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MEIOFAUNA IN FRESHWATER ECOSYSTEMS

Review Paper

Are meiofauna a standard meal for macroinvertebrates and juvenile fish?

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Abstract Due to the lack of empirical data, meiofauna are often underestimated as prey for freshwater animals and are commonly regarded as trophic dead ends. Here we present a synthesis of recent evidence showing that meiofauna are significant as prey, not only for many benthic macroinvertebrates (chironomids, shrimps, and flatworms) but also for juveniles of widespread freshwater bottom-feeding fish species (e.g., carps, gudgeons, catfish). In this review, we focus on the following questions: (1) Which groups consume meiofauna? (2) In what amounts are meiofauna ingested? (3) Does predatory feeding behavior influence natural meiofaunal communities? (4) Are meiofauna organisms actively ingested or are they bycatch? To answer these questions, we focused on studies that included gut/feces analyses of potential predators and empirical investigations conducted in the laboratory (e.g., functional response experiments and microcosm studies) and in the field (enclosure/exclosure settings). We were able to demonstrate that meiofauna taxa are consumed in high numbers by a wide range of larger organisms. This predation can significantly shape meiofaunal communities, by reducing the abundance, biomass, and production of certain members of the investigated assemblages. However, in most cases, it remains unclear if there is an active predation of meiofauna or a passive ingestion by unselective feeding.

Keywords Functional response · Predator prey interaction · Benthic food web · Macrofauna diet · Nematodes

Introduction

Meiofaunal communities comprise a broad diversity of small organisms, differing in their specific morphologies, phenotypes, and behavior patterns and reflect wide-ranging differences in feeding types and food preferences. For example, the diet of nematode species can consist of dissolved and particulate organic matter, microphytobenthos, macrophytes, fungi, bacteria, protozoans, or other meiofaunal organisms, depending on the species (summarized by Majdi & Traunspurger, 2015). The population dynamics of consumed organisms can be reduced or even stimulated by meiofaunal feeding pressure

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(Perlmutter & Meyer, 1991; Borchardt & Bott, 1995; Traunspurger et al., 1997; Bott & Borchardt, 1999). In addition to their impact on lower trophic levels, nematodes and rotifers themselves represent an abundant food source for a wide range of other meiofauna, including copepods, tardigrades, microturbellarians, other nematodes, and rotifers (Schmid-Araya & Schmid, 2000; Muschiol et al., 2008a, b; Hohberg & Traunspurger, 2009). A single individual of the predatory nematode *Prionchulus muscorum* can consume up to 86 smaller nematodes within 4 h (Kreuzinger-Janik et al., 2019). Furthermore, meiofauna may be threatened by predation even when "only" protozoans are present. As documented by Doncaster & Hooper (1961) and later by Geisen et al. (2015), these unicellular organisms are able to overwhelm and consume nematodes. These observations together with comprehensive examinations of freshwater benthic food webs (Schmid-Araya, 1997; Schmid-Araya et al., 2002) suggest that the meiofauna are key actors of benthic food web connectivity (Stead et al., 2005). In this review, we ask whether meiofauna are also a standard meal for much larger organisms such as macroinvertebrates and fish juveniles.

The ability of larger animals to ingest meiofaunal organisms has been recognized for several decades. Crisp & Lloyd (1954) analyzed the gut contents of several dipteran larvae and found meiofauna, mainly copepods. Similar findings were reported in fish (Bruun, 1949; Bregnballe, 1962). Following those early studies, the list of potential meiofaunal consumers has substantially increased (Gee, 1989; Coull, 1990; Schmid & Schmid-Araya, 1997; Schmid-Araya & Schmid, 2000). In 1990, Coull postulated that marine meiofauna serve as food for a wide range of animals of higher trophic level, including annelids, crustaceans, and fish. Supporting evidence was based on gut analyses and empirical approaches, which together resulted in the first description of the direct impact of predation on marine meiofaunal communities. By contrast, analogous ecological linkages in benthic freshwater ecosystems remained unconsidered. While organisms such as rotifers or microcrustaceans were regarded as inherent components of pelagic food webs (Sprules & Bowerman, 1988), the trophic relevance of their benthic pendants was not examined. Rather, investigations of the benthic food webs of lakes and streams mainly focused on macrobenthos and fish (Briand, 1983; Briand & Cohen, 1987; Sugihara et al., 1989; Diehl, 1992; Townsend et al., 1998) even though meiofauna are the largest contributors to metazoan abundance and species diversity (e.g., Robertson, 2000; Traunspurger, 2000; Majdi et al., 2017). The considerable efforts needed to collect, process, and identify these small organisms to the species level might be the reason why they have been largely ignored so far.

Studies considering a clearly larger taxonomic range and conducted at higher resolution finally integrated hard-bodied (Warren, 1989) and, to a lesser extent, soft-bodied meiofauna (Martinez, 1991) into benthic food webs. Schmid-Araya (2000) as well as Schmid-Araya et al. (2002) subsequently established the entire spectrum of meiofauna as an important part of the food web, based on the studies conducted in the Broadstone stream, a headwater in southeast England. After previous studies (Hildrew et al., 1985; Lancaster & Robertson, 1995; Woodward & Hildrew, 2001) were taken into account, by addition of meiofaunal organisms, the number of linked species increased and intermediate species feeding on more than one trophic level were dominant. However, connectance obviously declines in larger webs integrating meiofauna (Schmid-Araya et al., 2002; Thompson et al., 2012), due to the large size disparity and the associated limitations in foraging between the linked organisms (Warren & Lawton, 1987; Woodward et al., 2005). In other words, with increasing consumer size, it becomes increasingly difficult, if not impossible, to catch and retain small prey organisms. Nonetheless, this by no means implies that meiofauna are a dead end of benthic freshwater food webs.

Within the last 15 years, DNA-based procedures as well as stable isotope and fatty acid analyses of the characteristics of trophic networks have become well established (Traugott et al., 2013; Maghsoud et al., 2014). Genetically based examinations of the gut contents or feces of consumers are able to identify consumed organisms at a taxonomically high resolution (Pompanon et al., 2012; Tillner et al., 2015). In addition, approaches based on the use of stable isotopes or fatty acids can be applied to investigate trophic pathways, which allows the integration of meiofauna into benthic food webs, as shown by Goedkoop et al. (1998) and Schmid-Araya et al. (2016) for the meiofauna of streams and lakes. However, most of our knowledge on the role of meiofauna as food for larger organisms has been obtained in classical gut content analyses that were not confirmed in laboratory experiments (model ecosystems/microcosms) or field trials. This lack of validation has prevented meaningful statements on the quantity and quality of the trophic interactions involving meiofauna.

For example, in several studies, either no meiofauna or predominantly hard-bodied taxa (primarily microcrustaceans) were extracted from the digestive tracts of macroinvertebrates and fish, despite the presence of hard- and soft-bodied meiofauna in the habitat of interest (Coull, 1990; Smith & Smock, 1992; Smock et al., 1992; Tavares-Cromar & Williams, 1996; Schückel et al., 2012). In addition to the vertical distribution of meiofauna and differences in the feeding mechanisms of their consumers, the relative absence of soft-bodied taxa may be due to their fast digestion. Indeed, studies have shown that soft-bodied meiofauna such as nematodes are quickly (20 min up to hours) ingested beyond recognition by fish and invertebrates (Alheit & Scheibel, 1982; Hofsten et al., 1983; Scholz et al., 1991; Muschiol et al., 2008a; Ptatscheck et al., 2015). Consequently, studies that have focused only on data from the digestive tracts of larger organisms have probably underestimated the amount of meiofauna in their diet, and other potential consumers may not have been recognized (Schückel et al., 2012; Weber & Traunspurger, 2014a; Weber et al., 2018).

