

Free-Living Nematodes in the Freshwater Food Web: A Review

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Abstract: Free-living nematodes are well-recognized as an abundant and ubiquitous component of benthic communities in inland waters. Compelling evidence from soil and marine ecosystems has highlighted the importance of nematodes as trophic intermediaries between microbial production and higher trophic levels. However, the paucity of empirical evidence of their role in freshwater ecosystems has hampered their inclusion in our understanding of freshwater food web functioning. This literature survey provides an overview of research efforts in the field of freshwater nematode ecology and of the complex trophic interactions between free-living nematodes and microbes, other meiofauna, macro-invertebrates, and fishes. Based on an analysis of the relevant literature and an appreciation of the potential of emerging approaches for the evaluation of nematode trophic ecology, we point out research gaps and recommend relevant directions for further research. The latter include (i) interactions of nematodes with protozoans and fungi; (ii) nonconsumptive effects of nematodes on microbial activity and the effects of nematodes on associated key ecosystem processes (decomposition, primary production); and (iii) the feeding selectivity and intraspecific feeding variability of nematodes and their potential impacts on the structure of benthic communities.

Key words: algae, bacteria, ecology, fish, food web, free-living, freshwater, fungi, interaction, macrofauna, meiofauna, method, organic matter, predation, protozoa, selectivity.

Freshwater benthic micro-metazoans (also referred to as meiofauna or meiobenthos) have been fascinating and popular subjects of research ever since microscopy made them accessible to observation (e.g., Van Leeuwenhoek, 1677). This early enthusiasm led to important morphological (and taxonomical) descriptions during the 19th and the first half of the 20th century. Despite this promising start, there has been little quantitative evaluation of the role of meiofauna in freshwater ecosystems (Robertson et al., 2000; but see Schmid-Araya et al., 2002; Giere, 2009). By contrast, important progress in ecological research has been made by including mesofauna and meiofauna in models of soil and marine benthic food webs, respectively (e.g., Leguerrier et al., 2003; Wardle et al., 2004; Krumins et al., 2013).

Over the last 15 yrs, the inclusion of freshwater meiofauna within an ecological research framework has gained momentum, following the publication of comprehensive monographs in a special issue of *Freshwater Biology* (2000, volume 44) and of two books dedicated to this subject: *Freshwater Meiofauna* (Rundle et al., 2002) and *Freshwater nematodes: ecology and taxonomy* (Abebe et al., 2006). Yet, there are still substantial research gaps concerning the ecology of freshwater meiofauna. For instance, there is mounting consideration of the ecological role of meiofauna in streams; however, meiofauna is still excluded from our current conceptions of how large river ecosystems function. Ecosystems in large rivers are especially affected by human activities; it is therefore critical to understand their ecological functioning in an integrative way to propose a wide-range of solutions for decision-making or management contexts, leading Giere (2009) to plaid: “meiofauna

ecology of large rivers requires urgent investigation.” Furthermore, most available studies concern interstitial habitats (gravel, sediment, and mud, e.g., Hodda, 2006), and a proper assessment of the role of meiofauna in productive interface ecosystems, such as the microbial mats coating mineral and organic hard substrates (Pusch et al., 1998), is mostly lacking.

Free-living nematodes are a major component of freshwater meiofaunal communities, where they often attain very high densities (>1 million individuals per m²; Traunspurger, 2000; Traunspurger et al., 2012), and cover a body-size spectrum of several orders of magnitude (Traunspurger and Bergtold, 2006). Their variety of feeding types suggests their marked trophic specialization (Traunspurger, 1997, 2000, 2002; Moens et al., 2006), whereas their high-degree of intraguild species diversity may be a consequence of trophic niche specialization based on the diversity of available food sources (algae, bacteria, fungi, protozoans, meiofauna, and organic matter, e.g., Traunspurger, 2002; Moens et al., 2006). Nematodes, in turn, provide a food resource for larger benthic and pelagic invertebrates and vertebrates (Beier et al., 2004; Muschiol et al., 2008b; Spieth et al., 2011; Weber and Traunspurger, 2014b), highlighting their pivotal position in freshwater food webs as trophic intermediaries between benthic microbial production and macroscopic consumers.

Given their high diversity and rapid population turnover rates, nematodes are useful model organisms for testing general ecological theories (Reiss et al., 2010). The inclusion of free-living nematodes in conceptual models of freshwater food webs may help to disentangle pathways describing the “small-scale” control of some key ecological processes. There is mounting evidence that free-living nematodes have an important function in soil and marine food webs, by affecting the structure of microbial communities and connecting primary production and the decomposition of organic matter to higher trophic levels (De Mesel et al., 2004; Hohberg and Traunspurger, 2005; Pascal et al., 2008b; Evrad

Received for publication November 28, 2014.

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We thank Wendy Ran and two anonymous reviewers for helpful suggestions and Yang Liu for his help with bibliometric analyses. NM was supported by an Alexander von Humboldt Fellowship.

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This paper was edited by Jyotsna Sharma.

et al., 2010; Steel et al., 2013; Heidemann et al., 2014). Nonetheless, evidence of the role of nematodes in freshwater food webs is both relatively scarce and scattered across the literature, thus hampering both robust comparisons and validation of the patterns in freshwater benthic food webs (Ward et al., 1998; Moens et al., 2006; Thompson et al., 2012). The community structure of freshwater nematodes is a promising indicator of pollution in river sediments (Heininger et al., 2007; Höss et al., 2011; Hägerbäumer et al., 2015, this issue). Nematodes can occupy different trophic-levels in benthic food webs (e.g., bacterivorous, algivorous, and predators), hence their responses to pollutants may vary accordingly. Therefore, we also believe that a more complete knowledge of freshwater food webs using nematodes may be potentially beneficial to risk assessment and managerial approaches.

Here, we review the role of free-living nematodes in the freshwater benthic food web, with particular emphasis on research published during the last decade. After (i) a brief overview of recent research efforts, we focus on (ii) the trophic interactions of nematodes with microbes and the potential consequences on ecosystem processes, (iii) nematode feeding selectivity, (iv) predation on freshwater nematodes, and (v) emerging methodological approaches that may help in elucidating the complex interactions between freshwater nematodes, their prey, and their predators.

Throughout this literature review, we have given priority to studies of the trophic interactions of free-living nematodes from strict freshwater lotic and lentic environments. In some places, comparisons are made with other freshwater meiofaunal taxa or with the results of soil and marine studies, to avoid taxon- and habitat-based oversimplification and to place the discussion within the framework of the functional redundancy of similar-sized heterotrophic organisms in various ecosystems (Gilljam et al., 2011). For a broader overview, including nematode feeding type distribution and trophic ecology in terrestrial and marine ecosystems, we recommend that readers consult the reviews of Traunspurger (2002), Bilgrami and Gaugler (2004), Moens et al. (2006), Traunspurger et al. (2006a), Moens et al. (2013), and Traunspurger (2013).

