



REVIEW PAPER

The ability to get everywhere: dispersal modes of free-living, aquatic nematodes

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Received: 30 January 2020 / Revised: 30 July 2020 / Accepted: 1 August 2020 / Published online: 11 August 2020
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Abstract Nematodes colonize almost all aquatic habitats worldwide. Despite their small size, restricted locomotion and lack of pelagic larvae, they can reach even isolated habitats within a short time. In this review, we examine the underlying dispersal modes, considering their active movement in substrates and water, their drift by water and wind, rafting, zoochory as well as human-mediated vectors. These modes are limited by morphology and habitat structure, ecological factors and especially by hydrodynamics. Active dispersal is effective over short distances, but with increasing water-flow velocity, passive dispersal modes, which enable long-range transfer, become important. In fact, the transport of nematodes over thousands of kilometers via ship water tanks and by hitchhiking on sea turtles has been documented. Overland dispersal vectors include wind and birds whereas rafting enables an aggregated distribution because food is available, and reproduction is possible onboard the rafts. The diversity of possible dispersal modes is high and offers a reasonable chance for gravid females or groups of nematodes to be transferred even to remote environments. Their immigration is continuous, and supported by their rapid,

parthenogenetic reproduction, nematodes are effective pioneers with the ability to (re)colonize new or disturbed habitats or rebalance already existing communities.

Keywords Meiofauna paradox · Rafting · Zoochory · Drifting · Wind dispersal · Locomotion

Introduction

Nematodes are the most abundant metazoans in the biosphere and colonize nearly all aquatic and semi-aquatic habitats worldwide. They can be found in permanent lotic and lentic surface waters, such as lakes and streams, and in the seabed. They have also been collected from high-altitude lakes (up to 5,600 m above sea level) (Andrássy, 1978; Tsalolikhin, 2014), from deep-sea regions (down to 11,000 m below sea level) (Bik et al., 2010; Leduc & Rowden, 2018) and from caves and groundwater (Muschiol et al., 2015). In addition to these large-scale and permanent habitats, nematodes inhabit small, isolated and temporal environments, such as heat outlets or the volcanos of isolated islands (Muschiol & Traunspurger, 2009; Portnova, 2009; Schabetsberger et al., 2009; Portnova et al., 2011; Schabetsberger et al., 2013), ephemeral ponds with no connection to other waters or created by melt water or subject to sporadic desiccation and

Handling Editor: Diego Fontaneto

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surrounded by desert or ice (Suren, 1990; Pinder et al., 2000; Chan et al., 2005), as well as water collections in plant components (phytotelmata) (Kitching, 2000; Ptatscheck et al., 2015a; Robaina et al., 2015; Zotz & Traunspurger, 2016).

Within these marine and freshwater habitats, nematodes can occur in considerable abundances, reaching densities of millions of individuals per square meter (Traunspurger, 2000; Michiels & Traunspurger, 2005a; van Gaever et al., 2006; Schroeder et al., 2012; Traunspurger et al., 2012) and representing numerous species. For example, Beier & Traunspurger (2003a, b, c) identified up to 113 nematode species in $\sim 100\text{-cm}^3$ sediment samples (26-cm^2 sediment area) obtained from 2 streams during a 1-year period and Traunspurger (1996a, b) collected 116 species from a sediment sample of the same size from Lake Königssee. As an essential trophic link between the microbenthos (e.g., bacteria or rotifers) and larger organisms (macroinvertebrates or even juvenile fish), nematodes are crucial to nutrient cycling and energy flow in benthic environments.

A consideration of marine and freshwater nematodes on a global scale shows specific and non-random distribution patterns for many species (Artois et al., 2011; Moens et al., 2013; Zullini, 2014) whereas others were found to be ubiquitous. In their study of 18 nematode species from the Galapagos Islands, Abebe & Coomans (1995) showed that 10 were cosmopolitan, 6 were at least common in the southern hemisphere and the remaining 2 were newly described species. For example, *Rhabdolaimus terrestris* de Man, 1880 was collected from the Galapagos Islands but also inhabits bromeliad phytotelmata in Panama as well as European, Ethiopian and Himalayan lakes and Vietnamese streams (Traunspurger, 1995; Gusakov et al., 2011; Ristau & Traunspurger, 2011; Schroeder et al., 2012; Tsalolikhin, 2014; Zotz & Traunspurger, 2016). Genetic studies have provided evidence of gene flow between metacommunities separated by hundreds of kilometers and therefore of the possible dispersal range of nematodes (Bik et al., 2010; Apolônio Silva de Oliveira et al., 2017; de Groote et al., 2017). However, it is generally assumed that gene flow is mostly limited to distances < 100 km (Derycke et al., 2008, 2013; Hauquier et al., 2017). Cerca et al. (2018) showed in their review that, based on molecular investigations, even amphi-oceanic distribution of marine meiofauna taxa seldom occurs.

At local and habitat-based scales, the high distribution potential and importance of nematodes as pioneer organisms become obvious. Studies of artificial water-filled tree holes demonstrated their colonization by rotifers and especially by nematodes within a few days, despite the clear delimitation of these small island-like habitats and their isolation from other aquatic sources (Ptatscheck & Traunspurger, 2014; Ptatscheck et al., 2015a). Similarly, the rapid immigration of nematodes and other meiobenthic taxa, including rotifers and microcrustaceans, within a single tidal cycle or a few days was described in studies on the colonization of azoic substrate patches in tidal areas, lakes and streams (Boulton et al., 1991; Peters et al., 2007; Boström et al., 2010). However, in other studies from freshwater and marine environments (Chandler & Fleeger, 1983; Duft et al., 2002; Guilini et al., 2011; Zhou et al., 2015), even after weeks there was no complete adaptation of the species composition in the defaunated substrate or from the surrounding source habitats. Investigations on the colonization of ice after iceberg scouring and ice shelf collapses by meiofauna showed that nematodes, next to ostracods and copepods, are among the pioneer organisms, but the recovery process is slow (up to years) (Lee et al., 2001a, b; Hauquier et al., 2016). All those studies well demonstrated that dispersal is a key factor in understanding the structuring of nematode populations.

In addition to survivability, fecundity and sexual maturity, the dispersal potential of an organism is a crucial feature of its life history and sustained existence (Bonte & Dahiré, 2017). Dispersal describes all movements of an individual or a propagule that lead to a spatial gene flow (Ronce, 2007). It can be distinguished in three successive phases: (1) *emigration* from the source habitat, (2) active or passive *transfer* to another habitat and (3) the final *immigration* (Bowler & Benton, 2005; Bonte et al., 2012). The actual translocation (*emigration* and *transfer*) is often considered separately from the subsequent establishment processes comprising *immigration* (e.g., Nathan, 2001; Hessen et al., 2019). Dispersal enables individuals to avoid adverse living conditions (e.g., competition or predation) but also to recolonize habitats after catastrophic events or stabilize and expand the diversity of an existing community (Valanko et al., 2015). At the same time, high levels of interchange, for example between connected ponds

(Akasaka & Takamura, 2012), can lead to the homogenization of communities, a decrease in β -diversity or the dominance of a single, competitive taxon (Leibold et al., 2004; Matthiessen et al., 2010). The intensity of dispersal is thus a decisive factor in defining the diversity and stability of communities (Leibold et al., 2004; Cadotte, 2006; Howeth & Leibold, 2010; Matthiessen et al., 2010; Carrara et al., 2012; Valanko et al., 2015).

Dispersal also ultimately affects the distribution and composition of benthic invertebrates (Grönroos et al., 2013; Kärnä et al., 2015; Tonkin et al., 2018; Tornero et al., 2018; Gansfort & Traunspurger, 2019). However, these organisms are inhabitants of aquatic islands that are often not directly connected to similar habitats but are instead surrounded by a “dry ocean” (Incagnone et al., 2015). Furthermore, meiobenthic organisms such as nematodes are usually not associated with rapid movement and do not have pelagic larvae, such that dispersal within a habitat is unlikely. Thus, in referring to this so-called meiofauna paradox, Giere (2009) rightly asked: How can we explain a wide distribution of animals with almost no dispersive capacity? In this context, Cerca et al. (2018) already pointed out that the dispersal potential of meiobenthic organisms has been considerably underestimated in the past and the meiofauna paradox is rather to be regarded as a paradigm.

In this review, we consider the dispersal of free-living nematodes from permanent freshwater and marine habitats, although some of the discussed dispersal modes, such as wind drift and transport on/in larger animals, are also relevant for terrestrial species. However, due to their sometimes very (species-) specific dispersal, parasitic taxa were excluded. In focusing on the translocation (emigration and transfer) aspect of dispersal, we specifically asked: By what pathways can nematodes reach a given habitat? What are the triggers and influencing factors that determine nematode dispersal? How relevant are these modes for long-range dispersal?

A major difficulty in compiling this review was the comparability of the analyzed datasets since the included studies sometimes employed very different methodologies. Notably, the mesh sizes of the sieves used to extract the organisms of interest ranged from 1.2 to > 250 μm . In the study of Boulton et al. (1991), a mesh size of 63 μm did not hinder nematode entry into the investigated enclosures. Recent studies

showed that even a mesh size of 35 μm does not result in the retention of all nematodes from a suspension (Ptatscheck et al., 2015b; Kreuzinger-Janik et al., 2018). Consequently, nematode abundance and diversity are often underestimated. In addition, many studies included in this review were primarily designed to investigate larger organisms, with nematodes collected accidentally and thus mentioned only incidentally. Therefore, to avoid misinterpretations, we generally refrain from detailed comparisons of the nematode densities determined in different studies and habitats.