In the following, we summarize the empirical approaches developed within the last 20 years to investigate meiofauna as components of the diet of larger organisms in freshwater ecosystems. This includes functional response experiments, enclosure/exclosure studies from the laboratory and field, as well as direct observations of the feeding behavior of predators. Specifically, we want to answer the following questions:

1. What types of macroinvertebrates and fish consume meiofauna?
2. Can the number of ingested organisms be quantified?
3. What are the implications of meiofaunal consumption for the population dynamics of these organisms?
4. Do meiofauna serve as the main course, a side dish, or are they just the fly in the soup of higher trophic organisms?

Organisms consuming meiofauna

A very detailed list of species-specific gut contents was compiled by Schmid-Araya & Schmid (2000) for the numerous unicellular, meiofaunal, and macrofaunal organisms present in lotic systems. Among macrofaunal consumers (Table 1), dipteran larvae, especially chironomids, followed by plecopterans are the most common consumers of meiofaunal organisms. In the guts of all 19 investigated chironomid species, comprising carnivorous tanypodinae as well as deposit-feeding taxa, meiofaunal remains were found. Different species of trichopterans, megalopterans, and oligochaetes also ingested meiofauna. The majority of this meiofaunal diet was composed of rotifers, but nematodes, tardigrades, and microcrustaceans (cladocers, copepods, and ostracods) were also frequent. Larvae with body lengths of 1–2 mm were shown to already feed on rotifers (Schmid-Araya & Schmid, 1995). While larger insect larvae increasingly feed on other macrofaunal taxa, the meiofauna remain a part of their diet (Schmid-Araya & Schmid, 1995; Schmid & Schmid-Araya, 1997).

In addition to this compilation, we supplemented other freshwater macroinvertebrates that verifiably consume meiofauna (Tables 1 and 2), including the larvae of damselflies (odonata), chironomids, tricladid turbellarians, leeches, and crustaceans (adults and subadults). Note that for the species listed in Table 2, some were detected in laboratory experiments conducted under partly unnatural conditions and with the focused input of specific prey. Those studies, therefore, do not reflect the entire spectrum of meiofaunal food under natural conditions.

In the context of organismal groups consuming meiofauna, freshwater mollusks must also be included. Vaughn et al. (2008) described the diverse diet of mussels, which contains, but is not limited to, organisms from the water column, such as rotifers. Hicks & Marshall (1985) also collected microcrustaceans from the guts of marine bivalves. Yet, to our knowledge, there are no studies of the gut contents of freshwater mussels that definitively demonstrate the ingestion of meiofauna, in contrast to unicellular organisms (Yeager et al., 1994). However, the major part (80%) of the diet of mussels is composed of deposited material (Raikow & Hamilton, 2001), which may include attached meiofauna. Furthermore, Sudhaus (2018) reported that free-living nematodes,

Table 1 Macrobenthic organisms feeding on meiofauna, as determined in gut and feces analysis

Predator	Prey	Reference
Flatworms		
Polycelis nigra (Mueller, 1774)	Rotifers, Oligochaetes, Microcrustaceans	Reynoldson and Young (1963), Young (1981)
P. tenuis (Ijima, 1884)	Nematodes, Rotifers, Oligochaetes, Microcrustaceans	Reynoldson and Young (1963), Young (1981)
Dugesia polychroa (Schmidt, 1861)	Oligochaetes	Young (1981)
D. lugubris (Schmidt, 1861)	Rotifers	Reynoldson and Young (1963)
Dendrocoelum lacteum (Mueller, 1774)	Rotifers, Oligochaetes	Reynoldson and Young (1963), Young (1981)
Leeches		
Erpobdella octoculata (Linnaeus, 1758)	Oligochaetes, Microcrustaceans	Young (1981)
Oligochaetes		
Chaetogaster	Rotifers	Reviewed by Schmid-Araya and Schmid (2000)
Crustaceans		
Trichodactylus kensleyi (Rodríguez, 1992)	Microcrustaceans, Rotifers	Williner et al. (2014)
Damselflies (Zygoptera)		
Unspecified	Rotifers, Oligochaetes, Microcrustaceans	Lamoot (1977)
Pyrrhosoma nymphula (Saulzer, 1776)	Rotifers, Oligochaetes, Microcrustaceans	Lawton (1970)
Dipterans		
Chironomidae		
Macropelopiini		
Brundiniella	Tardigrades, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Procladius	Gastrotriches, Oligochaetes, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Macropelopia notate (Meigen, 1818)	Rotifers, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
M. goetghebueri (Kieffer, 1918)	Rotifers, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Apsectrotanypus	Rotifers, Oligochaetes, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Pentaneurini		
Ablabesmyia	Rotifers, Oligochaetes, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Conchapelopia pallidula (Kieffer, 1818)	Rotifers, Tardigrades, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
C. viator (Kieffer, 1911)	Rotifers	Reviewed by Schmid-Araya and Schmid (2000)
Krenopelopia	Rotifers	Reviewed by Schmid-Araya and Schmid (2000)
Labrundinia	Oligochaetes	Reviewed by Schmid-Araya and Schmid (2000)
Nilotanypus	Rotifers, Tardigrades, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)

Table 1 continued

Predator	Prey	Reference
Paramerina	Rotifers	Reviewed by Schmid-Araya and Schmid (2000)
Thienemannimyia laeta (Meigen, 1818)	Rotifers, Tardigrades	Reviewed by Schmid-Araya and Schmid (2000)
T. geijskesi (Goetghebuer, 1934)	Rotifers, Tardigrades, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Trissopelopia longimana (Staeger, 1839)	Rotifers, Tardigrades, Microcrustaceans, Nematodes, Oligochaetes	Reviewed by Schmid-Araya and Schmid (2000)
Zavrelimyia signatipennis (Kieffer, 1924)	Rotifers, Oligochaetes, Tardigrades, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Z. barbatipes (Kieffer, 1911)	Rotifers, Oligochaetes, Tardigrades, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Limoniidae		
Pedicia	Rotifers, Oligochaetes, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Dicranota	Oligochaetes	Reviewed by Schmid-Araya and Schmid (2000)
Limnophila	Oligochaetes, Nematodes	Reviewed by Schmid-Araya and Schmid (2000)
Stoneflies		
Isoperla	Rotifers, Tardigrades, Oligochaetes	Reviewed by Schmid-Araya and Schmid (2000)
Dinocras	Rotifers	Reviewed by Schmid-Araya and Schmid (2000)
Chloroperla	Rotifers, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Siphonoperla torrentium (Pictet, 1841)	Rotifers, Oligochaetes, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Caddisflies		
Plectrocnemia	Rotifers, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)
Alderflies		
Sialis	Rotifers, Microcrustaceans	Reviewed by Schmid-Araya and Schmid (2000)

rotifers, and tardigrades are incidentally ingested by gastropods with their food, but may survive gut passage. Present studies have shown that gastropods exert strong top-down effects on the meiofaunal communities of periphyton (Burgmer et al., 2010, Schroeder et al., 2010; Peters & Traunspurger, 2012).