BRIEF OVERVIEW OF RESEARCH EFFORTS IN THE FIELD

Through an extensive literature survey using the XML package in R (Nolan and Lang, 2014) for parsing and extracting XML content from the literature databases, ISI Web of Science and Google Scholar (last search: 11th November 2014), we obtained 540 publications issued within the last 60 yrs (1954–2014), retrieved by the search query in title–keyword–abstract of the words: “nematod*” AND (“freshwater” OR “river” OR “lake” OR “stream” OR “pond” OR “hyporheic”) NOT “soil”

NOT (“marine” OR “sea” OR “ocean” OR “tidal” OR “estuary” OR “lagoon” OR “brackish” OR “beach”) NOT (“elegans” OR “parasit*”), which potentially represents research conducted on free-living freshwater nematodes. Of these, 93 publications (listed in Table 1) were selected based on their report of field and/or laboratory evidence of at least one trophic interaction involving free-living freshwater nematodes. We recorded the location and type of the study sites recorded in those publications, the main approaches, and the participants in the described trophic interactions (Table 1). While numerous descriptive studies of nematode species and feeding type distribution have been conducted in various freshwater ecosystems, we selected only those studies in which a significant correlation between distribution pattern and potential prey/predator was reported.

Evidence based on distribution patterns made up a large share of the contributions (42% of studies) to knowledge of nematode trophic interactions in freshwater ecosystems. Although the information from those in situ surveys is mostly qualitative, evidence from various ecosystems collectively supports the existence of an important trophic link between nematodes and microbes (especially microphytobenthos [MPB] and bacteria) and foremost between nematodes and the availability of dissolved and particulate organic material (see scheme in Fig. 1). Note that this scheme does not really show the ecological importance of illustrated trophic links, but rather their occurrence as direct or indirect (correlative) evidence throughout relevant literature. As a result, this scheme must be interpreted with caution owing to (i) potential historical bias (e.g., to date, much attention has been paid to the microbe–nematode interaction) and (ii) links which do not necessarily imply a direct trophic interaction. Specifically it is unclear whether the correlation usually observed between nematodes and the amount of organic material is due to direct or to indirect trophic interaction such as ingestion of organic matter via its adsorption onto microbial cells (Höss et al., 2001).

Mounting evidence obtained from in situ manipulative experiments and analyses of the gut contents of predators supports reciprocal trophic linkages between nematodes and other permanent as well as temporary meiofauna (oligochaetes, harpacticoid copepods, tardigrades, water mites, rotifers, and chironomid larvae), with nematodes serving both as predator and as prey for these minute metazoans. Nematodes themselves are also the prey of larger invertebrates and vertebrates and are ingested by gastropod grazers (Table 1; Fig. 1). Nevertheless, trophic transfers from nematodes to higher trophic levels are still incompletely understood. Also, little attention has been paid to the complex trophic interactions between nematodes and protozoans/fungi (but see Bergtold et al., 2005), even though the latter are important regulators of ecosystem processes and contribute substantially to secondary production in

TABLE 1. Summary of strict freshwater studies providing evidence of nematode trophic interactions. Study location, habitat type, and main methodology applied are shown. Trophic interactions evidenced between nematodes and other organisms are listed and were used in the construction of Fig. 1. Parasitic interactions and trophic studies based solely on *C. elegans* are not included.

Country	Collection site(s)	Habitat type	Methodology	Prey	Predator	Reference
UK		River	Gut content		Chironomidae larvae	(Crisp and Lloyd, 1954)
Germany			Observation	Protozoa; meiofauna		(Meyl, 1961)
Poland		Lake; lab	Observation	OM; MPB		(Pieczyńska, 1964)
UK	Pond Imperial College	Pond; lab	Observation	OM; MPB		(Croll and Zullini, 1972)
Poland		Lab	Observation	Bacteria		(Duncan et al., 1974)
Belgium	Pond Uni-Ghent	Lab	Observation	Nematodes		(Grootaert and Maertens, 1976)
Germany	Weser	Lab	Observation	OM; Bacteria		(Riemann and Schrage, 1978)
Austria	Neusiedlersee	Lake; lab	Observation	Bacteria		(Schiemer et al., 1980)
Italy	Po	River	Distribution; observation	MPB; Bacteria; Protozoa; Fungi; Oligochaetes		(Zullini and Ricci, 1980)
Venezuela	Apure	Pond	Gut content		Fish (Characidae)	(Prejs and Prejs, 1987)
Sweden	Gardsjön	Lake	Distribution; observation	MPB; Bacteria; Meiofauna		(Prejs and Lazarek, 1988)
USA	Fish farm	Lab	Feeding experiment		Fish (Cyprinidae)	(Rotmann et al., 1991)
New Zealand	Moose stream; Tim's Creek	River	Distribution	Moss		(Suren, 1991)
USA	Mississippi	River	Distribution	OM; Macrophytes		(Anderson, 1992)
Norway	Dokka	River	Distribution; feeding experiment	Oligochaetes, Nematodes	Chironomidae larvae	(Prejs, 1993)
Canada	Duffin Creek	River	Distribution	Meiofauna; Chironomid		(Williams, 1993)
Romania	Mobile Cave	Cave	Distribution; observation	Bacteria		(Poinar and Sarbu, 1994)
USA	White Clay Creek	River	Fluorescent diatoms/bacteria	MPB; Bacteria		(Borchardt and Bott, 1995)
Austria	Oberer Seebach	River	Gut content	Rotifers; Oligochaetes		(Schmid-Araya and Schmid, 1995)
Sweden	Erken	Lake	Distribution	OM; MPB		(Goedkoop and Johnson, 1996)
Austria	Oberer Seebach	River	Gut content		Chironomidae larvae	(Schmid and Schmid-Araya, 1997)
USA		Hyporheic	Distribution	OM		(Strayer et al., 1997)
Sweden	Erken	Lab	Feeding experiment	Bacteria		(Traunspurger et al., 1997)
USA	Coweeta	River	Litter exclusion experiment	OM		(Wallace et al., 1997)
USA	White Clay Creek	River	Clearance rates	MPB; Protozoa		(Bott and Borchardt, 1999)
USA	Little Miami	River	Micro-distribution; SEM	OM; MPB		(Greenwood et al., 1999)
Croatia	Borovik reservoir	Lake	Distribution	OM		(Vidaković and Bogut, 1999)
China	Houhu; Biantang	Lake	Distribution	Macrophytes		(Wu and Liang, 1999)
Italy	Arnone	River	Distribution	OM		(Bazzanti, 2000)
USA	Goose Creek	River	Distribution	OM; Bacteria; Fungi		(Palmer et al., 2000)

(Continued)

TABLE 1. Continued.