The majority of studies on nematode dispersal have been carried out in marine environments, with an emphasis on water drift vs. active crawling/swimming. Reviews of the single dispersal modes of marine meiofauna (benthic invertebrates retained on a net with a mesh size of 44 μm); Giere (2009) can be found in Palmer (1988a), Armonies (1994) and Thiel & Gutow (2004b) whereas our review provides the first detailed descriptions of all relevant dispersal modes detected in both marine and freshwater nematodes, i.e., (1) active dispersal within a water body (swimming and crawling), (2) passive dispersal by water drift, (3) rafting on floating items, (4) hitchhiking in/on animals (endozoochory and epizoochory), (5) wind drift and (6) anthropogenic vectors (Fig. 1).

Traits relevant for dispersal

Locomotion

The alternating contractions of the dorsal and ventral longitudinal muscles of nematodes are solely responsible for their active locomotion. The resulting undulatory movement, in which backward pressure is exerted against different forms of external resistance, pushes the nematode body forwards along the substrate (Gray & Lissmann, 1964; Wallace, 1968). The form and frequency of these contractions and thus the nematode's progress depend on the surrounding medium. Due to its multilayer cuticula, the nematode body is less compressible such that the pore size of the sediment is an important parameter determining the speed of nematode movement. Larger nematodes move faster through the sediment than smaller ones, but the maximum speed is reached when particle diameters are three times smaller than the body length

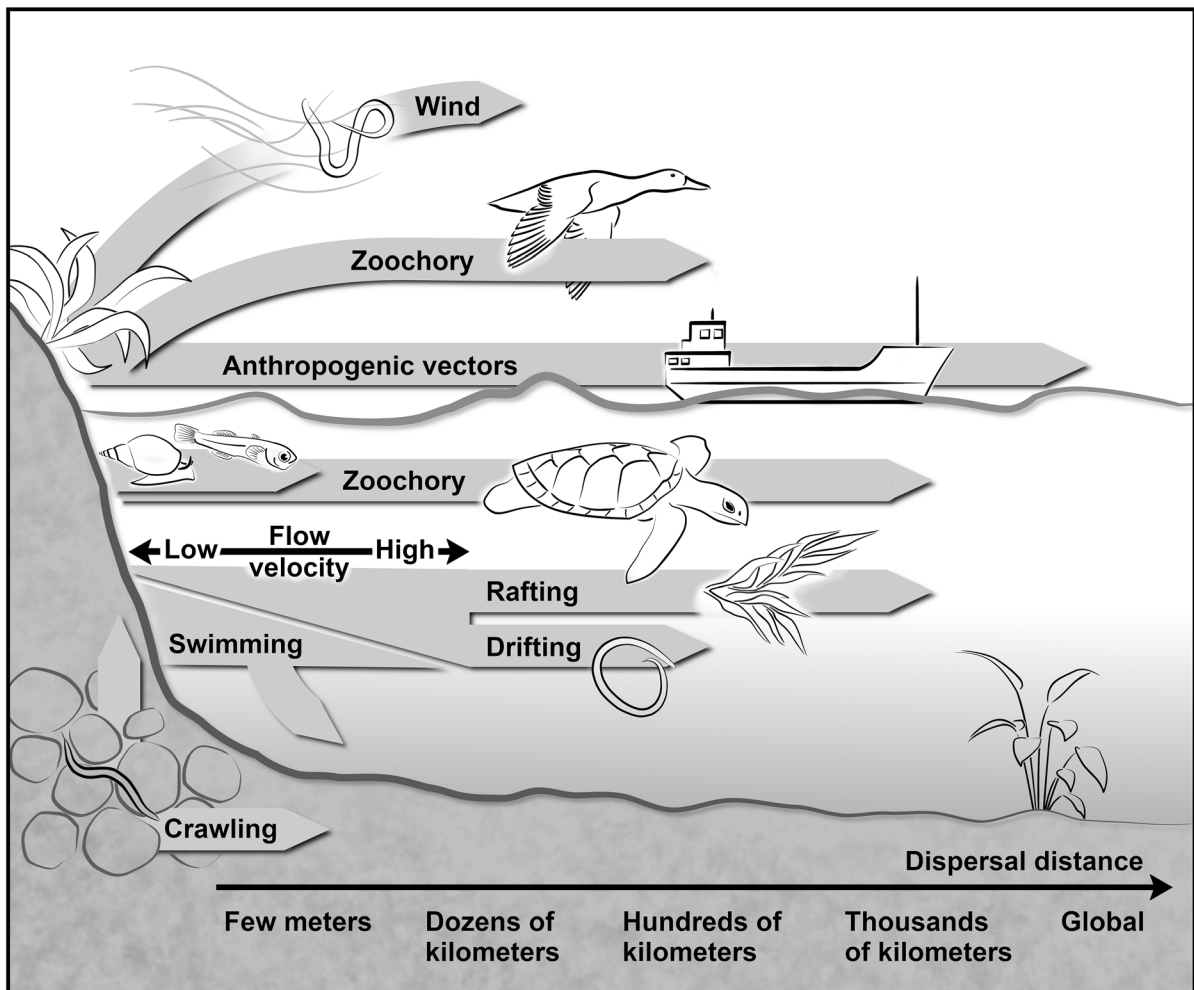


Fig. 1 Overview of the distribution modes and possible geographic ranges of nematodes based on the studies included in this review

of the worm (Wallace, 1968; Soetaert et al., 2002). With decreasing particle diameter, mobility is increasingly impaired because the interstitial spaces are narrower. In coarse sediment fractions, in which particle diameters exceed a third of the worm's length, locomotion is independent of particle size as the nematode then swims (Wallace, 1958, 1968). Thus, both sediment structure and nematode body width determine whether a nematode slides unimpeded through the interstitial or instead burrows (Wieser, 1959; Tita et al., 1999). In fine sediments with an incomplete interstitial system, nematodes with long, thin body shapes are at an advantage over those that are shorter and/or thicker. In addition to body length and width, the shape of the nematode tail provides insights into nematode locomotion, as long-tailed taxa

exhibit greater mobility and maneuverability and are thus largely found in fine sediments (Thistle & Sherman, 1985; Schratzberger et al., 2007).

In liquid medium, the wavelength, amplitude and frequency of the alternating contractions of nematodes are stronger and compensate for the reduced propulsion compared to that in sediments (Gray & Lissmann, 1964). In the water column, for example, the propulsive thrust must exceed the nematode's body weight; otherwise the nematode will sink (Wallace & Doncaster, 1964; Wallace, 1968). Small nematodes are better able to remain in the water column because, unlike larger individuals, their undulatory movement is not hampered by viscosity (Crofton, 1966). This was demonstrated experimentally by Ullberg & Ólafsson (2003b) while Thomas & Lana (2011) and Lins et al.

(2013) reported that, congruent with determinations of the most mobile nematode morphotypes in sediment, active swimmers were those with thin, uniform, long-tailed bodies. Together, these morphological adaptations suggest that nematode species disperse vertically and horizontally within the substrate to different extents and are able to enter the water column by active movement. Once in open water, nematodes can theoretically cover distances by swimming and then actively emigrate back to the sediment.

Little is known about the intrinsic speed of nematodes and most of the available studies have focused on terrestrial taxa (Table 1). Moreover, in most if not all cases, the speed of aquatic nematodes

was assessed in liquid or unnatural media, such as agar, but not in natural sediments. Jensen (1981) determined a swimming speed of 50 mm/min for the marine nematode species *Chromadorita tenuis* in still water. Another study showed that nematodes can swim continuously for at least 1–2 h (Ghosh & Emmons, 2008). The crawling speed of nematodes on or through a substrate is significantly slower than the swimming speed (Table 1). For example, when placed on agar *Panagrellus silusiae* can bridge distances of 30 mm within 1 min (Gray & Lissmann, 1964). The study of Hapca et al. (2007) convincingly showed that the crawling speed of nematodes in natural sediment is slower than that in or on agar. In

Table 1 Summary of studies that estimated the velocity (crawling or swimming) of different nematode species in different media

Taxon	Body length (µm)	Medium	Distance (mm) moved/ min	References
<i>Caenorhabditis elegans</i> (Maupas, 1900)	Different sizes	In/on agar	1–15	Ramot et al. (2008)
		In/on agar + food	1–13.5	
<i>Chromadorita tenuis</i> (G. Schneider, 1906)	~ 1,000	Water/swimming	50	Jensen (1981)
<i>Haemonchus contortus</i> (Rudolphi, 1803)	575	On 2% agar	3.1	Gray & Lissmann (1964)
		Water/swimming	9.9	
<i>Heterodera schachtii</i> (A.Schmidt, (1871)	Larvae (< 500)	On alginate jelly +		Wallace (1958)
		< 1 µm water film	< 0.05	
		2–5 µm	1.7	
		5–10 µm	0.7	
		10–20 µm	0.3	
		50 µm	0.2	
<i>Panagrellus silusiae</i> (de Man, 1913)	1,190–1,340	On 1% agar	30.1	Gray & Lissmann (1964)
		In 1% agar	27.6	
		On 1% gelatin	17.5	
		In 1% gelatin	23.2	
		Water/swimming	38.4	
<i>Phasmarhabditis hermaphrodita</i> (A. Schneider, 1859)	~ 1,000	On 1.2% agar	9.7	Hapca et al. (2007)
		On 1.2% agar + sand	6.9	
Rhabditis		In a suspension of starch grains	13.2–31.2	Gray & Lissmann (1964)
<i>Turbatrix aceti</i> (Müller, 1783)	1,500–1,570	On 0.5% agar	15.4	Gray & Lissmann (1964)
		In 0.5% agar	17.2	
		Water/swimming	43.1	

that study, the movement of *Phasmarhabditis hermaphrodita* was reduced by 29%, down to 6.9 mm/min, when a thin layer of sand was added to the agar. Among meiofauna, nematodes are rather slow, as copepods have a swimming speed of far over 400 mm/min and a burrowing speed of up to 16 mm/min while the burrowing speed of oligochaetes may reach 13 mm/min (Enright, 1977; Yen, 1988; Palmer et al., 1992).