Within the vertebrates, fish are the best documented taxon that consume meiofauna as observed by Gee (1989) for numerous marine and some freshwater taxa. Within the last 20 years, there has been a large increase in the number of studies of the meiofaunal diet of freshwater fish (Table 3). With the exception of smaller species such as zebrafish (Hofsten et al., 1983), the juveniles (up to 12 cm body length) and larvae of different taxa were observed to consume meiofaunal organisms, including microcrustaceans, oligochaetes, and nematodes. According to those studies, especially bottom-biting fish such as carps, gudgeons, or catfish but also, for example, roaches and, to a lesser extent, bream consumed meiofauna,

Table 2 Studies of the predation effect of different freshwater invertebrates on meiobenthic organisms

Predator	Offered prey	Prey size	Design	Substrate (particle size)	Effects on prey or ingestion rate	References
Crustaceans						
Neocaridina davidi (Bouvier, 1904)	Natural meiofauna community	Various	LE, GA	Fine-grained sediment	**Total Meiofauna** Abundance − 42% Biomass − 37% Sec. production − 22% after 42 days **Nematodes** Abundance -44% Biomass -40% Sec. production -28% after 42 days **Oligochaetes** Abundance -39% Biomass -37% Sec. production -22% after 42 days **Microcrustaceans** Abundance -43% Biomass -39% Sec. production -20% after 42 days	Weber and Traunspurger (2016b)
Procambarus clarkii (Girard, 1852)	Natural meiofauna community	Various	LE, GA	Gravel (3-5 mm)	**Total meiofauna** Biomass -42% Sec. production -22% after 14 days **Nematodes/Rotifers** No effect **Microcrustaceans** Biomass -51% after 14 days **Oligochaetes** Abundance -40% Biomass -37% after 14 days	Weber and Traunspurger (2017)
Astacus astacus (Linnaeus, 1758)	Natural meiofauna community	Various	LE, GA	Gravel (3–5 mm)	**Total meiofauna** Biomass − 37% Sec. production − 29% after 14 days **Nematodes/Rotifers** No effect **Microcrustaceans** Biomass − 49% after 14 days **Oligochaetes** Abundance − 45% Biomass − 58% after 14 days	Weber and Traunspurger (2017)

Table 2 continued

Predator	Offered prey	Prey size	Design	Substrate (particle size)	Effects on prey or ingestion rate	References
Eucyclops subterraneus scythicus (Plesa, 1989)	Nematodes					Muschiol et al. (2008b)
	Panagrolaimus sp.	–	FR	No substrate	26/20 min	
	Poikilolaimus sp.	–	FR	No substrate	38/20 min	
	Panagrolaimus sp.	–	LE	No substrate	238/24 h	
Diacyclops bicuspidatus	Nematodes					Muschiol et al. (2008a)
(Claus, 1857)						
	Panagrolaimus sp.	-	FR		45/2 h	
Flatworms						
Planaria torva	Nematodes					Kreuzinger-Janik et al. (2018)
(Mueller, 1774)						
	Caenorhabditis elegans (Maupas, 1900)	Juvenile	FR	No substrate	143/3 h	
		Adult	FR	No substrate	46/3 h	
		Adult	LE	Sand (< 1 mm)	1/3 h	
		Adult	LE	Gravel (2-4 mm)	26/3 h	
		Adult	LE	Leaf litter (50 µm-4 mm)	17/3 h	
Polycelis tenuis	Nematodes					Kreuzinger-Janik et al. (2018)
(Ijima, 1884)						
	Caenorhabditis elegans	Juvenile	FR	No substrate	927/3 h	
		Adult	FR	No substrate	51/3 h	
		Adult	LE	Sand (< 1 mm)	28/3 h	
		Adult	LE	Gravel (2–4 mm)	46/3 h	
		Adult	LE	Leaf litter (50 µm-4 mm)	7/3 h	
Dugesia gonocephala	Nematodes					Beier et al. (2004)
(Duges, 1830)						
	Caenorhabditis elegans	Juvenile	FR	No substrate	197/3 h	
		Adult	FR	No substrate	94/3 h	
		Adult	LE	Sand (0.56 mm)	19/3.5 h	
		Adult	LE	Gravel (3.21 mm)	0/3.5 h	
		Adult	LE	Gravel (6.83 mm)	0/3.5 h	
Chironomidae						
Chironomus riparius	Nematodes					Ptatscheck et al. (2015)
(Meigen, 1804)						
	Caenorhabditis elegans	Juvenile	FR	No substrate	763/4 h	
		Adult	FR	No substrate	557/4 h	
		Adult	LE	Sand (< 1 mm)	56/24 h	
		Adult	LE	Gravel (2–4 mm)	23/24 h	
		Adult	LE	Detritus (35 µm-2 mm)	44/24 h	
	Natural nematode community	Various	LE	Sand (< 1 mm)	80/24 h	

Table 2 continued

Predator	Offered prey	Prey size	Design	Substrate (particle size)	Effects on prey or ingestion rate	References
	Natural meiofauna community	Various	LE, GA	Sand (< 1 mm)	**Total meiofauna** Abundance − 40% Biomass − 60% after 8 days **Nematodes** Abundance -55% after 8 days **Oligochaetes** Abundance -54% after 8 days **Copepods** Abundance -66% Biomass -79% after 8 days	Ptatscheck et al. (2017)
Tardigrades						
Macrobiotus richtersii (Murray, 1911)	Nematodes					Hohberg and Traunspurger (2005)
	Pelodera teres (Schneider, 1866)	Juvenile	FR	No substrate	105/4 h	
	P. teres	Juvenile	LE	Agar	180/24 h	
	P. teres	Juvenile	LE	Sand (0.10-0.16 mm)	38/24 h	
	P. teres	Juvenile	LE	Sand (0.25-0.32 mm)	39/24 h	
	P. teres	Juvenile	LE	Sand (0.50-0.63 mm)	94/24 h	
	P. teres	Adult	FR	No substrate	54/4 h	
	Acrobeloides nanus (de Man, 1880)	Juvenile	FR	No substrate	99/4 h	
	A. nanus	Adult	FR	No substrate	58/4 h	
Nematodes						
Prionchulus muscorum (Dujardin, 1845)	Nematodes					Kreuzinger-Janik et al. (2019)
	Caenorhabditis elegans	Small	FR	No substrate	73/4 h	
	C. elegans	Large	FR	No substrate	52/4 h	
	C. elegans	Small	FR	Moss	86/4 h	
	C. elegans	Large	FR	Moss	54/4 h	
Stoneflies						
Chloroperlidae						
Unspecified	Natural meiofauna community	Various	FS	Leaf litter	**Nematodes** Biomass − 37% after 18 days Rotifers Biomass -26% after 18 days	Majdi et al. (2015)

Table 2 continued

Predator	Offered prey	Prey size	Design	Substrate (particle size)	Effects on prey or ingestion rate	References
Snails						
Theodoxus fluviatilis (Linnaeus, 1758)	Natural meiofauna community	Various	FS	Periphyton	**Total meiofauna** Abundance − 79%, especially that of nematodes and oligochaetes after 6 weeks	Peters and Traunspurger (2012)

FR functional response, *FS* field study in natural environments, *FE* field enclosures, *LE* laboratory experiment, *GA* gut analysis, *MG* investigations on the mortality and growth of the fish, *n.i.* not investigated

whereas sticklebacks that are not had no predation effect. For consumers, in addition to their feeding behavior, mouth cavity morphology and the structure and mesh width of the branchial basket determine the size of retained prey organisms (Spieth et al., 2011; Weber & Traunspurger, 2014a).Thus, Spieth et al. (2011) reported that the branchial apparatus of breams are apparently too large to retain meiofauna organisms, whiles roaches only had effects on larger meiofaunal taxa (oligochaetes).