Country	Collection site(s)	Habitat type	Sediment	Methodology	Prey	Predator	Reference
Croatia	Sakadas; Danube oxbow Lake	Lake	Sediment	Distribution	Nematodes	Gastropod	(Bogut and Vidaković, 2002)
Costa Rica		River	Epilithon	In situ enclosures			(Duft et al., 2002)
Mexico		Pond	Sediment	Distribution; modeling	OM; MPB		(Escobar-Briones et al., 2002)
Sweden	Erken	Lake	Epilithon	In situ enclosures	MPB	Gastropod (<i>Theodoxus fluviatilis</i>)	(Hillebrand et al., 2002)
Nigeria	Ogba	River		Gut content		Fish (Ciclidae)	(Omoigberale and Aruoture, 2002)
UK	Broadstone	River	Sediment	Gut content; modeling		Insect larvae	(Schmid-Araya et al., 2002)
Germany	Körsch; Krähenbach	River	Sediment	Distribution	OM		(Beier and Traunspurger, 2003)
Germany	Baderbach; Obersee	Lake; river	Sediment	Sediment microcosms		Flatworm	(Beier et al., 2004)
Germany	Brunnsee	Lake	Sediment	Distribution	Protozoa; Mei fauna		(Bergtold and Traunspurger, 2004)
China	Danchi	Lake	Wood	Observation		Fungi	(Hao et al., 2004)
Switzerland	Zurich	Lab		Behavior	MPB		(Höckelmann et al., 2004)
China	Donghu	Lake	Sediment	Distribution	OM		(Wu et al., 2004)
Brazil	Mineiro	River		Gut content		Shrimp (Aegidae)	(Bueno and Bond-Buckup, 2004)
China	Danchi	Lake	Sediment	Observation		Fungi	(Hao et al., 2005)
Italy	Taro; Ticino	River	Sediment	Distribution	OM; MPB		(Barbuto and Zullini, 2005)
Germany	Brunnsee	Lake	Sediment	Distribution	OM; Bacteria; Protozoa		(Bergtold and Traunspurger, 2005a)
USA	Coweeta Streams	River		Gut content		Salamander larvae (<i>Eurycea</i>)	(Johnson and Wallace, 2005)
New Zealand	Wanaka	Lake	Epiphyton	SLA; distribution	OM	Gastropod (<i>Potamopygus</i>)	(Kelly and Hawes, 2005)
Germany	11 Alpine Lakes	Lake	Sediment	Distribution	MPB		(Michiels and Traunspurger, 2005)
Sweden	17 Lakes	Lake	Epilithon	Distribution	OM; MPB		(Peters and Traunspurger, 2005)
Germany	Constance	Lake	Epilithon	Distribution	OM; MPB; Bacteria		(Peters et al., 2005)
Germany	Constance	River; lake	Sediment	Distribution	OM		(Wirthöft-Mühlmann et al., 2005b)
Germany	Constance	River; lake	Sediment	POM enrichment experiment	OM		(Wirthöft-Mühlmann et al., 2005a)
Germany	Rhine	River	Epilithon	Micro-flow chambers	OM; MPB; Bacteria; Protozoa		(Esser, 2006)
Canada	Sooke; Shawnigan	Lake	Sediment	Distribution	OM		(Furey et al., 2006)
Spain	Llobregat	River	Epilithon	Distribution	MPB		(Gaudes et al., 2006)
USA	Pascagoula; Escatawpa	River		Gut content		Fish (Centrarchidae)	(Peterson et al., 2006)
Germany		Lake	Sediment	Sediment microcosms		Chironomidae larvae; copepods	(Traunspurger et al., 2006b)
Croatia	Čonakut Channel	River	Epiphyton	Distribution	MPB; Protozoa; Macrophytes		(Vidaković and Bogut, 2006)
Germany	Schussen; Constance	River; lake	Sediment	Distribution	OM; MPB; Bacteria		(Wirthöft-Mühlmann et al., 2006)
France	Tarn	Lab	Epilithon	Optode measurements	MPB		(Mathieu et al., 2007)
Sweden	Erken	Lake	Epilithon	In situ enclosures		Gastropod (<i>T. fluviatilis</i>)	(Peters et al., 2007)
Argentina	Don Carlos; Pescado	River	Epipsammon	Distribution	MPB; Bacteria		(Sierra and Gomez, 2007)
Germany		Lab	Sediment	Distribution		Chironomidae larvae; Tubificidae	(Teiwes et al., 2007)

(Continued)

TABLE 1. Continued.

Country	Collection site(s)	Habitat type	Methodology	Prey	Predator	Reference
Italy	Bracciano	Lake	Distribution	Macrophytes		(Mastrantuono et al., 2008)
Romania	Mobile Cave	Lab	Functional-response experiment		Copepod	(Muschol et al., 2008b).
Spain	Fuerosos	River	Distribution	OM		(Gaudes et al., 2009)
Germany		River	Micro-flow chambers	Protozoa		(Norf et al., 2009)
Mexico	Cueva de Villa Luz	Cave	Micro-distribution	Bacteria	Water mite	(Borgonie et al., 2010)
Romania	Mobile Cave	Lab	Feeding experiment	OM; MPB		(Schroeder et al., 2010)
France	Garonne	River	Distribution		Fish (juvenile Cyprinidae)	(Majdi et al., 2011)
Germany	Obersee	Lab	Feeding experiment		Fish (Cyprinidae)	(Spieth et al., 2011)
Turkey	Tödürge	Lake	Gut content	OM; MPB; Bacteria		(Ünver and Erk'akan, 2011)
Croatia	Sakadas	Lake	Distribution	MPB		(Vidaković et al., 2011)
France	Garonne	River	Gut pigment	OM; MPB		(Majdi et al., 2012b)
France	Garonne	River	SIA; SIP	OM; MPB		(Majdi et al., 2012a)
Sweden	Erken	Lake	SIA	MPB; Bacteria		(Peters et al., 2012)
Sweden	Erken	Lake	In situ enclosures		Gastropod (<i>T. fluviatilis</i>)	(Peters and Traunsperger, 2012)
Sweden	Largen; Erken; Limmare	Lake	Distribution			(Schroeder et al., 2012a)
Germany	Constance	Lake	Distribution	OM; MPB; Bacteria		(Traunsperger et al., 2012)
Argentina		Lab	Gut content		Juvenile crayfish	(Viau et al., 2012)
Russia	Baikal	Lake	SIA	Bacteria		(Zemskaya et al., 2012)
Austria	Möll; Kleimelendbach	Glacier; river	Distribution	Fungi		(Eisendle-Flöckner et al., 2013)
Sweden	Erken	Lake; lab	SIA; SIP	MPB; Bacteria		(Estifanos et al., 2013)
Spain	Fuerosos	River; lab	Feeding experiment	Bacteria		(Gaudes et al., 2013)
Germany		Lab	Sediment microcosms	OM; MPB; Bacteria		(Ristau et al., 2013)
Sweden	Erken	Lake	In situ enclosures	Bacteria		(Schroeder et al., 2013b)
Romania	Mobile Cave	Lab	Feeding experiment		Gastropod (<i>T. fluviatilis</i>)	(Weber and Traunsperger, 2013)
Brazil	3 Streams in Pirapo catchment	River	Gut content		Fish (Heptapteridae)	(Tofoli et al., 2013)
Sweden	Largen; Erken; Limmare	Lake	Distribution; gut pigment	OM; MPB		(Kazemi-Dinan et al., 2014)
France	Bernazobre	River	In situ enclosures; modeling	OM; Bacteria	Chironomid; Flatworm	(Majdi et al., 2014)
Germany	Teutoburger Wald	Water tank	In situ mesocosms	OM		(Pratscheck and Traunsperger, 2014)
Germany		Lab	Feeding experiment		Fish (Cyprinidae)	(Weber and Traunsperger, 2014b)

OM = organic matter; MPB = microphytobenthos, POM = particulate organic matter; SEM = scanning electron microscopy, SIA = stable isotope analysis, SIP = stable isotope probing.