Surface adherence

Surface adherence is another factor that can affect the dispersal ability of an organism. In nematodes, adherence is enabled by the adhesive substances secreted by the caudal glands, adhesive tubes or strong setae (Adams & Tyler, 1980; Turpeniemi & Hyvärinen, 1996; da Fonsêca-Genevois et al., 2006; Giere, 2009; Tchesunov, 2015). The anchoring ability of nematodes allows them to stably colonize hard substrates even in high-energy environments, such that subsequent dispersal is mostly via rafting.

Behavior

Nematode mobility is also influenced by water parameters, the availability of food resources and the community composition (e.g., Wallace, 1968; Robinson, 1994; Ramot et al., 2008), all of which may lead to short-term translocations. de Meester et al. (2012, 2015) conducted a series of standardized laboratory experiments and showed that at high densities nematodes begin to emigrate from their source habitat. In this context competitive strength between species plays a decisive role, as species that are weak competitors emigrate earlier and at higher densities than strong competitors. Emigration is also determined by the availability of suitable food resources, as it is discouraged by sufficient food at the source habit but stimulated by the absence of food and by the presence of more suitable sources in adjoining areas (de Meester et al., 2012). Tita et al. (1999) showed that different nematode morphotypes are associated with specific feeding groups, with smaller ratios of body width:body length typical of microvores and higher ratios characteristic of epigrowth feeders and predators.

Additional information on the dispersal behavior of nematodes comes from observations of their

communities in natural environments. The oxygen content in benthic habitats is a crucial environmental factor that determines the dispersal depth of nematode communities (Platt, 1977; Strommer & Smock, 1989; Hendelberg & Jensen, 1993; Traunspurger, 1997; Teiwes et al., 2007). Studies from freshwater and marine environments have shown that nematodes mostly colonize the upper layers of the sediment, while in deeper layers, with their lower oxygen content, nematode density declines and their communities are composed by more adapted species. In well-aerated habitats, such as streams with a coarse (> 125 µm) sediment size, relocation to deeper layers is possible (Schmid-Araya, 1997; Eisenmann et al., 1998; Traunspurger et al., 2015) and reduces the risk of erosion by a strong flow velocity (Palmer & Gust, 1985; Palmer, 1986; Palmer & Molloy, 1986; Fegley, 1987; Palmer, 1988a; Traunspurger et al., 2015). Consequently, the tidal cycle can trigger the daily vertical migration of certain species of marine nematodes. However, the upwards migration of some species when the tide is strongest (Steyaert et al., 2001; Gallucci et al., 2005; Brustolin et al., 2013) suggests that factors other than protection from erosion must be invoked to explain vertical migration. For example, the occurrence of specific feeding types is determined by the allocation and quality of food sources (Soetaert et al., 2002; Neira et al., 2013). This was also observed by Traunspurger et al. (2015), who found that bacterial-feeding taxa are restricted to the upper sediments of streams, as also demonstrated for epigrowth feeders (Commito & Tita, 2002). Additionally, Traunspurger & Drews (1996) detected a predominance of juvenile individuals in these habitats. Experiments have shown that the active movement of nematodes is influenced by the suitability of habitats (e.g., the presence of food resources, or habitat structure) (Jensen, 1981; Ullberg & Ólafsson, 2003b; Lins et al., 2013; Mevenkamp et al., 2016). Thus, chemotaxis and the attraction of specific signal molecules (see also Choe et al., 2012 and literature therein) can be a powerful driver for the community composition of marine and freshwater nematodes.

The presence of predators and their physical disturbance of the sediment can restructure the distribution of nematodes and initiate active dispersal processes. Predators optimize their predation efforts by vertical migration while potential prey nematodes seek refuge in less vulnerable layers of the sediment

(Steyaert et al., 2001; Gallucci et al., 2008). In the presence of copepods and chironomids in sediment, the relative number of nematodes, especially juveniles, in the upper layers significantly increased, caused by an induced vertical relocation (Traunspurger et al., 2006). Ólafsson (2003) described the opposing effects of different organismal groups, including crustaceans, annelids and mollusks, on nematode dispersal in sediments. In that study, the presence of larger organisms often led to the migration of nematodes into deeper layers. However, whether this was an escape from predation, or induced by the physical disturbance caused by the bioturbation, or a response to the improved aeration in the disturbed deeper sediment was unclear.

In general, most of the considered studies conducted in natural environments could not clearly show whether nematode migration was triggered directly by the respective factor or whether the change in the community structure was due to environmental filtering. Further studies that minimize influencing factors such as emigration from adjacent areas or reproduction and, in the best case, allow observations of migratory nematodes (according to de Meester et al., 2012, 2015) would be an approach to investigate the distribution behavior of nematodes in response to certain environmental factors.

Dispersal units

According to Fontaneto (2019), the successful long-range dispersal of meiobenthic sized organisms requires, inter alia, the presence of propagules and the long-term resistance of these dispersal units. Propagules are especially relevant to dispersal outside the water (e.g., wind drift) (Panov et al., 2004; Nkem et al., 2006; Incagnone et al., 2015). For nematodes, dormant eggs, dauer larvae and stages of anhydrobiosis that facilitate resistance to high temperature, frost, desiccation and digestion (see the “Endozoochory” section) for periods partly as long as several decades (van Gundy, 1965; Watanabe, 2006; Mayer & Sommer, 2011) are of particular importance (Fontaneto, 2019). However, while eggs and dauer larvae are common dispersal units of nematodes, anhydrobiosis is known from other aquatic invertebrates such as microcrustaceans or rotifers. However, for nematodes anhydrobiosis is mainly restricted to terrestrial species and colonizers of ephemeral aquatic habitats (e.g.,

ponds) and is not a feature of species found in stable aquatic environments (Crowe & Madin, 1974; McSorley, 2003; Watanabe, 2006; Tahseen, 2012).

Several studies have investigated egg production by different freshwater nematodes and reported values of up to 49 eggs/day (Schiemer et al., 1980; Muschiol & Traunspurger, 2007; Kreuzinger-Janik et al., 2017). Those studies also showed that the number of laid eggs is strongly species-specific and depends on the age of the female nematode but also on environmental parameters (e.g., availability of food resources). As the hatching of juveniles is triggered by factors that include temperature and moisture, it can be delayed until environmental conditions are optimal (van Gundy, 1965). Egg clusters with sticky membranes are protected from dehydration or erosion and can thus be dispersed by rafting or zoochory (see later sections in this review) (Micoletzky, 1922; van Gundy, 1965).

Active dispersal through the sediment

Kappes et al. (2014) compared the dispersal potential of aquatic and terrestrial taxa (plants, mollusks, gastropods and dipterans) and showed that the former are especially successful in covering long distances. For organisms of meiobenthic size, dispersal mainly relies on passive modes (Incagnone et al., 2015), whereas in the case of active movement the maximal dispersal distance declines with decreasing body size (Jenkins et al., 2007).

