016. Fluxes of root-derived carbon into the nematode micro-food web of an arable soil. Food Webs 9: 32–38.

Perlmutter, D. G. & J. L. Meyer, 1991. The impact of a stream-dwelling harpacticoid copepod upon detritally associated bacteria. Ecology 72: 2170–2180.

Peters, L. & W. Traunspurger, 2005. Species distribution of free-living nematodes and other meiofauna in littoral periphyton communities of lakes. Nematology 7: 267–280.

Peters, L., H. Hillebrand & W. Traunspurger, 2007. Spatial variation of grazer effects on epilithic meiofauna and algae. Journal of the North American Benthological Society 26: 78–91.

Ptatscheck, C., B. Kreuzinger-Janik, H. Putzki & W. Traunspurger, 2015. Insights into the importance of nematode prey for chironomid larvae. Hydrobiologia 757: 143–153.

Ptatscheck, C., H. Putzki & W. Traunspurger, 2017. Impact of deposit-feeding chironomid larvae (Chironomus riparius) on meiofauna and protozoans. Freshwater Science 36: 796–804.

Radajewski, S., P. Ineson, N. R. Parekh & J. C. Murrell, 2000. Stable-isotope probing as a tool in microbial ecology. Nature 403: 646.

Raubenheimer, D., S. J. Simpson & D. Mayntz, 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. Functional Ecology 23: 4–16.

Reiss, J. & J. M. Schmid-Araya, 2008. Existing in plenty: abundance, biomass and diversity of ciliates and meiofauna in small streams. Freshwater Biology 53: 652–658.

Reiss, J. & J. M. Schmid-Araya, 2011. Feeding response of a benthic copepod to ciliate prey type, prey concentration and habitat complexity. Freshwater Biology 56: 1519–1530.

Riemann, F. & E. Helmke, 2002. Symbiotic relations of sediment-agglutinating nematodes and bacteria in detrital habitats: the enzyme-sharing concept. Marine Ecology 23: 93–113.

Ristau, K., M. Faupel & W. Traunspurger, 2012. The effects of nutrient enrichment on a freshwater meiofaunal assemblage. Freshwater Biology 57: 824–834.

Ristau, K., N. Spann & W. Traunspurger, 2015. Species and trait compositions of freshwater nematodes as indicative descriptors of lake eutrophication. Ecological Indicators 53: 196–205.

Robertson, J. R. & G. W. Salt, 1981. Responses in growth mortality, and reproduction to variable food levels by the rotifer, Asplanchna girodi. Ecology 62: 1585–1596.

Rossel, S. & P. Martínez Arbizu, 2018. Automatic specimen identification of Harpacticoids (Crustacea:Copepoda) using Random Forest and MALDI-TOF mass spectra, including a post hoc test for false positive discovery. Methods in Ecology and Evolution 9: 1421–1434.

Rossel, S. & P. Martínez Arbizu, 2019. Revealing higher than expected diversity of Harpacticoida (Crustacea:Copepoda) in the North Sea using MALDI-TOF MS and molecular barcoding. Scientific Reports 9: 9182.

Rothstein, M. & P. Götz, 1968. Biosynthesis of fatty acids in the free-living nematode, Turbatrix aceti. Archives of Biochemistry and Biophysics 126: 131–140.

Rubin, D., 1976. Inference and missing data. Biometrika 63: 581–592.

Ruiz, T., A. Bec, M. Danger, A.-M. Koussoroplis, J.-P. Aguer, J.-P. Morel & N. Morel-Desrosiers, 2018. A microcalorimetric approach for investigating stoichiometric constraints on the standard metabolic rate of a small invertebrate. Ecology Letters 21: 1714–1722.

Rzeznik-Orignac, J., A. Puisay, E. Derelle, E. Peru, N. Le Bris & P. E. Galand, 2018. Co-occurring nematodes and bacteria in submarine canyon sediments. PeerJ 6: e5396.