It should be noted that most of the studies listed in Table 3 were conducted within the framework of aquaculture and focuses on the suitability of nematodes as food for farmed fish. The prey organisms (mainly nematodes) used in those studies were offered directly in the water column and in water tanks without sediment. Under natural conditions, different results will likely be obtained.

However, fish are not the only vertebrate consumers of meiofauna. Gut content and feces analysis of waterfowls showed evidence of their uptake of meiofaunal organisms (Gaston, 1992; Frisch et al., 2007). Their ability to rework sediment (Cadée, 1990) and filter even small organisms (Gurd, 2007) leads to assume a strong top-down effect on the meiobenthic community that has already been shown for macroinvertebrates (Rodríguez-Pérez & Green, 2012).

Quantification of ingested meiofauna

In general, the quantity of ingested meiofauna organisms is difficult to determine with gut analysis alone. Nevertheless, quantitative estimations of feeding behavior are needed to enable predictions of food web stabilities, ecosystem functions, and population dynamics (Kreuzinger-Janik et al., 2018). Laboratory approaches are particularly suitable for this purpose and can provide first insights into the trophic relationships between specific predator and prey species within hours and without excessive workload. Furthermore, in these kinds of experiments, defined prey densities can be offered and specific biotic (e.g., interactions between prey species, immigration) and abiotic factors (e.g., temperature, light) can be adapted or excluded. Only few laboratory studies have already quantitatively examined the amount of meiofaunal organisms ingested by larger predators (Fig. 1). All present laboratory experiments testing single meiofaunal prey species were conducted with nematodes that are predominant in benthic environments and easy to cultivate and handle during trials.

Laboratory investigations on the predator–prey relationship between macroinvertebrates and nematodes have been reported most commonly in studies that included functional response experiments. Those experimental setups enable an examination of the ingestion rates of prey by a predator as a function of prey density and provide information on the strength of certain predator–prey relationships. Most of the quantitative data generated from functional response experiments investigating the feeding behavior of macrofaunal organisms derive from flatworm species (Beier et al., 2004; Kreuzinger-Janik et al., 2018). Three widespread flatworm species were investigated in those studies, with juvenile as well as adult nematodes serving as prey. The highest ingestion of adult nematodes was by *Dugesia gonocephala*, which consumed up to 94 *Caenorhabditis elegans* within 3 h (Beier et al., 2004). For juvenile nematodes as prey, the maximum ingestion was by *Polycelis tenuis*, which consumed 927 *C. elegans* in 3 h (Kreuzinger-Janik et al., 2018). Ptatscheck et al. (2015) analyzed the

Table 3 Empirical studies of the predation effect of different freshwater fish on meiobenthic organisms

Fish species/ predator	Body length/ life stage	Offered prey	Design	Substrate	Effects on prey (consumption)	References
Common carp						
Cyprinus carpio (Linnaeus, 1758)	Larvae	Nematodes				
		Panagrellus redivivus (Linnaeus, 1767)	LE, MG	No substrate	n.i.	Schlechtriem et al. (2004a)
		P. redivivus	LE, MG	No substrate	n.i.	Schlechtriem et al. (2004b)
		Panagrellus redivivus *Panagrolaimus* sp.	LE, GA	No substrate	n.i.	Tillner et al. (2015)
	3–4 cm (juvenile)	Nematodes				Weber and Traunspurger (2014a)
		Caenorhabditis elegans	LE	Fine sand	234,000/24 h	
	6–8 cm (juvenile)	Nematodes				Weber and Traunspurger, (2014a)
		Caenorhabditis elegans	LE	Fine sand	204,000/24 h	
		Natural meiofauna community	LE	Fine-grained, natural sediment	**Nematodes:** Abundance -82% Biomass -94% after 48 h. No effect on Nematode diversity **Oligochaetes:** Abundance -97% Biomass -96% after 48 h **Microcrustaceans** Abundance -94% Biomass -98% after 48 h **Rotifers** No effect Effects on the meiofauna size structure	Weber and Traunspurger (2014b)
		Natural meiofauna community	FE	Mud and woody and leafy debris	**Total meiofauna** Sec. production -65% after 80 days. **Nematodes** Sec. production -77% after 80 days. No effect on Nematode diversity **Oligochaetes** Sec. production -74% after 80 days **Microcrustaceans** Sec. production -61% after 80 days **Rotifers** No effect Increase of smaller meiofauna size classes	Weber and Traunspurger (2015)

Table 3 continued

Fish species/ predator	Body length/ life stage	Offered prey	Design	Substrate	Effects on prey (consumption)	References
		Natural nematode community	FE	Mud and woody and leafy debris	**Abundance and Biomass** reduction of the most common species **Nematodes composition** but not the diversity was affected by fish	Weber and Traunspurger (2016a)
		Natural meiofauna community	FE, GA	Mud and woody and leafy debris	**0–2 cm sediment depth** **Total Meiofauna** Abundance -62% Biomass -79% after 32 days **Nematodes** Abundance -80% Biomass -80% after 32 days **Oligochaetes** Abundance -85% Biomass -84% after 32 days **Microcrustaceans** Abundance -70% Biomass -71% after 32 days **Rotifers** No effect **2–4 cm sediment depth** **Total Meiofauna** Abundance -49% Biomass -77% biomass after 32 days **Nematodes** Abundance -65% Biomass - 67% after 32 days **Oligochaetes** Abundance -80% Biomass -80% after 32 days **Rotifers** No effect	Weber et al. (2018)
	9–12 cm (juvenile)	Nematodes				Spieth et al. (2011)
		Caenorhabditis elegans	FE	Sand	Abundance -52% after 2 days	
		Natural meiofauna community	LE	Fine-grained, natural sediment	Significant reductions in oligochaete microcrustacean and nematode abundance	
		Nematodes				Weber and Traunspurger (2014a)
		Caenorhabditis elegans	LE	Fine sand	201,000/24 h	