The dispersal of nematodes through the sediment has been less intensively studied than dispersal in the water column. In studies on the recolonization of sediments by meiofauna (Table 2), the immigration of sediment-crawling organisms was often prevented by the placement of azoic sediments on impassable barriers such as trays. Chandler & Fleegeer (1983) were the first to demonstrate that the degree of immigration of nematodes in azoic sediments by sediment crawling and water column dispersal was very similar in a tidal pond. However, whereas nematodes were the predominant meiofaunal taxon in the undisturbed sediment (> 80%), with an abundance sufficient to allow recruitment, even after 29 days their densities in the azoic sediment were less than a third of those in the source sediment. The further demonstration that even copepods, which are very effective dispersers in the water column, could

Table 2 Studies on the recolonization of azoic or disturbed substrates by nematodes in which the abundances of settling individuals were compared with those of nematodes from the natural background substrate

Location/habitat	Colonization area (grain size)	Area size (cm ²)	Flow (cm/s)	Depth (m)	Comparison with the background density	Pathway	References
Marine							
Baltic Archipelago	Azoic clay sediment	1,200	Low wave activity	1–1.5	9% After 2 weeks	W	Aarnio & Bonsdorff (1992)
	Azoic sandy sediment	1,200	High wave activity	1–1.5	30% After 2 weeks		
Deep sea	Azoic sediment + food sources	15*		2,475	2% After 10 days	S	Guilini et al. (2011)
Estuary pond	Azoic sediment (38 µm)	374–420		0.1–0.5	19–31% After 29 days	AP	Chandler & Fleeger (1983)
Intertidal mudbar	Dug-up sediment	90,000		Up to 1.5	No differences after 0.5 days	AP	Sherman & Coull (1980)
Intertidal mudflat	Sediment disturbed by artificial spots	0.65*		–	No differences after 5 h	AP	Billheimer & Coull (1988)
Intertidal sand flat	Sediment disturbed by ray feeding	~ 1,206		–	No differences after 4–14 tidal cycles	AP	Cross & Curran (2004)
Intertidal shoal	Azoic sediment (141 µm)	177	Up to 35	–	20% After one tidal cycle	AP	Fegley (1988)
Intertidal zone	Azoic sediment (38 µm)	755	1.2–6	–	10% After 3 days	AP	Sun & Fleeger (1994)
Intertidal zone	Azoic sediment (< 63 µm)	6*		1.5	21% After 60 days	AP	Zhou et al. (2015)
Intertidal zone	Sediment traps	1.3	130–730	–	11% After 1 days	W	Commito & Tita (2002)
Subtidal zone	Azoic sediment	875		11	No differences after 1 month	AP	Olafsson & Moore (1990)
Subtidal zone	Sediment disturbed by stingray feeding	–	4.3	2–3	No differences after 4 days	AP	Sherman et al. (1983)
Subtidal zone	Azoic sediment + oil contamination	1,000		1	No differences after 16 days	W	Alongi et al. (1983)
Subtidal zone	Azoic sand (207 µm)	49		0.7–1.0	No differences after 1 day	W	Colangelo & Ceccherelli (1994)
Subtidal zone	Artificial seagrass bed	217		At least 1	No differences after 2 days	AP	de Troch et al. (2005)
Swedish fjord	Azoic sediment (175 µm)	2,035		27	30% After 525 days	W	Widborn (1983)
Laboratory	Azoic sediment	2*	No flow		5–20% After 9 days	AP	Gallucci et al. (2008)
Laboratory	Azoic sediment (< 2 mm)	17*	No flow		32–90% After 14 days	AP	Schratzberger et al. (2004)
Laboratory	Azoic sediment	1,369	No flow		10–18% After 49 days	AP	Ullberg & Ólafsson (2003a)
Freshwater							
Littoral zone	Aluminum plates						Peters et al. (2007)
	Bottom	2,500		0.6–0.8	~ 16.5% After 57 days	W	
	30 cm above bottom	2,500		0.6–0.8	~ 16.5% After 57 days	W	
Littoral zone	Sediment disturbed by carp	4,900		0.7	No differences after 45 days	AP	Weber & Traunspurger (2016)
Stream	Standpipe traps (30 µm to 9 mm)	35*	3.9–705.1	0.32–0.37	95% After 5 days	S	Schmid-Araya (2000)
Stream pool	Azoic sediment (240 µm)	314	30	0.29	~ 11% After 21 days	AP	Duft et al. (2002)
Artificial stream	Washed gravel (2.5–3.5 cm) and sand	6,000	1–12	0.08–0.10	No differences after 5 days	W	Smith & Brown (2006)

Possible colonization pathways (W primarily through the water column, S primarily through sediment, AP all pathways possible) are also presented

*The whole area was investigated; in other cases, subsamples were taken

not approximate their sediment density during the same period showed that colonization through the sediment is a slow process. Much higher recolonization rates for nematodes were reported by Schmid-Araya (2000) in a study of a fast-flowing stream with coarse gravel. In that setting, recolonization by nematodes and harpacticoids was completed within 5 days and that by other meiofaunal organisms (cyclopoids, rotifers and ostracods) within approximately 2 days. Whether this immigration was primarily due to downstream movement was not investigated. Although other studies of azoic stream sediments found evidence of nematode colonization by upstream movement (Williams & Hynes, 1976; Williams, 1977), migration by downstream drift cannot be excluded because in those investigations the 125- μm nets used to prevent immigration from other directions would not have been an effective barrier for nematodes.

Active dispersal in the sediment includes not only horizontal movement but also vertical displacement. Nematodes in sediments exhibit a typical vertical distribution, with time-related and species-specific vertical preferences discerned in seasonally affected habitats such as streams or the littoral and profundal of lakes (Traunspurger & Drews, 1996; Traunspurger et al., 2015). The constant upward and downward dispersal of nematodes within relatively short time intervals may allow the colonization of deposited substrates from below. Using the same experimental design, Williams & Hynes (1976), Williams (1977) and Benzie (1984) showed that up to 62% of the immigrating nematodes that had colonized the azoic substrates had done so by vertical movement.

The importance of crawling in the sediment

Both Schratzberger et al. (2004) and Gallucci et al. (2008) found that large (long and wide) nematodes are the first to enter azoic sediment by sediment burrowing. The two studies also showed that active dispersal has significantly different effects on the species composition of the recolonized and source sediments. Thus, despite the strong influence of active crawling on nematode diversity, this type of motility is restricted to small areas around the source habitat. In the study of Ullberg & Ólafsson (2003a), the number of nematodes arriving at a location 36 cm away was only half that at an area adjacent to the source habitat.

Among the studies on the recolonization of the azoic substrates listed in Table 2, only one was able to attribute the alignment (95%) of nematode densities in the new vs. the background substrate to in-sediment movement alone. Accurate insights into the active spread of organisms within the sediment will require further studies that specifically examine this pathway.

Nematodes are classified as mainly passively dispersed organisms. While this applies to large distances, active movement over smaller ranges should not be underestimated, as demonstrated in a study of the colonization of disturbed habitats after predation (Weber & Traunspurger, 2015). The advantages of active locomotion include that emigration is determined by the organism itself, adverse environmental conditions can be avoided, and favorable conditions directly pursued. However, the active dispersal of nematodes in sediments is restricted to station-keeping movement within a home range (according to Schlägel et al., 2020) and is largely associated with behavior patterns such as foraging or reproduction (see the “Behavior” section). As such, because it is unlikely to result in spatial gene flow, it does not correspond to the definition of dispersal provided above.

Nematodes in the open water

Numerous studies have described the presence of nematodes in open waters. For example, Mott & Harrison (1983) collected up to 46,000 nematodes/ m^3 in a fast-running stream. In a very early study by Eddy (1927) and a much later one by Abdel-Aziz & Aboul-Ezz (2004), the number of nematodes in plankton samples from lake littorals was as high as 11,000 nematodes/ m^3 . Nematode densities in the water column are summarized in Table 3. In several of the cited studies, nematodes are only casually mentioned or are discussed as bycatch obtained by resuspension of the sediment during sampling (e.g., Fernando, 1980; Dimas-Flores et al., 2008).

The majority of studies describing nematodes in open waters were conducted in relatively high-energy environments, i.e., those affected by wind, waves, tides or waterflow along a stream, and in most cases samples were obtained at heights not more than 1 m above the substrate. Boeckner et al. (2009) demonstrated that with increasing height above the substrate

Table 3 Studies on the number of water-drifted nematodes vs. their benthic densities, other drifted invertebrates, different flow levels and different water column heights

Location/ habitat	Flow	Depth (cm)	Height in water column (cm)	Mesh size (μm)	Drifting nematodes	Percentage (reference value of 100%)			References
						Nematodes (drifting meiofauna)	Nematodes (benthic community)	Bottom nematodes (drifting nematodes)	
Marine									
Coastline	Sheltered site	1,000	Up to 650	53	113 m^{-3}	21.5			Boeckner et al. (2009)
	Exposed site	1,000	Up to 650		63 m^{-3}	22.4			
Intertidal sediment		2	50	42	Up to 7,900 m^{-3}				Rodriguez (2004)
Intertidal sediment		6	1.5	50			72		Palmer (1986)
Mud									
	No flow				3 m^{-3}			0.12	
	1 cm/s				6 m^{-3}			1.67	
	> 1 cm/s				53 m^{-3}			5	
Plant cover							71.2		
	No flow				2 m^{-3}			0.06	
	< 0.44 cm/s				28 m^{-3}			0.79	
	> 0.44 cm/s				84 m^{-3}			2.37	
Intertidal sediment		Up to 120	Up to 57	63		26.6–32	60.1–64.9	0.004–0.092	Palmer & Gust (1985)
Tidal channel*	50 cm/s		5	100	70 m^{-3}	0.5			Sibert (1981)
			30		34 m^{-3}	0.9			
Tidal creek**	0–60 cm/s		7	63.5	1–3 on 5.2 cm^2	4.5–30	80–89	1.6–2.6	Bell & Sherman (1980)
Shallow lagoon	10–60 cm^{-1}	160–220	Surface	33	151–850 m^3				Hagerman & Rieger (1981)
Microcosms***	No flow		At least 12	–		< 9.8	83–87%	< 6	Walters & Bell (1986)
Freshwater									
Stream	2–60 m^3/s			1.2	Up to 8,000 m^3				Mott & Harrison (1983)
	50–560 m^3/s				1,500–46,000 m^3				
Stream*				80		0.1	10.1		Williams (1980)
Stream*	1–12 cm/s			80		0.3	5.0		Smith & Brown (2006)
Stream	8.5–100 m^2/s	15–150	5	44	Up to 21 m^{-3}	2.4	3.1	Up to 0.03	Palmer (1992)

*Meiofauna as well as larger invertebrates such as insect larvae were considered

**Because of the sampling design, abundances are reported per area, not per volume

***Only individuals entering the water column by active swimming were considered

the number of nematodes in the water column declines. In that study, 58% of the nematodes were collected at a height of 0.5 m but only 2% above 6.5 m. Most of the organisms in the water column are apparently directly (< 5 cm) above the ground (Sibert, 1981). However, even water layers not in direct exchange with the substrate may contain nematodes. This was shown by Khalifa et al. (2015), who detected nematodes at a height > 15 m above the lake bottom. In the open ocean, nematodes may be associated with marine snow, which can also be found a few meters below the surface (Shanks & Walters, 1997).