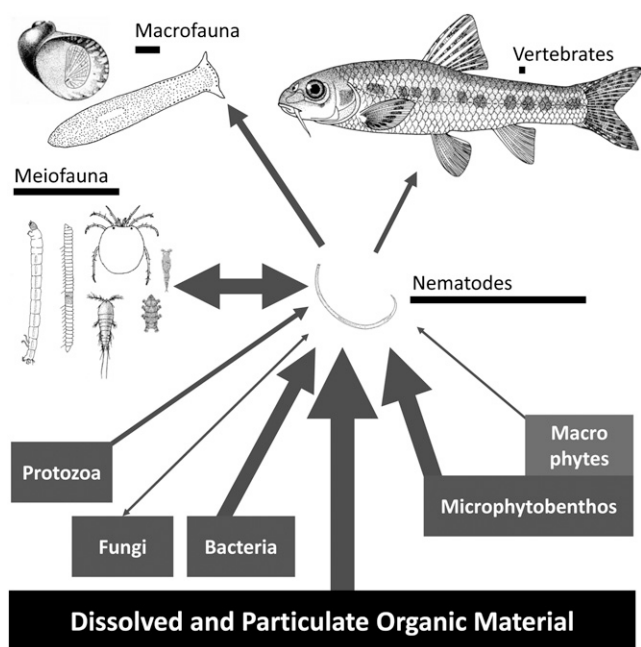


FIG. 1. Trophic interactions involving nematodes in freshwater ecosystems based on their frequencies of occurrence in literature. Arrow size is relative to the number of trophic interactions directly or indirectly evidenced in the relevant literature (93 studies; listed in Table 1). Arrow trajectory shows the trajectory of energy. Scale bar for metazoans is 1 mm. Meiofauna include permanent meiofaunal taxa, such as rotifers, tardigrades, water mites, harpacticoid copepods, and oligochaetes; as well as temporary meiofauna, such as larvae of chironomids. Macrofauna include gastropods, flatworms, and shrimps; Vertebrates include fishes and amphibian larvae. Macrophytes also include bryophytes.

freshwater ecosystems (Gessner and Chauvet, 1994; Bergtold and Traunspurger, 2005b; Risse-Buhl et al., 2012; Faupel and Traunspurger, 2012).

For the period between 2003 and 2013, there was neither a decrease nor an increase in the number of studies that showed trophic interactions of freshwater nematodes (Fig. 2A; Mann-Kendall; $\tau = 0.2$; $P = 0.53$), in contrast to the total number of studies dealing with freshwater nematodes, which increased significantly during the same period (Fig. 2B; Mann-Kendall; $\tau = 0.6$; $P = 0.01$). This striking difference should foster further evaluation of the role of nematodes in freshwater food webs. Moreover, 73% of the research efforts on the trophic ecology of freshwater nematodes were concentrated in European inland waters (Fig. 2B), whereas food web dynamics in tropical and subtropical rivers and lakes, i.e., areas currently experiencing acute anthropogenic pressure (Dudgeon et al., 2006), have largely been ignored.

INTERACTIONS WITH MICROBES AND ECOSYSTEM PROCESSES

There is a large body of evidence supporting the intimate association of nematodes with bacteria and decaying detritus, with potential consequences on the

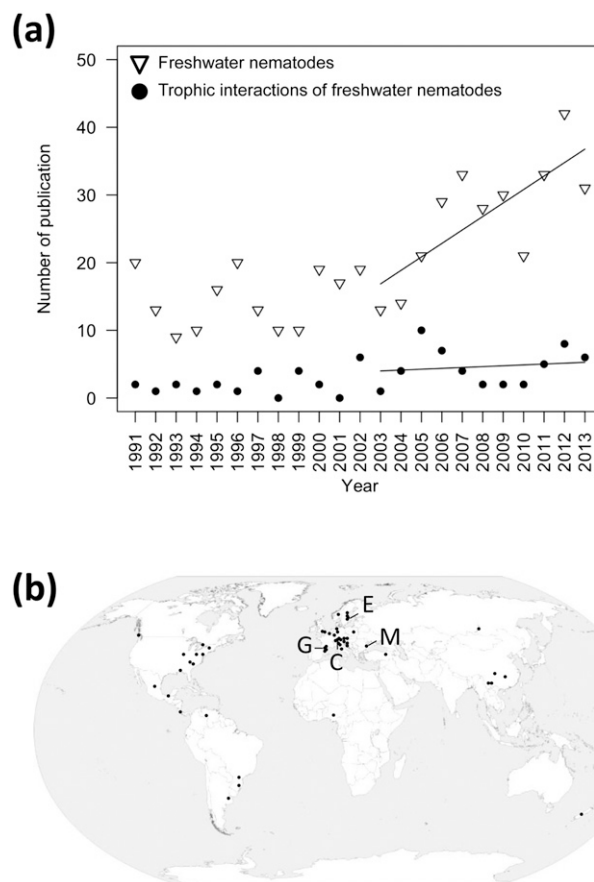


FIG. 2. (A) Yearly publication rate of studies considering broad aspects of free-living freshwater nematodes versus studies highlighting their trophic interactions, from 1991 to 2013. (B) Global distribution of study/collection sites where evidence of trophic interactions involving free-living freshwater nematodes has been obtained (collection/study sites listed in Table 1). Some sites have been investigated repeatedly ($N > 3$ different studies): Lake Erken (E), Lake Constance (C), Garonne River (G), and Movel Cave (M).

decomposition process in lentic and lotic ecosystems. For instance, Goedkoop and Johnson (1996) observed a rapid increase in nematode densities in Lake Erken (Sweden) after the sedimentation of a pelagic diatom bloom on the lake bottom. Within 35 days, bacteria had mineralized an average of 12.4% of the detrital C pool, while sediment-dwelling meiofauna had assimilated 7.2% and chironomids 6% of detrital C. In a 1-yr study of Lake Constance (Germany), Witthöft-Mühlmann et al. (2005a) recorded a similarly strong positive response of nematode densities to river-borne particulate organic matter sedimentation on the lake bottom. Surprisingly, the response of nematodes to organic matter availability was much stronger than that of the lake's benthic microbial communities. A possible rationale for this could be the importance of top-down control and/or indirect effects of nematodes on microbial communities (see below), in analogy to the green world hypothesis proposed by Hairston et al. (1960). Taken together, these findings highlight the involvement of nematodes in energy turnover in sediment patches enriched with allochthonous organic material.