Table 3 continued

Fish species/predator	Body length/life stage	Offered prey	Design	Substrate	Effects on prey (consumption)	References
	11–14 cm (juvenile)	Nematodes				Spieth et al. (2011)
		Caenorhabditis elegans	LE	Sand (0.5-2 mm)	50% reduction in abundance after 24 h	
Gudgeon						
Gobio gobio (Linnaeus, 1758)	2.5–5 cm (juvenile)	Nematodes				Weber and Traunspurger (2014a)
		Caenorhabditis elegans	LE	Fine sand	183,000/24 h	
	5–7 cm (juvenile)	Nematodes				Spieth et al. (2011)
		Caenorhabditis elegans	LE	Sand (0.5-2 mm)	Abundance -50% after 24 h	
		Natural meiofauna community	LE	Mud and woody and leafy debris	**Nematodes** Abundance -56% Biomass -80% after 48 h **Oligochaetes** Abundance -90% Biomass -99% after 48 h **Microcrustaceans** Abundance -87% Biomass -86% after 48 h **Rotifers** No effect Effects on the meiofauna size structure but not on diversity	Weber and Traunspurger (2014b)
	6–8 cm (juvenile)	Nematodes				Weber and Traunspurger (2014a)
		Caenorhabditis elegans	LE	Fine sand	165,000/24 h	
	10–12 cm (juvenile)	Nematodes				Spieth et al. (2011)
		Caenorhabditis elegans	LE	Sand (0.5-2 mm)	Abundance -30% after 24 h	
		Nematodes				Spieth et al. (2011), Weber and Traunspurger (2014a)
		Caenorhabditis elegans	LE	Fine sand	81,000/24 h	
Roach						
Rutilus rutilus (Linnaeus, 1758)	1–2 cm (juvenile)	Natural meiofauna community	LE, GA	Coarse sediment overlain with fine material	Significant reduction of copepods > 1 mm after 11 days	Dineen and Robertson (2010)
	3–8 cm (juveniles)	Nematodes				Spieth et al. (2011), Weber and Traunspurger (2014a)
		Caenorhabditis elegans	LE	Fine sand	No detectable predation	
	10–13 cm (juvenile)	Natural meiofauna community	LE	Fine-grained, natural sediment	**Oligochaetes** Abundance -50%	Spieth et al. (2011)

Table 3 continued

Fish species/ predator	Body length/ life stage	Offered prey	Design	Substrate	Effects on prey (consumption)	References
					after 24 h	
					Rotifers/Nematodes/Copepods	
					No effect	
Armored catfish						
Corydoras aeneus	2–3 cm	Nematodes				Majdi et al. (2018)
(Gill, 1858)	(juvenile)					
		Poikilolaimus sp. (*regenfussi*), *Caenorhabditis elegans*	LE	Sand (3-5 mm)	76,000 nematodes per day	
		Panagrolaimus cf. *thienemanni*				
		(Hirschmann, 1952)				
		Panagrellus redivivus				
Tilapia						
(*Oreochromis niloticus*)	Juvenile–adult	Nematodes				Abada et al. (2017)
(Linnaeus, 1758)						
		Adoncholaimus	FS	No substrate	n.i.	
		Punctodora				
		Labronema				
		Oncholaimus				
		Odontolaimus				
Common whitefish						
Coregonus lavaretus	Larvae	Nematodes				Schlechtriem et al. (2004b, 2005)
(Linnaeus, 1758)						
		Panagrellus redivivus	LE, MG	No substrate	n.i.	
Grass carp						
Ctenopharyngodon idella	Larvae	Rotifers, Nematodes				Rottmann et al. (1991)
(Valenciennes, 1844)						
		Brachionus rubens	LE, MG	No substrate	n.i.	
		(Ehrenberg, 1838)				
		Panagrellus sp.				
Bighead carp						
Hypophthalmichthys nobilis	Larvae	Rotifers, Nematodes				Rottmann et al. (1991)
(Richardson, 1845)						
		Brachionus rubens	LE, MG	No substrate	n.i.	
		Panagrellus sp.				
		Nematodes				Santiago et al. (2003)
		Panagrellus redivivus	LE, MG	No substrate	n.i.	
		Nematodes				Santiago et al. (2004)
		Panagrellus redivivus	LE, GA, MG	No substrate	300 nematodes gut^{-1}	
Asian catfish						
(*Clarias macrocephalus*)	Larvae	Nematodes				Santiago et al. (2003)
(Günther, 1864)						

Table 3 continued

Fish species/ predator	Body length/ life stage	Offered prey	Design	Substrate	Effects on prey (consumption)	References
		Panagrellus redivivus	LE, MG	No substrate	n.i.	
Catfish						
Synodontis petricola	Larvae	Nematodes				Sautter et al. (2007)
(Matthes, 1959)						
		Panagrellus redivivus	LE, MG	No substrate	n.i.	
Zebrafish						
(*Danio* sp.)	Adult	Nematodes				Hofsten et al. (1983)
		Panagrellus sp.	LE, GA, MG	No substrate	n.i.	
		Turbatrix aceti				
		(Müller, 1783)				
		Caenorhabditis elegans				
		C. hriggsae				
		(Dougherty and Nigon, 1949)				
Brook charr						
Salvelinus fontinalis	< 1 year	Copepods, Ostracods	FS, GA, MG	No substrate	n.i.	McNicol et al. (1985)
(Mitchill, 1814)						
Bream						
Abramis brama	7–12 cm (juvenile)	Nematodes				Spieth et al. (2011)
(Linnaeus, 1758)						
		Caenorhabditis elegans	LE,	Sand	No detectable effect	
		Natural nematode community	FE	Sand (0.5–2 mm)	Significant reduction	
Ninespine stickleback						
Pungitius pungitius (Coste, 1848)	2–4 cm (juvenile)	Nematodes				Spieth et al. (2011), Weber and Traunspurger (2014a)
		Caenorhabditis elegans	LE	Fine sand	No detectable predation	

FS field study in natural environments, *FE* field enclosures, *LE* laboratory experiment, *GA* gut analysis, *MG* investigations on the mortality and growth of the fish, *n.i.* not investigated

feeding behavior of the chironomid larvae *Chironomus riparius* on nematode prey. In this study, up to 763 juvenile and 557 adult *C. elegans* were eaten within 4 h by the insect larvae, which are commonly considered to be detritus feeders.

Studies investigating predator–prey relationships among meiofauna have shown that even within the meiofaunal size class ingestion rates can be very high. Thus far, tardigrades, copepods, and predatory nematodes have served as model predators of nematodes (Hohberg & Traunspurger, 2005; Muschiol et al., 2008a, b; Kreuzinger-Janik et al., 2019). In the case of copepods, nematode ingestion was highest for *Eucyclops subterraneus scythicus,* which consumed 38 nematodes of the species *Poikilolaimus* sp. within 20 min and a maximum of 238 *Panagrolaimus* sp. per day (Muschiol et al., 2008b). Hohberg & Traunspurger (2005, 2009) evaluated the feeding behavior of the tardigrade *Macrobiotus richtersii* when offered different nematode species as prey and found that up to 105 small *Pelodera teres* were eaten by the predator within 4 h. Moreover, juvenile tardigrades ingested 56 small *Pelodera teres*, which corresponded to an uptake of 65% of the predator's own biomass within the same time frame. For the predatory nematode *Prionchulus muscorum*, the relationship between ingested prey and predator biomass was even more impressive; Kreuzinger-Janik et al. (2019) calculated a daily per capita