Nematodes typically account for < 33% of the meiofauna in open water (Table 3) whereas copepods and, in streams, rotifers and chironomid larvae are encountered above the substrate in higher numbers. For example, Palmer (1992) reported that only 2.4% of the drifting meiofauna collected in a fourth-order stream were nematodes, while rotifers, oligochaetes, chironomids and copepods represented 86.2%, 6.9%, 2.9% and 1.5%, respectively. These latter organisms are more efficient active dispersers and have higher dispersal rates (Palmer, 1988a; Commito & Tita, 2002; da Fonsêca-Genevois et al., 2006). As shown in Table 3, most nematodes remain in the substrate, with < 3% reaching the open water. However, given the high abundance of nematodes in the substrate, the resuspension of even a small percentage may be sufficient for an effective dispersal in the water column. According to Artois et al. (2011), 300 million nematodes representing 38 freshwater species are transported in the Adda River per day. However, the composition of those species in the open water may not be entirely congruous with the composition within the substrate (Commito & Tita, 2002; da Fonsêca-Genevois et al., 2006). Therefore, either specific taxa enter the water column by active movement or not all species are passively suspended.

Active emigration from sediment

Active entry into open water has been investigated in microcosm experiments without any flow and thus able to exclude passive processes. Jensen (1981) examined active emigration from the substrate and was able to demonstrate that nearly all nematodes left the sediment and swam 5 cm upwards, in the direction of food sources. In the studies of Alldredge & King (1977) and Walters & Bell (1986), only a small

fraction of the natural nematode composition (< 6%) entered the water from the sediment when no food sources were offered. Armonies (1988a) similarly showed that in the absence of a food incentive nematodes did not leave the sediment; however, 96%, 65% and 35% of the copepods, ostracods and flatworms, respectively, actively emigrated within 24 h.

The entry of meiobenthic organisms into the water column may depend on the time of day. Palmer (1992) and Armonies (1994) found that copepods, oligochaetes and rotifers mainly leave the sediment during nighttime, consistent with active emigration, while a similar behavior was not exhibited by nematodes. Clifford (1972) collected higher numbers of meiobenthic organisms, including nematodes, from the water column during the day, but whether the time of day influenced nematode emigration could not be established.

Passive emigration from sediment

A widely discussed factor in the passive emigration of nematodes into open water is erosion by flow. An increase in the number of nematodes and other meiobenthic organisms in the open water with increasing flow (e.g., tidal cycles, wave action, storms or flood events) was demonstrated in several studies of freshwater and marine habitats (Mott & Harrison, 1983; Palmer, 1986; Armonies, 1988b; Palmer, 1990; Armonies, 1994; Ullberg, 2004; de Meester et al., 2018). The dispersal of other meiofauna, mainly copepods, is significantly less dependent on flow velocity because these organisms have a higher potential for active dispersal into the water column (Palmer, 1988a; Commito & Tita, 2002). Near-bed flow and the resultant shear stress have an especially strong impact on organismal transport (Eckman, 1983; Palmer, 1986). However, for the erosion of nematodes from sandy sediment, relatively low flow velocities of 9–12 cm/s are sufficient (Palmer, 1992; Thomas & Lana, 2011) and even a flow rate of < 3 cm/s allows the resuspension of single nematodes (Armonies, 1988b). The threshold for the erosion of nematode individuals can be less than that for the surrounding sediment; thus, nematodes are not only eroded together with the sediment but are also leached from the sediment (Palmer, 1992). For flatworms and copepods, abundances in the water column are highest

at low flows (Armonies, 1994), indicating a larger role of active emigration. However, as more nematodes are not consistently resuspended in high-energy vs. low-flow habitats (Boeckner et al., 2009), additional factors must also determine the number of eroded nematodes.

Allredge & King (1977) observed a higher transfer of nematodes to the open water above fine, sandy sediments than above coarse particles, although similar velocities were measured at the two sites. Because the critical erosion threshold is lower in fine, sandy sediments, nematodes are probably removed together with the sand, while coarser sediment would provide protection up to a certain flow level. Near-bed hydrodynamics are mainly affected by the topography of the sediment and the presence of above-ground structures (e.g., plants) (Eckman, 1983). For example, sediment-covering vegetation and surface depressions lower the shear stress, thus reducing the erosion of small organisms while simultaneously enhancing passive immigration by the deposition of nematodes and other meiobenthic organisms (Anderson & Charters, 1982; Fonseca et al., 1982; Eckman, 1983; Nowell & Jumars, 1984; Atilla et al., 2005).

Nematodes of the upper sediment layers are highly likely to be resuspended (Eskin & Palmer, 1985; Palmer, 1988a; da Fonsêca-Genevois et al., 2006; Thomas & Lana, 2011). While thin, agile taxa avoid erosion by migrating to deeper areas, more lethargic nematodes (especially epistrate feeders) remain in the surface sediment and are washed away (Eskin & Palmer, 1985; Tita et al., 1999; Thomas & Lana, 2011) and their dispersal rates are accordingly higher (Olafsson & Moore, 1990; Commito & Tita, 2002). Therefore, the active vertical distribution of nematodes within the substrate (see the “Active dispersal through sediment” section) determines their passive dispersal by water drift. While, as discussed above, the presence of predators in the sediment contributes to shaping the vertical distribution of nematodes and other meiobenthic organisms, few studies have investigated the impact of predators on meiofaunal dispersal. Ullberg & Ólafsson (2003a) found that the presence of amphipods had no effect on the active dispersal of nematodes. Since their study was conducted in microcosms without flow, passive dispersal processes could be excluded. By contrast, potential predators (fish, *Leiostomus xanthurus*) in more energetic habitats significantly increase the number of

nematodes and other meiobenthic taxa (copepods and foraminiferans) in the water drift (Palmer, 1988b). This can be explained rather by the biting behavior of bottom-feeding fish, which would result in the resuspension of the nematodes, than by active emigration. Other types of fish, rays, sharks, manatees, walruses, waterfowl and even some whales can also cause large sediment disturbances and thus favor a considerable erosion of small benthic organisms. Such disturbances can alter the vertical distribution of meiofauna and enhance the water dispersal of deep-sediment-dwelling taxa.

Drifting

Unlike the emigration of nematodes from the substrate to the open water, which can include active and passive components, subsequent transfer in high energetic and possibly also low flow freshwater and marine systems is primarily due to passive drift (Palmer, 1984; Palmer & Gust, 1985; Palmer, 1990). In high-energy habitats, the transfer and emigration of nematodes and other meiobenthic organisms such as copepods can be attributed to passive particles because even a low flow velocity can prevent active progress (Hagerman & Rieger, 1981; Palmer & Gust, 1985). This was convincingly demonstrated by Palmer (1990), who showed equal sinking/swimming rates of living and anesthetized nematodes (0.09 cm/s). Flood events can also cause organisms to drift between waters that are otherwise spatially isolated. This dispersal mode is relevant for several aquatic taxa, including zooplankton (Dias et al., 2016), macrobenthos (Petsch et al., 2017) and macrophytes (Akasaka & Takamura, 2012), and can markedly influence their local species composition. The spread of nematodes through flooding has not been reported so far but is likely.

Transfer back to the substrate

Although nematodes in the open water have essentially no influence on the direction of their journey, they can delay their sedimentation until suitable substrates are in range. The body length, flexibility, activity level and adhesiveness of nematodes are essential factors that determine where nematodes become deposited in the sediment (Bertelsen, 1997). Species with the morphological adaptations that allow

swimming (slim body, long tail) remain in the open water longer than less active species (de Meester et al., 2018). In addition, specific behaviors, such as coiling, which reduces the projected body area of the organism, can enhance the sinking rate (Bertelsen, 1997). The accumulation of drifting nematodes attached to objects (see the “Rafting” section) or to larger organisms (see the “Animal dispersal vectors” section) can increase the time spent in the open water. Active immigration into substrates by swimming was observed in laboratory investigations only under no-flow conditions (Jensen, 1981; Ullberg & Ólafsson, 2003b; Lins et al., 2013; Mevenkamp et al., 2016), but all of those studies consistently showed that the settling locations were those with the most suitable food sources or habitat structure.