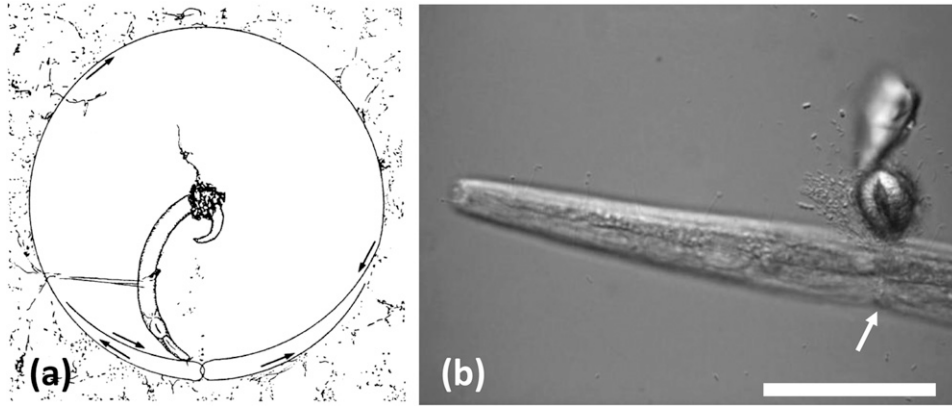


FIG. 3. (A) Scheme of detritus-pellet formation by a Chromadoridae nematode. After adherence of the nematode's tail to the substrate via caudal secretions, the surrounding particles are collected by oscillation movements and further agglutinated into a pellet (after Meschkat 1934; modified in Riemann and Helmke 2002). (B) Anterior part of a living *Chromadorina bioculata* retrieved from epilithic biofilms of the Garonne River (France). The white arrow shows the constriction of the nematode cuticle due to the attachment of secretions. A diatom cell and detrital particle are trapped in secretions. Bacterial density is high in the pellet and around the trapped diatom. Scale bar is 50 μm .

In forested streams, where shading by the riparian canopy can alter primary production, the decomposition of plant litter is an essential ecological process that fuels stream food webs. During a 3-yr litter exclusion experiment, Wallace et al. (1997) observed a significant reduction of nematode densities in reaches that were prevented from litter fall inputs. Other field evidences also support the ability of nematodes to aggregate preferentially in leaf packs with the highest biomass of microbial decomposers (fungi and bacteria) and/or the largest amount of organic matter clumps (Palmer et al., 2000; Swan and Palmer, 2000; Gaudes et al., 2009). Nematodes may influence decomposition rates in forested streams by affecting microbial decomposers, although the relative importance of this mechanism in freshwater ecosystems is discussed controversially in the literature (Cummins, 1974; Abrams and Mitchell, 1980). Yet, it is broadly accepted that nematodes significantly affect decomposition processes in soil and marine ecosystems (e.g., Freckman, 1988; Alkemade et al., 1992).

Although fungal biomass is generally several orders of magnitude greater than bacterial biomass in leaf packs, typical fungal-feeding nematodes (e.g., *Aphelenchoides* spp., *Filenchus* spp.) were rarely found in the streams of southwestern France and Canada whereas bacterial-feeding nematodes (e.g., *Eumonhystera* spp., *Plectus* spp.) dominated consistently (Majdi et al., 2014, unpubl. data). This suggests either low access to the mycelial biomass embedded in leaf tissues or competitive exclusion due to the greater diet flexibility and/or greater colonization success of bacterial-feeding species in leaf packs. Interestingly, aquatic fungi are not only nematode prey, they are also nematode predators, as several hyphomycete species were shown to prey on litter-dwelling nematodes (Peach, 1950; Hao, et al., 2005; Swe et al., 2009).

In lotic systems, it is still difficult to separate the distribution trends of nematode species from the multiple influences of intraguild interference, environmental

forcing, and trophic interactions with microbes. Nematode distribution in exposed riverine patches such as litter packs or epibenthic biofilms may undergo important variations according to fluctuations in the hydrological regime and the downstream transport of dissolved and particulate resources (Palmer et al., 2000; Swan and Palmer, 2000; Majdi et al., 2012c). Under laboratory controlled conditions, Perlmutter and Meyer (1991) showed that harpacticoid copepods can remove >30% of bacterial biomass from decaying leaf surfaces. Additional experimentally based evaluations of the role of nematodes in lotic detritus-based food web are needed, especially studies focusing on the pathway of top-down control on microbial decomposers and examining the potential indirect consequences on decomposition rates. In fact, insights gained from laboratory investigations of bacteria–nematode interactions (Traunspurger et al., 1997; Gaudes et al., 2013) tend to support the importance of indirect control pathways (bioturbation, excretion) on microbial activity, but whether this mechanism operates in natura remains to be determined.

Primary production is another key ecosystem process in which nematodes exert top-down regulation. Consistent surveys of nematodes dwelling in phototrophic biofilms (or periphyton) have provided increased evidence of a tight linkage between the biomass of MPB and that of nematodes (especially Chromadoridae) in lakes (Traunspurger, 1992; Hillebrand et al., 2002; Peters and Traunspurger, 2005; Schroeder et al., 2012b; Kazemi-Dinan et al., 2014) and rivers (Esser, 2006; Gaudes et al., 2006; Majdi et al., 2011, 2012c). The dominance of Chromadoridae within nematode communities in shallow freshwater periphyton has been consistently reported for the last 100 yrs (Micoletzky, 1914; Schneider, 1922; Meschkat, 1934; Meuche, 1938; Young, 1945; Pieczynska, 1964; Croll and Zullini, 1972; Traunspurger, 1992; Majdi et al., 2011; Schroeder et al., 2012a, 2013a). In some cases, Chromadoridae were

observed to collect and agglutinate particulate material using their caudal sticky secretions to form a so-called detritus pellet (Fig. 3). Croll and Zullini (1972) ascribed this behavior to the predominantly epilithic lifestyle of Chromadoridae, in which fixation to the substratum allows these nematodes to overcome epibenthic shear-stress constraints. It may also be related to mucus-trap feeding and enzyme sharing (Riemann and Schrage, 1978; Riemann and Helmke, 2002), two proposed mechanisms whereby nematodes directly feed on items trapped in their secretions and/or benefit from the enzymatic activity of bacteria that cleaves the refractory material agglutinated in secretions into more edible labile compounds. Moens et al. (2005) further show experimentally that a specific bacterial assemblage can develop on nematode secretions, underlining a potential example of nematode–bacterium cooperation (see also Murfin et al., 2012). Based on combined assessments of the gut contents of nematodes and of their assimilation of freshly photosynthesized carbon (C) in the Garonne River (France), Majdi et al. (2012a,b) showed that Chromadoridae can derive 1% to 27% of their energetic demand from the direct ingestion of diatom cell contents and that the assimilation of freshly photosynthesized C completely (104%) fulfills their energetic demand. A major part of the C fixed by photosynthesis is rapidly exuded by diatoms as exopolymeric substances (EPS) and then processed by bacteria (Romaní and Sabater, 1999). These results suggest that Chromadoridae for the most part feed on the EPS exuded by diatoms, possibly through “gardening” interactions with bacteria, and to a lesser extent graze directly on diatom cells.