Schenck, J. & D. Fontaneto, 2019. Biodiversity analyses in freshwater meiofauna through DNA sequence data. Hydrobiologia. https://doi.org/10.1007/s10750-019-04067-2.

Schiemer, F., 1982. Food dependence and energetics of free-living Nematodes. Oecologia 54: 108–121.

Schiemer, F. & A. Duncan, 1974. The oxygen consumption of a freshwater benthic nematode, Tobrilus gracilis (Bastian). Oecologia 15: 121–126.

Schiemer, F., A. Duncan & R. Z. Klekowski, 1980. A bioenergetic study of a benthic nematode, Plectus palustris de Man 1880, throughout its life cycle. Oecologia 44: 205–212.

Schmid, P. E. & J. M. Schmid-Araya, 1997. Predation on meiobenthic assemblages: resource use of a tanypod guild (Chironomidae, Diptera) in a gravel stream. Freshwater Biology 38: 67–91.

Schmid, P. E. & J. M. Schmid-Araya, 2002. Trophic relationships in temporary and permanent freshwater meiofauna.

In Rundle, S. D., A. L. Robertson & J. M. Schmid-Araya (eds), Freshwater meiofauna biology and ecology. Backhuys Publishers, Leiden: 295–320.
Schmid-Araya, J. M. & P. E. Schmid, 1995. Preliminary results on diet of stream invertebrate species: the meiofaunal assemblages. Jahresbericht der Biologischen Station Lunz 15: 23–31.
Schmid-Araya, J. M., A. G. Hildrew, A. Robertson, P. E. Schmid & J. Winterbottom, 2002a. The importance of meiofauna in food webs: evidence from an acid stream. Ecology 83: 1271–1285.
Schmid-Araya, J. M., P. E. Schmid, A. Robertson, J. Winterbottom, C. Gjerløv & A. G. Hildrew, 2002b. Connectance in stream food webs. Journal of Animal Ecology 71: 1056–1062.
Schmid-Araya, J. M., P. E. Schmid, S. P. Tod & G. F. Esteban, 2016. Trophic positioning of meiofauna revealed by stable isotopes and food web analyses. Ecology 97: 3099–3109.
Schroeder, F., D. Muschiol & W. Traunspurger, 2010. Fluctuating food availability may permit coexistence in bacterivorous nematodes. Fundamental and Applied Limnology 178: 59–66.
Schroeder, F., W. Traunspurger, K. Pettersson & L. Peters, 2012. Temporal changes in periphytic meiofauna in lakes of different trophic states. Journal of Limnology 71: 216–227.
Sieriebriennikov, B., H. Ferris & R. G. de Goede, 2014. NINJA: an automated calculation system for nematode-based biological monitoring. European Journal of Soil Biology 61: 90–93.
Taylor, W. D., 1980. Observations on the feeding and growth of the predacious oligochaete Chaetogaster langi on ciliated protozoa. Transactions of the American Microscopical Society 99: 360–368.
Traunspurger, W., 1997. Bathymetric, seasonal and vertical distribution of feeding-types of nematodes in an oligotrophic lake. Vie et Milieu 47: 1–7.
Traunspurger, W., M. Bergtold & W. Goedkoop, 1997. The effects of nematodes on bacterial activity and abundance in a freshwater sediment. Oecologia 112: 118–122.
Traunspurger, W., S. Höss, A. Witthöft-Mühlmann, M. Wessels & H. Güde, 2012. Meiobenthic community patterns of oligotrophic and deep Lake Constance in relation to water depth and nutrients. Fundamental and Applied Limnology 180: 233–248.
Traunspurger, W., B. Wilden & N. Majdi, 2019. An overview of meiofaunal and nematode distribution in lake ecosystems differing in their trophic state. Hydrobiologia. https://doi.org/10.1007/s10750-019-04092-1.