Palmer (1984) estimated the passive settlement rate of nematodes and reported a settling velocity (calculated for the total meiofauna) of ~ 0.15 cm/s. However, in that study only 36% of the nematodes in the water column were returned to the sediment. In the study of Commito & Tita (2002), emigration rates of drifting nematodes ranged from 1 to 135 individuals/cm²/day and were mainly influenced by the background densities in the sediment and by the flow velocity. At higher flow rates, more nematodes were collected in bottom traps. As already noted, depressions (e.g., bottom traps, feeding pits, tunnels of sediment dwellers) promote immigration back to the sediment. According to Palmer (1986), benthic organisms can affect the roughness of the substrate by reworking processes and thus influence the critical erosion velocity, as demonstrated for invertebrates such as crabs and polychaetes (Luckenbach, 1986; DePatra & Levin, 1989) but also for fish (Sherman et al., 1983; Billheimer & Coull, 1988; Cross & Curran, 2004). The latter studies examined the recolonization of fish feeding pits by meiofauna and showed that nematode densities in the disturbed area became comparable to those in the surrounding sediment within a relatively short time (5 h to 7 days, see Table 2), presumably due to the suitable hydrodynamic conditions around the pits and the lower shear stress.

Atilla et al. (2005) demonstrated that artificial above-ground structures (e.g., bottle brushes) retain drifting organisms. With the increasing complexity of the structure (in this case, bristle density), both the retention and diversity of the captured nematodes increase significantly due to flow reduction.

Importance of drifting

The distances covered by drifting nematodes are difficult to determine because tracking over longer distances under field conditions is challenging. To our knowledge, only Thomas & Lana (2011) were able to localize the exact source of nematodes collected from the water column. In that study, stained nematodes were trapped 2 m away from the site of their release. Bell & Sherman (1980) and da Fonsêca-Genevois et al. (2006) determined the distance to the next known natural occurrence of the collected species and concluded that nematodes are able to cover distances of 500 m. Both Hagerman & Rieger (1981) and Derycke et al. (2007) reported distances of at least 10 km. In general, the studies presented in this section suggest that the continuous transport of small organisms (planktic and benthic) by drift occurs in all bodies of waters with a minimal flow velocity. Furthermore, for organisms with the necessary traits (e.g., propagules), drift enables a long-range dispersal as well as translocation between waters and may thus be the most important transport mode for nematodes and other mainly passively dispersed aquatic organisms.

Rafting

Rafting, the passive transport of organisms on floating biotic (e.g., algae, driftwood, marine snow) or abiotic (e.g., plastic debris or tar balls) items, is a common dispersal mode for a wide range of terrestrial and aquatic vertebrates as well as invertebrates in marine and fresh waters (Thiel & Gutow, 2004b). The organic items frequently derive from benthic habitats that were detached by water flow or wind, such that they contain a complete organismal community. On the other hand, the raft may be initially unoccupied, as is often the case for anthropogenic items. In both cases, new organisms may arrive on the raft during its journey (Thiel & Gutow, 2004b). Rafting nematodes are mainly transported on floating substrates (algae, bacterial mats, marine snow) or on vehicles with at least temporal contact with the benthos (e.g., ice; Macfarlane et al., 2013) (Table 4).

Rafting is an important dispersal mechanism that enables the transfer of organisms especially between shore areas (Thiel & Gutow, 2004a, b), given the erosion of benthic substrates together with their

Table 4 Investigations of marine and freshwater environments in which rafting nematodes were found on different floating items

Habitat	Floating substratum	References
Marine		
Estuary	Algae	Phillips (1963)
Offshore waters > 100 km	Algae	Abe et al. (2013)
Offshore waters 0.9–115 km	Algae	Ingolfsson (1995)
Microcosms	Algae	Arroyo et al. (2006)
Microcosms	Algae	Highsmith (1985)
Shallow embayment	Algae	Ólafsson et al. (2013)
Diff. habitats in the Sargasso Sea	Algae	Micoletzky (1922)
Shallow archipelagic waters	Algae	Norkko et al. (2000)
Oligohaline eulittoral zone	Bacterial mats	Vopel & Arlt (1995)
Bermuda Islands	Coconut	Gerlach (1977)
Mangrove embayment	Detritus	Faust & Gullede (1996)
Intertidal mudflat	Ice	Macfarlane et al. (2013)
Pack-ice	Ice	Schünemann & Werner (2005)
Offshore waters 3 km	Marine snow	Shanks & Walters (1997)
Shallow bay	Marine snow	Shanks & Edmondson (1990)
Sheltered intertidal sandflat	Seafoam	Armonies (1989)
Tidal drainage channel	Sediment	Hicks (1988)
Freshwater		
Pond	Algae	Phillips (1958)
Stream	Bacterial biofilm	Gaudes et al. (2006)
Cave waters	Bacterial mats	Riess et al. (1999); Muschiol et al. (2015)
Mesocosm	Periphyton mats	Liston (2006); Liston et al. (2008)
Stream	Water hyacinths	Sazima & Zamprogno (1985)

resident organisms that mainly occurs in high-energy waters. Rafts washed up on the shore may be colonized by the benthic community and then drifted by water flow. In low-energy and shallow shore environments, substrate fragments that float up during the daytime via photosynthetic processes may be relocated by wind and then sink to the bottom at night, thereby enabling at least a short-term dispersal (Phillips, 1958; Faust & Gullede, 1996). The sinking rate of nematodes rafting on marine snow was temporally lower than of free-drifting nematodes but, which enabled their longer persistence in the water column (Shanks & Edmondson, 1990).

Ingolfsson (1995) and Abe et al. (2013) found living nematodes on floating algae > 100 km away from the shoreline, indicative of long-range transport across the ocean. Covered distances of hundreds of kilometers have also been determined for other organisms, including oligochaetes and plathelminths (reviewed by Thiel & Gutow, 2004b). In addition to

wind and flow velocity, the durability of the floating item can limit the covered distance. For example, sea foam mediates a short dispersal as it quickly decays (Armonies, 1989) whereas more durable items, such as floating algae and especially driftwood, persist over many years and favor longer dispersal distances (Thiel & Gutow, 2004a).

Requirements for successful rafting

Studies on nematodes on floating items from coastal waters showed their lower abundance and different species composition compared to nematodes in the substrate below (Hicks, 1988; Arroyo et al., 2006). For example, Faust & Gullede (1996) found that although nematodes were the predominant taxon in the upper sediment (~ 2,740 individuals/l), only ~ 1% of that population was present on floating detritus, where they accounted for ~ 7% of the rafting metazoans, which were dominated by crustacean larvae (~ 87%). By

contrast, Gaudes et al. (2006) reported significantly higher nematode densities on floating bacterial mats (up to 752 individuals/cm²) than on attached mats. Since in many cases only single individuals are transported (Micoletzky, 1922; Abe et al., 2013), it is likely that not all nematodes associate with the raft or that some become lost during the voyage, resulting in a sorting process for rafting species.

Thiel & Gutow (2004b) described the three features that determine the rafting of organisms: (1) the ability to cling to the potential raft, (2) successful survival on the raft and (3) the establishment of persistent populations during transport. For nematodes, their caudal glands and the adhesion of their eggs allow them to withstand the water flow and to remain on the raft for long periods of time (Micoletzky, 1922). Biotic rafts tend to host high densities of microfauna, including bacteria, protozoans, diatoms, and other algae, that constitute the basis of the rafting food web. The review of Thiel & Gutow (2004b) also noted the presence of predatory, grazing and detritivore organisms on rafts, but suspension feeders able to optimally exploit the renewable resources predominated. Accordingly, studies on rafting nematode communities mostly identified bacteria- and algae-feeding species (Micoletzky, 1922; Riess et al., 1999; Gaudes et al., 2006; Muschiol et al., 2015). However, Micoletzky (1922) observed that the body sizes of nematodes on floating macroalgae were smaller than those of related species in the sediment. The authors attributed this finding to the limited food resources during long-range dispersal. Furthermore, during their voyage, rafting organisms are exposed to competition and predation as well as rapidly changing environmental parameters (e.g., flow velocity, temperature, salinity, UV radiation) (Thiel & Gutow, 2004b). Nonetheless, with their ability of parthenogenetic reproduction, especially in freshwater environments, nematodes are able to compensate for losses and establish durable populations (Thiel & Gutow, 2004b).

In contrast to drifting organisms, the chance of surviving long-range dispersal is higher for rafting individuals and whole communities, especially if structure-forming or engineering species colonize the raft. Reproduction during transfer will result in more individuals reaching a new habitat simultaneously, thereby facilitating its colonization. Nematodes investigated in a microcosm study showed almost no tendency to leave floating algae and recolonize the

underlying sediment, as also reported for other organisms (Arroyo et al., 2006 and literature therein). However, in that study, whether the algae had direct contact with the sediment, thus enabling active immigration, or colonization was possible only over the water column was not resolved. Shanks & Edmondson (1990) found that 94% of the vertical nematode flux in a shallow bay was due to individuals rafting on marine snow.