Quantitatively, freshwater nematode communities exert rather low grazing pressure on MPB (Borchardt and Bott, 1995; Majdi et al., 2012a,b; Graba et al., 2014). However low grazing pressure does not mean unimportant impacts on microbial communities (e.g., De Mesel et al., 2004; Hubas et al., 2010), and in a laboratory experiment, Mathieu et al. (2007) determined a threshold of 100 individuals/cm², above which diatom biofilms show much higher rates of oxygen production. As this density threshold is often exceeded in the periphyton (Gaudes et al., 2006; Majdi et al., 2011; Schroeder et al., 2012b, 2013a), primary production may well be substantially affected by nematodes (Fig. 3). The result is a greater spatial heterogeneity of microbial mats and thus higher rates of solute transport within those mats (Derlon et al., 2013). The presence of nematodes in phototrophic biofilms likely stimulates primary production, by enhancing both the porosity of biofilms to nutrients and light penetration in the mat, as was observed in the upper few millimeters of muddy estuarine sediments by Pinckney et al. (2003). Qualitatively, nematode feeding preferences are also expected to affect the assemblage of phototrophic communities, as discussed in Food Recognition and Selection. In return,

bottom-up control is likely to influence the local diversity of nematode communities. For instance, nematode communities dwelling diatom-dominated periphyton in rivers and lakes consistently show both a low diversity and an overwhelming dominance of one or two chromadorid species (Peters et al., 2005; Gaudes et al., 2006; Majdi et al., 2011; Schroeder et al., 2012a). Nonetheless, it is not clear whether this pattern was due to bottom-up structuring (diatom feeding), or to environmental forcing such as the important exposition to flow or wave disturbance of these habitats which could favour again Chromadorids able to anchor themselves efficiently using their sticky caudal secretions (Croll and Zullini, 1972). More generally, it is beyond the scope of this review and still premature to elaborate much about the drivers of nematode diversity, due to the scarcity of comparable datasets from which general patterns can be drawn (Hodda et al., 2009).

FOOD RECOGNITION AND SELECTION

Free-living nematodes forage in small-scale patchy environments. Hence, they are likely able to discriminate among the many different food items they encounter (bacteria, algae, fungal hyphae and spores, protozoans, particulate, and dissolved organic matter), selecting the highest quality food available at the lowest possible cost (e.g., in their closest vicinity). Food recognition and specific handling can translate into typical behavioral and morphological traits that are identifiable during *in vivo* observations and in behavioral assays (e.g., Jensen 1982; Moens and Vincx 1997; Moens et al., 1999b; Höckelmann et al., 2004; Bilgrami and Gaugler 2005; Salinas et al., 2007; Hohberg and Traunspurger 2009; Weber and Traunspurger 2013). Recognition of food hotspots can lead to intra-specific agglutination mechanisms. Agglutination can be provoked by kairomones (e.g., Höckelmann et al., 2004; detailed below). In addition, intra-specific chemical communication using pheromones also mediates a variety of behavioral responses from avoidance to attraction (Choe et al., 2012), supporting the existence of complex mechanisms for food recognition and exploitation in nematodes. The presence of selectively feeding nematodes changes the size spectra and species composition of soil and marine microbial communities (Romeyn and Bouwman, 1983; Jensen 1987; De Mesel et al., 2004; Salinas et al., 2007; Rzeznik-Orignac et al., 2008; Moens et al., 2014), and thus microbial activity as well as the rates of associated ecological processes. Although often advocated as a rationale for the high diversity and apparent species redundancy of freshwater nematodes (Hodda et al., 2009), feeding selectivity has nonetheless received scant attention, and large-scale quantitative investigations are, for the most part, lacking (Moens et al., 2006). In this context, there is still considerable controversy about how specialist

nematodes can be in their selection of food items. Trophic opportunism is widespread in nature, and the number of feeding-types undoubtedly underestimates the real number of feeding modes in free-living freshwater nematodes. In the following paragraphs, we listed some arguments to this debate.

In their laboratory study of chemotaxis by the freshwater nematode *Bursilla monhystera* (Rhabditidae) toward odors of cyanobacterial strains present in biofilms, Höckelmann et al. (2004) provided the first evidence of the selective attraction of nematodes to axenic cyanobacterial biofilms of *Plectonema* sp. but not to those of *Calothrix* sp. *B. monhystera* was also not attracted by single volatile organic compounds (or odors) isolated from cyanobacterial biofilms, clearly indicating the specificity of the chemotaxis response for complex multi-component odors. The same authors also observed that *B. monhystera* moved toward attractive odor spots at a rate of ~1.5 cm/min, although upon its arrival it did not ingest the cyanobacterial filaments directly, but rather browsed in search of associated bacteria or EPS.

Using a “cafeteria-design” in laboratory microcosms, Weber and Traunspurger (2013) further observed the different and marked food choices of two nematode species, *Panagrolaimus* cf. *thienemanni* (Panagrolaimidae) and *Poikilolaimus* sp. (Rhabditidae), isolated from the submerged Movile Cave (Romania). *Panagrolaimus* preferred high densities, and *Poikilolaimus* low densities of *Escherichia coli* (10^9 cells per ml and 10^6 cells per ml, respectively). Despite a cell size similar to that of *E. coli*, the green algae *Chlorella minutissima* was rarely preyed upon by nematodes. Moreover, the two nematode species were rarely found at the same *E. coli* density spot, suggesting the absence of competition due to trophic niche specialization based on the recognition of food density levels. Those results corroborated with the autecological characteristics and distributional patterns of both species in the cave ecosystem (Muschiol and Traunspurger, 2007; Schroeder et al., 2010; Muschiol et al., 2015).

In a laboratory experiment, Estifanos et al. (2013) offered a diet consisting of either *E. coli*, *Matsuebacter* sp., or both to cultures of *Caenorhabditis elegans*, *Acrobeloides tricornis*, *Panagrolaimus* sp., and *Poikilolaimus* sp. Differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of these nematode species were recorded and were shown to be linked to their differential assimilation capacities of the monobacterial diet offered. Feeding selectivity was quantified in mixed bacterial diet experiments showing that *E. coli* contributed 71% to the C supply of *C. elegans*, whereas *Matsuebacter* sp. contributed >90% to that of *A. tricornis*. In their further study of the natural periphytic communities of Lake Erken (Sweden), Estifanos et al. (2013) similarly followed the fate of C and nitrogen (N) from algae and bacteria in a stable isotope probing (SIP) experiment. Their results, showing that nematodes quickly

incorporated freshly photosynthesized material, highlighted the importance of algal-derived material (i.e., diatoms, green algae, and their EPS) in the diet of periphytic nematodes. This conclusion confirmed a previous in situ SIP experiment that showed the rapid incorporation of freshly photosynthesized C by periphytic nematodes from the Garonne River (France) (Majdi et al., 2012a).