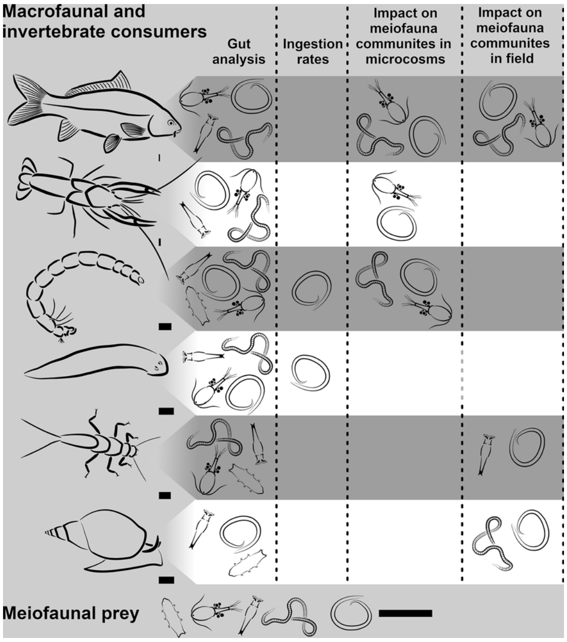

Fig. 1 Aspects of trophic relationships (gut content, ingestion rates, and impact on communities) between meiofauna (prey) taxa and potential consumers that have already been documented by empirical studies. Consumers include fish, crustaceans, chironomid larvae, flatworms, stonefly larvae, and snails. Meiofauna include nematodes, rotifers, microcrustaceans, oligochaetes, and tardigrades. The scale bars of the depicted organisms (consumers and prey) correspond to 1 mm

ingestion rate of up to 4.8 times the predator's own biomass.

Although functional response experiments are able to give insights into the strengths of predator–prey relationships, they are limited in three aspects: (1) this kind of approach is most of all practical for small predators because here the prey density that must be offered to attain exact and useful results is much lower than that required for larger predators such as fish, crayfish, and shrimp. (2) With the exception of Kreuzinger-Janik et al. (2018), the effects of substrate were not considered in functional response investigations. (3) Results include only data on single prey species and not on whole meiofauna communities. For these reasons, other or follow-up experimental designs, which we will discuss below, are necessary to generate meaningful datasets.

For fish, the reworking of sediments is an important component of their feeding behavior. Thus, substrate was added to experimental setups, investigating their consumption of meiofaunal prey. In those laboratory experiments on the quantifications of nematode consumption by different fish species, only single nematode densities were offered. Spieth et al. (2011), Weber & Traunspurger (2014a), and Majdi et al. (2018) showed that in particular bottom-biting fish like common carps (3–4 cm body length), gudgeon (2.5–5 cm), and armored catfish (2–3 cm) are able to consume considerable amounts of nematodes (*Caenorhabditis elegans*) as shown by feeding rates of 234,000, 183,000, and 76,000 nematodes per day, respectively. At a body length of 9–12 cm (carps) and 10–12 cm (gudgeons), their nematode ingestion was reduced by 14% and 6% and was caused by increasingly larger meshes of the gill apparatus. Thus, the retention of meiofauna organisms is mainly restricted to small fish species or juvenile fish. In the course of their development, young bottom-biting fish tend to increasingly prefer macrofauna-sized prey (Coull et al., 1995).

In addition to the determination of feeding rates, nearly all cited studies on potential invertebrate predators (Table 2) investigated the influence of habitat complexity on predation success in experiments conducted in microcosms. Substrates (e.g., sediment, leaf litter, periphyton) are an essential refuge for benthic organisms that determine their horizontal and vertical distribution. Distribution patterns of meiofauna reflect a trade-off between residence in the high-risk (Hölker & Stief, 2005; Traunspurger et al., 2006), but productive, sediment surface and the safer, but physiologically harsher, conditions (e.g., Low oxygen content; Strommer & Smock, 1989; Traunspurger et al., 2015; Majdi et al., 2017) of the deeper sediment.

For instance, meiofaunal prey are much more ingested by flatworm and chironomids, in experiments using no sediment in comparison to experiments using complex substrates where meiofauna could seek refuge (Beier et al., 2004; Hohberg & Traunspurger, 2005; Ptatscheck et al., 2015; Kreuzinger-Janik et al., 2018, 2019). Nevertheless, some predators can follow-up with their prey as Kreuzinger-Janik et al. (2019) showed; the addition of moss did not affect the food intake of predatory, moss-dwelling nematodes.

In combination with the substrate complexity, feeding behavior of macroinvertebrate predators determine their influence on meiofauna. For example, the consumption of nematodes by epibenthic flatworms is reduced in fine sediment but is less affected by coarse gravel or leaf litter (Beier et al., 2004; Kreuzinger-Janik et al., 2018). The small interstices of fine sediment offer considerable protection for meiofaunal prey and hinder the ability of flatworms to deeply penetrate the sediment. Therefore, smaller flatworm species showed higher nematode feeding rates on sediments than larger species. By contrast, for chironomids, which are endobenthic organisms, feeding on nematodes is more efficient in sandy than in coarse-grained substrates (Ptatscheck et al., 2015).

In field experiments also, the sediment depth influences the feeding success of juvenile fish (Gallucci et al., 2005). Meiofauna organisms colonizing deeper sediment layers have a higher protection against predating by juvenile fish as has been reported by Weber et al. (2018). While in the upper sediment layers (0–2 cm), common carps (6–8 cm body length) caused a higher reduction of meiofauna (62%); in a depth of 2–4 cm, a reduction of only 42% was observed. Very similar observations were made by Coull et al. (1989) for juvenile spots.

Furthermore, an impact of substrate on the feeding effort have already been reported from field investigations on predatory nematodes in marine environments (Gallucci et al., 2005).

All those studies illustrate that laboratory experiments considering the complex landscape in which meiofauna dwells are essential to estimate the effect of a given predator in the field. Finally, the large numbers of meiofaunal organisms consumed in those laboratory experiments provide evidence of the strong feeding pressure exerted by fish, crustaceans, and organisms of macrofaunal (and even meiofaunal) size. Nevertheless, the predatory impact on meiofauna, whether through direct predation or as bycatch, is likely to have been greatly underestimated. Since most of the studies examining the influence of predators on single meiofauna species used nematodes as prey, investigations with other prey organisms and additional potential predators are needed. Beyond that, for a complete picture of top-down impact by larger organisms on meiofauna, supplementary studies conducted over longer period and in which the prey consists of whole meiofaunal communities are indispensable.

Laboratory model ecosystems (microcosms) offer nearly optimal systems for such approaches because of the reproducibility and efficiency of those approaches in terms of time, space, and cost. Microcosms are often used in population- and community-level studies and provide a bridge between theory and the natural environment (Fraser & Keddy, 1997). However, a limitation of their use in laboratory experiments is that they cannot reproduce the influence of environmental factors, such as wave action and current velocity, nor such factors as emigration and immigration (Blanchet et al., 2008; Englund & Leonardsson, 2008; Ludlam & Magoulick, 2009). Thus, extrapolation of their results to natural conditions (field studies) has been accordingly problematic (Aarnio, 2000; Petersen & Englund, 2005; Meissner & Muotka, 2006). For example, in small-scale (microcosm and laboratory) experiments, some freshwater fish species were shown to alter the abundance and composition of meiobenthic communities (Table 3), but the studies were conducted in the absence of the abovementioned environmental factors.