Animal dispersal vectors

Dispersal by larger animals consists of transfer on those organisms (epizoochory) or within their digestive tracts (endozoochory). In epizoochory, contact of the animal with nematode-containing water, substrate or other structures (e.g., plants) suffices to initiate transfer. In general, the overland transport on/in invertebrates and vertebrates is especially relevant for the meiofauna of littoral zones, wetlands, mudflats and other shallow waters, where direct contact with the sediment is likely. The dispersal distance resulting from zoochory depends on the range of the transporting animal, which for birds can be ~ 1,000 km. Processes that may limit epizoochory include dehydration. In the case of endozoochory, success requires the survival of ingestion (by direct predation or as bycatch) and digestion whereas subsequent transfer may be limited by the time required until digestion or the next defecation.

Epizoochory

Frisch et al. (2007) suggested that the transport of meiobenthic organisms on the feathers and feet of birds is more decisive than endozoochory. While this has been documented for benthic taxa such as cladocerans, copepods and bryozoans (Green & Figuerola, 2005 and literature therein), it may not be the case for nematodes (Maguire, 1959). However, the use of coarse-meshed sieves for organism collection could have resulted in insufficient sampling and therefore biased conclusions.

Nematodes can also be dispersed via their transport in the fur of mammals. Vanschoenwinkel et al. (2008c) identified nematodes, rotifers copepods, ostracods, cladocerans, tardigrades and flatworms in the fresh mud left behind by wild boars on the trees

they had rubbed themselves against. However, that study did not differentiate between living individuals and eggs, and nematodes accounted for only a very small percentage (1%) of the collected meiobenthic organisms, which consisted mostly of microcrustaceans. Nematodes were the only taxon that did not emerge from boar feces incubated in water, indicating the complete digestion of living individuals and their eggs. Meiobenthic organisms have also been detected on the fur of nutrias (Waterkeyn et al., 2010a), whereby the percentage of nematodes was < 1% (five nematodes collected from three nutrias). While mammals of a large number of taxa can be assumed to transport meiobenthic organisms, current evidence suggests that fewer nematodes are transferred by mammals than by birds.

Another mode of dispersal is via turtle shells, as the backs of marine turtles are colonized by a diverse array of micro-, meio-, and macrobenthic organisms, all of which are associated with food webs and energy flows (Corrêa et al., 2014; dos Santos et al., 2018; Ingels et al., 2020). In contrast to all other dispersal modes discussed herein, apart from rafting, turtle shells allow the reproduction of the transferred organisms. Nematodes may reach densities on turtle shells of 21.6 individuals 10 cm^{-2} (1.08 m^2 shell size) on average, with up to 41 genera/species per shell, and were the third most dominant taxon, behind ostracods and copepods. Although the meiobenthic community on turtle shells resembles that occurring in reef environments, turtle shells represent hotspots of nematode diversity. Moreover, because millions of turtles, with their standing stock of meiobenthic organisms, traveling thousands of kilometers between foraging grounds and nesting beaches (Luschi et al., 2003; Ingels et al., 2020), they must be considered as one of the most important epizoochoric dispersal vectors in marine environments.

Given the success of this dispersal pathway, other animals with outer shells or carapaces may also disperse nematodes by epizoochory. For example, Schejter et al. (2011) described nematodes associated with ascidian colonies on the shells of gastropods. Other epibiotic organisms, such as rotifers and protozoans, have also been found on various crustaceans, including aquatic sow bugs, lobsters and the crustaceans living on whales (Fernandez-Leborans & Tato-Porto, 2000a, b; Fernandez-Leborans, 2001; Cook et al., 2002).

Endozoochory

Intact nematodes ingested by insect larvae, juvenile fish or crustaceans usually do not survive gut passage but are instead quickly (20 min up to hours) digested beyond recognition (Alheit & Scheibel, 1982; Hofsten et al., 1983; Scholz et al., 1991; Muschiol et al., 2008; Ptatscheck et al., 2015b; Weber & Traunspurger, 2017, 2015). However, this is not the case for all nematode species. The free-living nematode *Panagrellus redivivus* survives in the gut of larval coregonids for a few hours and is able to pass through the intestine, leaving by active movement (Schlechtriem et al., 2005). Nematodes exiting the fish gut are subsequently located in the open water, which enables their further dispersal (water drift, rafting or swimming). Similarly, unscathed gut passage has been reported for numerous *Rhabditida* species ingested by gastropods (Sudhaus, 2018), with the nematodes surviving for up to 5 days until their excretion. Gastropods exert strong top-down effects on the meiofaunal communities of periphyton (Burgmer et al., 2010; Schroeder et al., 2010; Peters & Traunspurger, 2012; Schroeder et al., 2013), which implies the regular consumption and thus the endozoochory of nematodes. Transport by fish larvae and gastropods provides a larger dispersal radius for nematodes than allowed by their own locomotion but not a dispersal over long distances or between different waters, as occurs with transport by birds. Gaston (1992) found up to 2,300 nematodes and 5,000 copepods in the gut of waterfowl (green-winged teal) that had fed for 20 min on a mud flat. Overall, nematodes together with ostracods and copepods represented up to 36% of the ingested meiofauna, which was about the same proportion as collected from 1 m^2 of sediment from the examined area. An analysis of waterfowl feces revealed living adult nematodes but their occurrence strongly varied between bird species (3–60%) and their numbers increased after several days when the feces were incubated in water (Green et al., 2008). The latter observation leads to the conclusion that some nematodes survived the passage as propagules, probably as eggs, as also suggested by the investigation of Frisch et al. (2007). According to the results of Green et al. (2008), the feces of one grey goose may contain ~ 13 nematode individuals, but considering that a flock of waterfowl at a particular site may comprise several thousand individuals, the transfer of

meiobenthic organisms by endozoochory may well be substantial. Additionally, this study also showed that the eggs of crustaceans are found much more frequently and in greater numbers in the feces of waterfowl than nematodes.

In addition to primary zoochory, secondary zoochory via the seeds and invertebrates (e.g., daphnia) ingested by fish and dispersed by piscivorous birds such as cormorants has been described (van Leeuwen et al., 2017). However, this pathway has not yet been demonstrated for nematodes or other typically meiobenthic organisms.

Hessen et al. (2019) concluded that the only conceivable vector for the long-distance endozoochory of pelagic microcrustaceans is waterfowl, which can cover distances of hundreds of kilometers. Nonetheless, the authors also noted that this dispersal pathway is less likely because of the different feeding grounds (the birds forage in terrestrial or coastal habitats) and the fast gut turnover of these birds, but dispersal over short distances was likely to be common.

Gone with the wind

An omnipresent vector for the overland dispersal of unicellular organisms (e.g., bacteria, algae) and microscopic metazoans (e.g., nematodes, microcrustaceans, flatworms, acari, rotifers) is wind (Frankland, 1886; Vanschoenwinkel et al., 2008b). Wind erosion primarily affects terrestrial organisms, while inhabitants of benthic habitats are exposed to wind mostly in eulittoral zones, floodplains, desiccated substrates and thus especially in temporal waters and semiaquatic habitats (e.g., ponds or phytotelmata).

In contrast to other benthic organisms or zooplankton, there is little consistent information on the wind drift of nematodes, especially regarding the resultant dispersal rates (individuals collected at a certain time in a certain area). Furthermore, many of the studies did not identify nematodes to the genus/species level, which complicates determination of their source and favored habitat. To the best of our knowledge, only Ptatscheck et al. (2018) examined nematodes from aquatic habitats drifted by wind. Among the 27 wind-dispersed nematode species that were collected, only 1 preferentially colonized aquatic environments whereas at least 9 were known from both terrestrial

and aquatic or semiaquatic habitats. The most common species were typically terrestrial, consistent with the results of other studies (Baujard & Martiny, 1994; Nkem et al., 2006).

While in the study of Vanschoenwinkel et al. (2008a) nematodes accounted for ~ 1% of the aeroplankton (~ 94% crustaceans), in the study of Ptatscheck et al. (2018) nematodes comprised ~ 46% of the sampled animals (crustaceans were not found) and their dispersal rate within 4 weeks was as high as 3,020 individuals/m² in a study conducted in central Europe. Other investigations of different locations reported much lower rates of < 5 individuals/m² within 1 year (Nkem et al., 2006: in Antarctica) and 14 individuals/m² within 1 month (Vanschoenwinkel et al., 2008a: South Africa during the dry season). An important reason for the large differences in these results is the fundamentally different methods that were used. Thus, while Ptatscheck et al. (2018) collected the organisms using formaldehyde-filled funnels and 5- μ m mesh-size filters, Vanschoenwinkel et al. (2008a) collected aeroplankton in windsocks (100 μ m) and Nkem et al. (2006) analyzed soil samples as well as the contents of open-top chambers and Bundt pan soil traps. Difficulties in comparing the results of studies on wind-drifted organisms were noted by Vanschoenwinkel et al. (2009).

Not all organisms are dispersed equally, with clear limitations as well as different sorting processes described for wind-drifted nematodes, rotifers, cladocerans, copepods and tardigrades (Jenkins, 1995; Cáceres & Soluk, 2002; Ptatscheck et al., 2018). In the case of nematodes, their form and weight determine the wind energy necessary for their erosion and the transfer range. For example, resting eggs are less effectively transported by wind than are later stages (Cáceres & Soluk, 2002). Nkem et al. (2006) and Ptatscheck et al. (2018) showed that aerial plankton mainly contains small individuals (< 0.75 mm) and juvenile nematodes with low body weights. Furthermore, anhydrobiosis and the associated weight reduction through water loss enable a more effective wind transfer than possible for hydrated forms (van Gundy, 1965). It is often assumed that the presence of propagules, which are not known from aquatic nematodes, is a prerequisite for the successful wind drift of microscopic aquatic organisms (Panov et al., 2004; Nkem et al., 2006; Incagnone et al., 2015). However, Ptatscheck et al. (2018) found only living stages in

their collection of wind-drifted organisms and thus argued that the climatic conditions are a crucial determinant of wind drift and that propagules are a feature only of harsher environments.