Algal biomarker pigments in the guts of periphytic nematodes were quantified using high-performance liquid chromatography in studies carried out at a single date in three Swedish lakes, Largen, Erken, and Limmaren (Kazemi-Dinan et al., 2014), and over a 1-yr period in the Garonne River in southwestern France (Majdi et al., 2012b). Through comparisons of the ratios of biomarker pigments in periphyton and in nematodes, nematode algivory was examined regarding the relative availabilities of the main MPB groups (diatoms, green algae, and cyanobacteria). Diatom biomarkers were found in all nematodes. In fact, diatoms consistently dominated the MPB in the studied lakes and river. However, in the shallow zones of Lake Erken (mesotrophic) and in Lake Largen (oligotrophic), green algae were preferentially ingested, based on the accumulation of the respective pigments in nematode guts. In the Garonne River, the ingestion of chlorophyll *a* was proportional to its availability in the periphyton, suggesting the nonselective opportunistic ingestion of diatom cells. As grazing on diatom cells only covered a small fraction of the energetic demands of periphytic nematodes, diatom-derived polymeric substances were proposed to be an important additional food resource (see Interactions with Microbes and Ecosystem Processes for details).

There is little information on the diet of predatory nematodes in freshwater ecosystems, but Prejs (1993) and Schmid-Araya and Schmid (1995) observed the ingestion of various meiofauna (rotifers, naidid and enchytraeid oligochaetes, other nematodes, and chironomids) by *Anatonchus dolichurus*, *Anatonchus tridentatus*, and *Prionchulus punctatus*. Although still understudied, predatory nematodes in freshwater ecosystems are likely able to exhibit prey selectivity, based on compelling evidence gained from laboratory observations of the feeding behavior of soil and marine predatory nematodes on nematode prey (e.g., Bilgrami, 1993; Moens et al., 1999a, 2000; Bilgrami and Gaugler, 2005; Bilgrami et al., 2005). Those studies showed that predatory nematodes tend to select their prey according to their physical, chemical, and behavioral characteristics (e.g., thickness of the cuticle, secretion of deterrent substances, and capacity to adopt escape strategies). However, the placement of predatory nematodes in agar medium may affect their perception of prey cues. For this reason, we stress that the feeding selectivity of predatory nematodes in natural communities remains to be ascertained.

NEMATODES AS PREY

Few studies of freshwater ecosystems have tackled the energy fluxes between fungi, protozoans, and nematodes (Fig. 1). Although trophic interactions between nematodes and eukaryotic microbes are thought to be nonreciprocal, those microbes indeed prey upon nematodes. For example, nematodes can be preyed upon by specialized aquatic hyphomycetes (e.g., Hao et al., 2005), and there is evidence from soil ecosystems of predatory ciliates (*Urostyla* sp. and testate amoebae) attacking and consuming even relatively large nematode taxa, such as *Ironus*, *Clarkus*, and *Tobrilus* spp. (Doncaster and Hooper, 1961; Yeates and Foissner, 1995). In the benthos, reciprocity in the trajectory of trophic interactions is certainly plausible, given the coexistence of a diverse assemblage of protozoan and metazoan species with overlapping body sizes. Intraguild predation may well be intense, since the most efficient way to cope with competitors surely is to devour them! Several studies have reported reciprocal predation between nematodes and other metazoan meiofauna (Fig. 1; Table 1). In this context, the timing of colonization (“priority-effects”) becomes crucial for determining species distribution and food web structure—a topic that deserves, again, further evaluation.

Nematodes are by no means a “trophic dead-end” in freshwater ecosystems, as increasing evidence supports the consumption of nematodes by macrofauna and vertebrates that are several orders of magnitude larger (Table 1). For instance, the massive consumption of nematodes together with algae by “peaceful” herbivorous snails grazing the periphyton has been clearly demonstrated (Hillebrand et al., 2002; Kelly and Hawes, 2005; Peters and Traunspurger, 2012; Schroeder et al., 2013b). Whether the presence of nematodes and other meiofauna increases the palatability of periphyton to grazers has not been thoroughly examined, but periphyton containing nematodes probably fuel grazers with nonnegligible sources of high-quality protein and essential polyunsaturated fatty acids. Voracious macroinvertebrate predators, such as flatworms can also affect nematodes, either negatively, by direct top-down consumption (Beier et al., 2004), or positively, by the bottom-up stimulation of sediment retention and bacterial biomass through copious mucus secretions (Majdi et al., 2014). The latter authors showed that in intricate detritus-based habitats, the indirect effects of predators on habitat structure may have potentially larger consequences than consumptive effects. In the same context, a recent experiment using Chloroperlidae larvae as predators showed negative effects on the nematode community due to sediment resuspension by these active predators (N. Majdi, unpubl. data).

The consumption of nematodes by a variety of juvenile and adult freshwater fishes (Characidae, Cyprinidae, Ciclidae, and Centrarchidae; see Table 1) has

been reported, strengthening the hypothesis of direct top-down control of meiofauna by fishes (Weber and Traunspurger, 2014b). That same study determined a strong reduction of nematode biomass (80–94%) in sediment exposed to the predation of juvenile carp (*Cyprinus carpio*) and gudgeon (*Gobio gobio*). Effects of fish predation on the body-size distribution of nematode prey appear to be species-specific (Spieth et al., 2011; Weber and Traunspurger, 2014a). The rationale is that many benthivorous fish species are size-selective feeders because of the different morphologies of their oral cavities and gill rakers. An interesting implication of trophic transfer from nematodes to highly mobile organisms, such as fishes, is that the localized benthic secondary production of nematodes can be exported both vertically and horizontally, thereby enhancing the ecological connectivity of freshwater ecosystems.

EMERGING APPROACHES

Many different approaches have been applied to disentangle the trophic interactions of freshwater nematodes, including descriptions of nematode species and feeding-type distribution patterns (see Table 1), the quantification of gut pigment contents (Majdi et al., 2012b; Kazemi-Dinan et al., 2014), the assessment of predator–prey functional responses (Beier et al., 2004; Hohberg and Traunspurger, 2005; Muschiol et al., 2008a, 2008b), food tactism assays (Höckelmann et al., 2004; Weber and Traunspurger 2013), and the use of fatty acid (FA) profiling, SIP, and other biomarkers/tracers to investigate the trophic positioning and fluxes of matter that are mediated by freshwater nematodes and other meiofaunal organisms (Borchardt and Bott, 1995; Bott and Borchardt, 1999; Caramujo et al., 2008; Majdi et al., 2012a, 2012b; Peters et al., 2012; Estifanos et al., 2013; Mialet et al., 2013; Kazemi-Dinan et al., 2014). In this section we briefly describe the approaches (SIP, FA, profiling, gut DNA content, and automated image tracking) that may fully reveal the composition of the nematode diet, allowing nematodes to be properly placed within a more comprehensive picture of freshwater food webs. For more detailed descriptions of these approaches, the reader is referred to the reviews of King et al. (2008), Crotty et al. (2012), Traugott et al. (2013), and Dell et al. (2014). Most of our knowledge about nematode feeding ecology has been grasped at the level of feeding-types or, at best, at the level of species. Understanding the variation of individual traits is a key constraint to resolve population-level effects (Violle et al., 2012). However, we still have a very limited knowledge of intraspecific variability in nematodes. In this context, this section deals first with approaches requiring (many) individuals in one analysis, and then present some approaches that have the potential to reveal feeding variability at the individual level.