The need to close the knowledge gap between highly replicable small-scale experiments and field studies with respect to the effects of fish predation on meiobenthic communities in natural freshwater ecosystems (Weber & Traunspurger, 2015) has been addressed in relatively few studies thus far. Nevertheless, Spieth et al. (2011) and Weber & Traunspurger (2015) used field enclosures and exclosures to provide the first evidence that the presence of benthivorous freshwater fish, specifically carps, significantly influences the structure and composition of a natural meiobenthic community.

Predation effects on meiofaunal composition and population dynamics

In the study of Dineen & Robertson (2010), the influence of juvenile roaches (*Rutilus rutilus*) on natural benthic meiofaunal and macrofaunal communities was investigated. The results showed that up to 78% of the items identified in the gut contents of the fish were of meiofauna-sized origin (e.g., copepods, ostracods and temporal meiofauna) despite larger organisms, and therefore, more rewarding food sources were present in the sediment. Within the copepods, mainly the larger individuals (1 mm) were consumed. Interestingly, nematodes were found in the sediment, but not in the fish guts. Both Weber & Traunspurger (2014a) and Spieth et al. (2011) also reported no significant consumption of nematodes by this fish species under laboratory conditions, regardless of whether only nematodes (Weber &

Traunspurger, 2014a) or a natural meiofaunal community (Spieth et al., 2011) was offered as prey. In the latter study, *Rutilus rutilus* also had no predatory effect on crustaceans, but the fish reduced the number of oligochaetes by 50%. This example indicates that meiofauna organisms are ingested under natural conditions, but selectively feeding fish species differentially influence meiofaunal communities.

The immediate predation effects of fish and macroinvertebrates on the abundance and biomass of meiofauna in freshwater ecosystems may be quite strong (Tables 2 and 3). Especially populations of oligochaetes, microcrustaceans, and nematodes can be severely reduced (summarized in Fig. 1). Juvenile carps (6–8 cm) caused a maximum abundance reduction of 82–97% and a biomass reduction of 94–98% in these meiofaunal groups (Weber & Traunspurger, 2014b). Moreover, the fish reduced the total secondary production of the meiofauna down to 35% within 80 days (Weber & Traunspurger, 2015). Although it is known from studies with an aquaculture background (Rottmann et al., 1991) that juvenile fish can ingest rotifers (tested without sediment), empirical investigations in natural environments revealed no top-down impact on benthic rotifers.

In comparison, macroinvertebrate organisms have a very similar meiofaunal prey spectrum than juvenile fish (Fig. 1). The guts of the invasive red swamp crayfish (*Procambarus clarkii*) and of the native noble crayfish (*Astacus astacus*) were shown to contain, in addition to detritus, fragments of meiofaunal organisms, including nematodes, microcrustaceans, and oligochaetes (Weber & Traunspurger, 2017). The quantitative examination of the feeding behavior of these crayfish species revealed no effect on the total abundance, but a significant effect on the total biomass of the meiofaunal community (42% and 37% reductions in *Procambarus clarkii* and *Astacus astacus*, respectively). This study provided the first evidence of feeding pressure by crayfish on meiofauna in general. Also, fragments of meiofauna were found in the guts of the ornamental cherry shrimp *Neocaridina davidi*. In this experiment, Weber & Traunspurger (2016b) observed a reduction on both density and biomass of meiofaunal communities after 42 days. For nematodes, oligochaetes, and microcrustaceans, these effects even were significant. Further investigations of a natural meiofaunal community revealed the effects of the feeding of *Chironomus riparius* (Ptatscheck et al., 2017). The total meiofaunal density was reduced to 56% by a single chironomid larvae after one day already. These results indicate predatory pressures on meiofauna by macrofaunal organisms that, based on the feeding preferences reported in the literature, were not expected. Both Peters & Traunspurger (2012) and Majdi et al. (2015) found that the presence of plecopterans and gastropods in enclosures reduced the biomass and the abundance of meiofaunal taxa. However, whether these impacts were caused by predation or by indirect engineering effects (e.g., changes of the habitat structure by grazing or predator's movements) could not be surely determined.

Several studies pointed out the reason for selective feeding on meiofauna was prey's body size. Because of the morphology of their branchial apparatus and the distance of their gill rakers, growing fish no longer retain smallest food particles. Hence, observing the effect of fish predation on the size structure of a meiofaunal community, Weber & Traunspurger (2015) found that juvenile carp reduced the abundance of large-bodied meiofauna, thereby increasing the relative abundance of small-bodied meiofauna, suggesting indirect facilitation. Abada et al. (2017) investigated the abundance and diversity of nematode assemblages in response to the presence of Nile tilapia in rearing basins in Egypt. Tilapia predation and/or disturbance reduced nematode abundance, especially of the largest taxa, whereas smaller taxa were unaffected. Beyond that, Dineen & Robertson (2010) reported food preferences of roach for large copepods > 1 mm. For macroinvertebrates that ingest their prey intact, engulfing large meiofauna may be challenging. For example, *Chironomus riparius* with body length of 11.4 mm significantly reduced only the medium-sized nematodes (0.125–1 mm) from natural sediments, while larger larvae (13.5 mm) were able to consume larger nematodes with body length of 1–2 mm (Ptatscheck et al., 2015, 2017). In contrast, chironomids of the taxon Tanypodinae that crush their prey can consume much larger prey organisms like oligochaetes or other chironomids (Baker & McLachlan, 1979). These studies demonstrate the ability of benthivorous fish and macroinvertebrates to change the structure and composition of a meiobenthic invertebrate community in a natural ecosystem. However, the predation by larger organisms does not necessarily has an effect on meiofauna species composition and diversity as demonstrated by Weber &

Traunspurger (2014b) for juvenile gudgeons and carps. In another study by Weber & Traunspurger (2016a), conducted in a field enclosure/exclosure in a natural freshwater pond, the presence of carp was shown to depress the abundance and biomass of free-living freshwater nematode assemblages, especially those of the dominant nematode species, resulting in changes in species density and species composition. By contrast, fish predation had no effect on the diversity and feeding type of the nematode assemblages.

Based on all these results, especially on those from field investigations, at least a short-term top-down effect of larger organisms on the meiofauna in freshwater ecosystems is confirmed. Abundance, biomass, secondary production, size structure, and species composition of meiofauna have shown to be shaped by the predation of larger organisms.

In many studies, only the influence of single individuals on the meiobenthic community was investigated, whereas the high densities of macroinvertebrates [e.g., 90,000 chironomid larvae per m^2 (Berg & Hellenthal, 1992)] in freshwater sediments suggest that the effects of predation in natural environments may be much higher (Ptatscheck et al., 2017).