Vafeiadou, A.-M., P. Materatski, H. Adão, M. De Troch & T. Moens, 2014. Resource utilization and trophic position of nematodes and harpacticoid copepods in and adjacent to Zostera noltii beds. Biogeosciences 11: 4001–4014.
Van Gaever, S., L. Moodley, F. Pasotti, M. Houtekamer, J. J. Middelburg, R. Danovaro & A. Vanreusel, 2009. Trophic specialisation of metazoan meiofauna at the Håkon Mosby Mud Volcano: fatty acid biomarker isotope evidence. Marine Biology 156: 1289–1296.
Van Oevelen, D., L. Moodley, K. Soetaert & J. J. Middelburg, 2006. The trophic significance of bacterial carbon in a marine intertidal sediment: results of an in situ stable isotope labeling study. Limnology and Oceanography 51: 2349–2359.
Vecchi, M., I. L. Newton, M. Cesari, L. Rebecchi & R. Guidetti, 2018. The microbial community of tardigrades: environmental influence and species specificity of microbiome structure and composition. Microbial Ecology 76: 467–481.
Vestheim, H., B. Edvardsen & S. Kaartvedt, 2005. Assessing feeding of a carnivorous copepod using species-specific PCR. Marine Biology 147: 381–385.
Vidakovic, J., G. Palijan & D. Cerba, 2011. Relationship between nematode community and biomass and composition of periphyton developing on artificial substrates in floodplain lake. Polish Journal of Ecology 59: 577–588.
Volland, J.-M., A. Schintlmeister, H. Zambalos, S. Reipert, P. Mozetič, S. Espada-Hinojosa, V. Turk, M. Wagner & M. Bright, 2018. NanoSIMS and tissue autoradiography reveal symbiont carbon fixation and organic carbon transfer to giant ciliate host. The ISME Journal 12: 714.
Walsberg, G. E. & T. C. Hoffman, 2005. Direct calorimetry reveals large errors in respirometric estimates of energy expenditure. Journal of Experimental Biology 208: 1035–1043.
Watts, J. L. & J. Browse, 1999. Isolation and characterization of a Δ5-fatty acid desaturase from caenorhabditis elegans. Archives of Biochemistry and Biophysics 362: 175–182.
Weber, S. & W. Traunspurger, 2013. Food choice of two bacteria-feeding nematode species dependent on food source, food density and interspecific competition. Nematology 15: 291–301.
Wegener, G., M. Y. Kellermann & M. Elvert, 2016. Tracking activity and function of microorganisms by stable isotope probing of membrane lipids. Current Opinion in Biotechnology 41: 43–52.
Weitere, M., M. Erken, N. Majdi, H. Arndt, H. Norf, M. Reinshagen, W. Traunspurger, A. Walterscheid & J. K. Wey, 2018. The food web perspective on aquatic biofilms. Ecological Monographs 88: 543–559.
Wieser, W., 1953. Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nernatode. Arkiv für Zoologie 439–484.
Wilden, B., N. Majdi, U. Kuhlicke, T. R. Neu & W. Traunspurger, 2019. Flatworm mucus as the base of a food web. BMC Ecology 19: 15.
Witte, U., F. Wenzhöfer, S. Sommer, A. Boetius, P. Heinz, N. Aberle, M. Sand, A. Cremer, W.-R. Abraham, B. B. Jørgensen & O. Pfannkuche, 2003. In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. Nature 424: 763–766.
Wu, X., T. Campinas Bezerra, D. Van Gansbeke & T. Moens, 2019. Natural stable isotope ratios and fatty acid profiles of estuarine tidal flat nematodes reveal very limited niche overlap among co-occurring species. PeerJ 7: e7864.
Yeates, G. W., T. d Bongers, R. G. M. De Goede, D. W. Freckman, & S. S. Georgieva, 1993. Feeding habits in soil nematode families and genera—an outline for soil ecologists. Journal of Nematology 25: 315–331.