Despite their disadvantages—mostly their low resolution when multiple food sources are consumed by the study organisms—SIP and FA profiling are powerful approaches that enable the assessment of the feeding history of consumers and a quantification of their assimilation of ingested food items. Furthermore, the two techniques can be merged (compound-specific stable isotopic analysis) to better examine the use of a labeled basal food source by various consumers (Ruess and Chamberlain, 2010). However, the most challenging aspect of including nematodes into a broader picture of freshwater food webs is the low individual biomass of most free-living nematodes, which makes such approaches time-consuming because of the copious amounts of nematode individuals needed to achieve proper signal detection. For instance, minimum N and C requirements for most standard mass spectrometry platforms are approximately 20 μg of N and C per sample, which practically means sorting, cleaning, and encapsulating tens to hundreds of nematodes to meet the minimum sample amount required for signal detection. While mass spectrometer systems can be specifically modified to allow the analysis of smaller samples (>1 μg N and 2 μg C; Carman and Fry, 2002), the inclusion of nematodes is far from routine in the vast majority of trophic studies. One way around this methodological limitation is to use nematode species reared in the laboratory on strains of labeled microbes, which allows high individual recovery rates and thus a reliable assessment of nematode assimilation rates and metabolic pathways at the level of species (e.g., Ruess et al., 2002; Pascal et al., 2008a; Estifanos et al., 2013).

In a wider sense, individuals can be seen as the “single-cell” components of ecosystems. Individual-based approaches enable individual traits to be linked to the properties of the systems they compose; this is achieved using well-developed statistical tools such as individual-based modeling (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005). It is possible to merge SIP with Raman microspectroscopy to detect enrichment from a ^{13}C -labeled source at the individual level (Li et al., 2013). Using this approach, the latter authors detected ^{13}C assimilation by *C. elegans* fed on ^{13}C -labeled *E. coli* based on the Raman spectra of a single *C. elegans* individual, which showed distinctive red shifts similar to that of its prey. Li et al. (2013) showed that the Raman shift of the thymine band provides a simple indicator of ^{13}C incorporation into nematode cells. Further application of this method in laboratory and field conditions may be a relevant alternative approach to examine more finely the C flows in freshwater food webs.

The detection and identification of prey DNA contained in the guts of nematodes is a recent and potentially complementary qualitative approach. It brings the advantages of a higher specificity and sensitivity and thus the possibility to obtain more detailed insights into trophic network complexity. With sufficient temporal

replication, a reduction of the possibility of contamination, and the establishment of a prey molecular database as a reference, this approach could bring valuable information on nematode selectivity in situ and could be even applied to individual-based diet analyses. To the best of our knowledge, the use of molecular techniques to unravel the diet of nematodes is an as yet untested strategy. However, it has been applied to analyze the gut contents of marine copepods, with the detection of DNA of algae, cyanobacteria, and invertebrate preys (Nejstgaard et al., 2003; Vestheim et al., 2005; Motwani and Gorokhova, 2013). These examples of the successful use of this approach should pave the way for its application to nematodes and other meiofauna. Conversely, the detection of nematode DNA in the guts of predators will reveal the connections of nematode species with higher trophic levels, provided that DNA target primers take into account the degradation dynamics of nematode DNA during its passage through the guts of predator species (e.g., Heidemann et al., 2014). A growing number of studies in soil and marine ecosystems detecting nematode DNA ingested by a variety of micro-predators have provided empirical support for the role of nematodes as an important trophic resource for many terrestrial and marine invertebrates (Read et al., 2006; Heidemann et al., 2011, 2014; Maghsoud et al., 2014).

Direct in vivo observations of nematode feeding behavior have established a robust benchmark for understanding the participation of nematodes in the trophic dynamics of various ecosystems (e.g., Wood, 1973; Romeyn and Bouwman, 1983; Jensen, 1987; Moens and Vincx, 1997). This approach was used in 13% of the studies examining the trophic interactions of nematodes in freshwater ecosystems, as determined in our literature search (Table 1). Approaches based on image tracking and computer-aided analysis are a logical continuum of traditional observational studies and can provide a high-throughput evaluation of nematode feeding behavior, with minimum commitments of time and effort. They have been applied to study nematode locomotion (Tsibidis and Tavernarakis, 2007; Buckingham and Sattelle, 2009; Wang and Wang, 2013) and may prove useful for monitoring a variety of behaviors in vivo, including attraction to food, mechanisms of physical food recognition, feeding strategy, and behavioral responses to the presence of predators, competitors, or conspecifics. Live observations can be recorded in semi-natural conditions using home-made miniature flow cells (e.g., Esser, 2006; Norf et al. 2009), and the availability of open-source software for recording and processing images (e.g., Stuurman et al., 2007; Wang and Wang, 2013) make automated image tracking of nematodes very accessible. It is fairly possible to complement those observations with other in vivo imaging techniques, such as confocal laser scanning microscopy with differential fluorescent probing, which may lead us

to the answers to some of the outstanding questions in nematode ecology, including the selective feeding by nematodes on bacteria, algae, and EPS and the in vivo consequences of nematode bioturbation on biofilm architecture.

CONCLUSION

The following conclusions/recommendations can be drawn from our literature review:

- (i) Knowledge on the trophic ecology of freshwater nematodes is heterogeneous and for the most part insufficient. Although some studies suggest that nematodes are key intermediaries between microbial production and macro-organisms, many significant gaps remain in our understanding of their role for instance in mediating the decomposition of organic matter in lakes and streams. Investigations into this aspect of nematode ecology as well as the interactions between nematodes and protozoans and nematodes and fungi will yield important information.
- (ii) There is recent mounting evidence of the influence of nematodes on primary production in phototrophic microbial mats. As grazing pressure is rather low, it is suggested that indirect effects such as bioturbation may affect biofilms more deeply by increasing their porosity to nutrient fluxes for instance. However, further research is needed to disentangle the relative importance of nematode controls on the architecture of these productive interface ecosystems.
- (iii) The ability of freshwater nematodes to discriminate and select food items is increasingly recognized based on laboratory experiments. However, large-scale investigations of feeding-selectivity in natural or semi-natural conditions are still needed to better understand the effects of nematode selectivity on complex benthic communities.
- (iv) Thus far, only a few studies, using the typical methodologies of trophic ecology (e.g., isotopic tracers), have attempted to unravel the position of nematodes in freshwater food webs. The paucity of quantitative studies may be due to the large number of nematode individuals that need to be sorted to allow significant signal detection in the various probing methods. We believe that emerging techniques, such as SIP coupled with Raman microspectroscopy, gut DNA contents of nematodes and their predators, and automated image tracking used in the framework of individual-based modeling, would provide the high-throughput of the data needed for large-scale investigations of nematode positioning within freshwater benthic food webs.

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