However, the studies listed in Tables 2 and 3 are conducted within days, weeks, or few months. Long-term studies with durations of over 1 year indicating a clear top-down control on the meiofauna population dynamic are lacking. A very similar data situation has been reviewed by Coull (1999) for marine environments. While it has been demonstrated that young fish consumed meiofauna organisms and reduces their abundance in microcosms or enclosure experiments, field studies revealed no effects of a top-down control. It is very likely that large-scale events like flow disturbances or especially migration of meiofauna organisms could overwhelm the effects those that were observed under controlled conditions (Coull, 1999; Dineen & Robertson, 2010). Meiofauna organisms can recolonize disturbed substrates within hours (e.g., within one tidal cycle) or a few days, by active movement or passive drift by water or even air (Fegley, 1988; Palmer, 1988; Boulton et al., 1991; Cross & Curran, 2004; Incagnone et al., 2015; Ptatscheck et al., 2018). Their short generation times, high reproduction rate, and partly asexual reproduction strategies promote the fast population recovery. Weber & Traunspurger (2015, 2016a) showed that young carps significantly shaped meiofaunal communities. However, within 45 days of their removal from enclosures (6 ind. per m2) meiofauna abundance, biomass, secondary reproduction, as well as nematodes species composition recovered. The traceability of a top-down control of larger organisms on meiofauna is thus highly dependent on predation intensity and frequency. When predation occurs continuously and with a high intensity, it should be more detectable than single or seasonal dependent predation. The predation on meiofauna is highly variable because predators can, for example, move to adjacent areas, grow, and change their feeding preferences, leave the habitat (adult insects), or are consumed by larger predators. Finally, periodic predation enables the meiofauna community to regenerate. The influence of seasonality, but even of species turnover and habitat structure must, therefore, be considered in further investigations.

The importance of meiofauna as food for larger organisms

Yet, the question remains, whether meiofauna are a worthwhile target prey or simply a bycatch?

Meiofauna organisms that colonize substrates of aquatic habitats in large numbers are mostly multivoltine and, as pointed out above, can easily absorb the adverse effects of predation. It seems that a standing stock is available throughout the year that theoretically can provide food for larger organisms. Taken together, the studies in this review provide convincing evidence that meiofaunal organisms are frequently consumed by a wide range of larger invertebrates and vertebrates (Fig. 1). It can be expected that the list of evaluated species is far from being complete and species-specific differences in feeding behavior must of course be considered. For example, Schmid-Araya & Schmid (1995) reported that not all of the examined plecopteran species contained meiofauna within their guts.

For freshwater fish (Weber et al., 2018), insect larvae (Schmid-Araya & Schmid, 1995; Tavares-Cromar & Williams, 1997; Schmid & Schmid-Araya, 1997; Schmid-Araya & Schmid, 2000; de Carvalho & Uieda, 2009), and crustaceans (Weber & Traunspurger, 2016b, 2017) from natural substrates, most of their gut contents consist of fine particulate organic matter and meiofauna is rather underrepresented. By contrast, for young brook charr, McNicol et al. (1985) showed only a small proportion of detritus, but a higher content of macroinvertebrates than of meiofauna, while meiofauna-sized organisms represent the major part of roaches diet (Dineen & Robertson, 2010). The proportion may strongly fluctuate over the course of the year as in summer, microcrustaceans accounted for 95% of the ingested food of juvenile fish, but in winter the amount declined to 13% (Ahlgren, 1990). Accordingly, the author of that study concluded that juvenile fish can specifically separate detritus from invertebrates and that detritus is ingested intentionally, when preferred invertebrate prey are scarce.

However, several studies in marine environments conclude that the nematodes and especially copepods contained in a few 10 cm^2 sediment cover the daily nutrient need of young fish (Ceccherelli et al., 1994; Feller & Coull, 1995; Street et al., 1998). In numbers, this means ingestion rates of up to 750 marine copepods and 7.000 nematodes per fish and day. Also, in these studies, the meiofauna partly accounted for only 2-3% of the total stomach content, which is in line with the observations from freshwater organisms mentioned above. The nutritional value of different meiofaunal taxa probably depends on their own diet, for example, discussed for bacterial feeding nematodes and algal feeding copepods by Coull (1999). In aquaculture, meiofauna organisms like copepods, nematodes, and even rotifers have established for several decades as suitable food sources that promote the growth and survival of young fish (Fernández-Reiriz et al., 1993; Sargent et al., 1997; Farhadian et al., 2008). In fish farm cultivating freshwater fish, mainly nematodes are used as food (Schlechtriem et al., 2004a, b, 2005; Rottmann et al., 1991). The high proportion of polyunsaturated fatty acids and amino acids makes meiofaunal organisms a “good quality food” promoting growth (Watanabe et al., 1983; Coull, 1990, 1999; Sargent et al., 1997).

Consequently, meiofauna, regardless of whether ingested selectively or not by freshwater fish or macroinvertebrates, may at least represent a qualitative enhancement of diet. Young bottom-biting fishes can retain small nutritious particle and segregate the preferred components by the morphology of their mouth and branchial basket as well as specific feeding behavior. Therefore, and based on the results reviewed in this text, it can be expected, that meiofauna organisms are an important standard meal for young fish before they switch to larger prey during their development. This assumption is supported by studies on the stable isotope signature of juvenile marine fish (e.g., Lugendo et al., 2006; Carpentier et al., 2014), which demonstrate the great importance of meiofauna as food resource. Contrary, tube-building chironomids that are characterized as nonselective feeder with fast gut passage and low digestion efficiency (Mclachlan et al., 1978; Pinder, 1986; Welton et al., 1991; Hirabayashi & Wotton, 1999) prefer the most common food source (Ptatscheck et al., 2017). Therefore, the larvae consume meiofauna organisms and can shape the community, but rather ingest them as bycatch. Similar omnivores feeding behavior of various freshwater crustaceans has been observed by Weber & Traunspurger (2016b, 2017). However, for these organisms as well as for the majority of freshwater macroinvertebrates that are known to consume meiofauna (Table 1, Fig. 1), the literature is not rich enough to draw clear conclusions on the importance of a meiofaunal diet.

Conclusion

With regard to our initial questions and based on the current data situation, the following can be summarized: (1) Gut analysis revealed that a wide spectrum of macroinvertebrates and juvenile fish consume meiofauna organisms in natural environments. However, (2) only for single predators this ingestion of meiofauna was experimentally quantified so far and data are still sparse. Present investigations show a high intake of nematodes, microcrustaceans, and oligochaetes. In line with these results, (3) an at least short-term top-down control (< 1 year) of meiofauna populations by larger organisms was demonstrated. (4) The meiofauna represents a nutritiously and omnipresent food source in benthic environments and can be considered as a standard meal for young fish, but probably rather a bycatch for invertebrates.

It has become clear that, finally, not only gut analysis, but rather the combination with laboratory experiments under controlled conditions, microcosm studies and field investigations using enclosure/exclosure settings improve the results and enable to gain better insights. Especially, long-term field investigation would help to understand the top-down impact of larger organisms on the population dynamics of meiofauna. Beyond these empirical studies, analysis of stable isotopes and fatty acids are also suitable tools for examining the position of the meiofauna in benthic food webs. Currently, only a few such investigations have been conducted in freshwater habitats (e.g., Schmid-Araya et al., 2016; Majdi & Traunspurger, 2017). Although our knowledge of this trophic interactions has significantly increased over the last 20 years (summarized in Fig. 1), much remains to be learned about the impact of these interactions on the abundance, biomass, secondary production, and composition of meiofaunal communities in freshwater habitats and the benefits for predator species.

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