Additional parameters affecting the wind dispersal of nematodes are wind speed and humidity. More nematodes were collected from the air during periods of higher wind speed (Ptatscheck et al., 2018), suggesting a stronger erosion effect and longer transport distances. The same study showed that dispersal was enhanced by higher humidity, although it is usually assumed that small organisms are mainly dispersed during dry periods because dry surfaces facilitate erosion (Incagnone et al., 2015). Thus, the wind dispersal of nematodes and other microscopic organisms is likely to be strongly seasonal (Ptatscheck et al., 2018).

The distances covered by the aeroplankton range from a few meters (Jenkins & Underwood, 1998; Vanschoenwinkel et al., 2008a, 2009), to several hundred meters (Maguire, 1963) and up to several dozen kilometers (Carroll & Viglierchio, 1981). With increasing distance, the number of wind-dispersed nematodes declines (Ptatscheck et al., 2018). However, wind-drifted nematodes can be collected at least 35 m above the ground, such that transport on a larger scale is plausible (Ptatscheck et al., 2018). While little is known about the colonization success of wind-drifted nematodes, it can be assumed that overland dispersal is an important mode of transport for isolated habitats such as tank bromeliads. Studies on the colonization of azoic sediments in streams by aerially transported organisms revealed that, in contrast to other benthic invertebrates such as ostracods or copepods, there was no evidence of the establishment of nematode communities (Williams & Hynes, 1976; Williams, 1977; Benzie, 1984).

Human-mediated transfer

Wyatt & Carlton (2002) pointed out that in discussions of the global distributions of microscopic organisms such as nematodes, not only natural processes but also anthropogenic vectors must be considered, because they are also effective and well documented. In fact, since contact between larger organisms and the sediment often leads to the displacement of meiofauna, nematodes are likely to be common “travel

companions” including of humans. Both Waterkeyn et al. (2010b) and Valls et al. (2016) showed that nematodes can be transferred in the mud residue of clothes (here, footwear). Because aquatic nematodes (probably their eggs) in dried sediment are highly viable (Gerlach, 1977), human-mediated transfer is likely to be an important mechanism leading to the dispersal of organisms across different wetland habitats, especially those in highly frequented areas but also sites separated by long distances.

Ships transit lakes, river systems and oceans and with the emptying of their ballast tanks they contribute to the global dispersal of numerous, sometimes invasive, species. Nematodes are the predominant and most diverse meiobenthic taxon collected from the sediments of ballast tanks (Duggan et al., 2005, 2006; Radziejewska et al., 2006). Duggan et al. (2005) identified 48 different freshwater nematode taxa in the tanks of several ships traveling the Great Lakes, which border parts of the USA and Canada. The results of Radziejewska et al. (2006) suggested the transport of > 100,000 nematodes (66% of the collected meiofauna) within the sediment contained in the ballast tank of a bulk carrier. Moreover, depending on the location of sediment uptake, nematode abundance in transported sediments may be even higher.

Finally, even tap water enables the dispersal of nematodes, as these and other meiobenthic organisms (e.g., rotifers, oligochaetes, gastrotrichs, flatworms, microcrustaceans) are present in drinking water distribution systems (Funch et al., 1995; Schreiber et al., 1997; Christensen, 2011; Inkinen et al., 2019). In fact, guideline values for finished water from the Netherlands (in 1993) and North America include the allowance of 0.3 and 2.5 nematodes/l (reviewed by Christensen, 2011). Other studies found up to 156 individuals, belonging to 41 species/l drinking water (reviewed by Artois et al., 2011).

What is left to say?

The ability to get everywhere

The picture that emerges from this review is that the dispersal pathways of marine and freshwater nematodes are as diverse as the habitats they inhabit, and they include both water but also overland routes (Fig. 1). While active locomotion, whether by

sediment crawling or by swimming in open waters, enables nematodes to spread over centimeter and meter ranges, passive modes are essential for longer-range dispersals from freshwater and marine environments. Under favorable conditions nematodes can disperse by drift, rafting and zoochory but also as stowaway on ships to reach opposite shores, cross the (dry) ocean and cover distances > 10,000 km. Since the survival rate (e.g., the avoidance of death by starvation, digestion) and recruitment from source habitats decline with increasing time and distance, most distribution probably takes place over smaller ranges, in line with the results of studies based on genetic approaches (Derycke et al., 2007; Bik et al., 2010; Derycke et al., 2013; Hauquier et al., 2017). However, according to the review of Cerca et al. (2018), the presented studies suggests that the meiofauna paradox most likely does not exist because the dispersal of these small organisms is more diverse and effective than often assumed, but not entirely unrestricted (see next section). Finally, although the basic distribution pathways of nematodes have already been demonstrated, the picture is far from complete. For example, the entire spectrum of larger organisms (e.g., crustaceans or even whales) that may transport nematodes by primary or secondary zoochory has yet to be examined in depth and thus offers a wide field for further studies. In addition, most of the studies cited in our review addressed the dispersal of nematodes in marine environments whereas studies from freshwater ecosystems are underrepresented. Indeed, processes that have primarily been described in marine environments, such as rafting, presumably also occur in lakes or streams, but very few studies have examined the importance of water drift for the dispersal of nematodes in lakes (e.g., littoral vs. profundal).

Limitations of dispersal

This review explored the dispersal modes of nematodes and included comparisons with studies on other meiofaunal organisms to assess the extent of these processes in various environments. However, because microcrustaceans (mainly copepods) and other meiofauna have already been extensively examined in this context, a consideration of all existing studies would have been far beyond the scope of this review, which is why we focused on single examples. The authors of

previous studies on the dispersal of marine nematodes (e.g., Palmer, 1988a; Armonies, 1994) concluded that dispersal is primarily passive, with active locomotion playing a more important role in copepods. Our review also shows that nematodes can actively move in water or sediment but as crawlers and swimmers they are less effective than other meiofaunal organisms, in addition to being vulnerable to even low flow velocities of water. While epibenthic organisms such as microcrustaceans or plathelminths immigrate to the water column by active movement, this is the case for only a small percentage of endobenthic nematodes, whose presence in the water column is instead largely due to erosion. Indeed, our review also provides considerable evidence of the limitation of nematode dispersal (Fig. 1) due to (1) organismal morphology, (2) ecological factors, (3) habitat structure and (4) hydrodynamics, which together result in the sorting of species, size classes and feeding types. Morphological characteristics such as body shape determine how fast and how far a nematode can disperse on its own in any direction. This active dispersal is usually triggered by several fundamental ecological factors that act in concert and also determine local population dynamics (Bowler & Benton, 2005; Matthysen, 2012). For nematodes, these factors include the availability of food resources but also predation, competition, oxygen level and the amount of disturbance. Overland dispersal, which relies on wind and the mobility of larger organisms, is mainly restricted to species of shallow and ephemeral waters as well as littoral zones. In habitats characterized by a high flow velocity, such as streams or shore areas subject to wind, waves and tides, the number of drifting or rafting nematodes originating from the upper substrate layers increases, although additional factors, such as the vertical distribution and habitat structure of the organisms, also play important roles.

If their dispersal is by no means unrestricted, then why are nematodes so successful in entering new habitats? A crucial advantage is the high densities in which nematodes occur. Even if only a small percentage of the nematodes emigrate from the sediment, it is enough to allow a continuous spread of numerous individuals, especially since only a few gravid females can sustain a population. For example, Palmer (1992) showed that 24 h of nematode immigration by open water dispersal can result in the settling of a larger number of individuals than previously located in the

home substrate. Further reasons may be found in the subsequent establishment processes described by *immigration*, which were not considered in this review and have so far hardly been investigated for nematodes in general.

A quick glance at colonization

Studies that investigated the succession of empty habitats (Table 2) have shown that colonization by nematodes starts immediately, with densities comparable to those of the surrounding habitats reached within a few days. However, for successful dispersal not only the arrival of organisms but also their ability to prevail in the new habitat is crucial. In the case of passive distribution, organisms can reach locations that differ completely in their biotic and abiotic parameters from the source habitat, such that a high degree of adaptability is necessary for survival and reproduction. According to Bongers & Bongers (1998), nematodes with fast reproduction rates, the ability of parthenogenesis and a tolerance of unfavorable environmental conditions will be successful colonizers. Bacterial (Monhysteridae, Plectidae) and hyphal (Aphelenchoidae) feeding taxa were identified as pioneer organisms in streams, lakes (Duft et al., 2002; Peters et al., 2007; Weber & Traunspurger, 2016) and ephemeral waters (Ptatscheck & Traunspurger, 2014; Ptatscheck et al., 2015a), indicative of the important role of food availability during the establishment of nematode communities. Predatory nematodes often occur in higher abundances in more nutritious environments (Michiels & Traunspurger, 2005b; Schroeder et al., 2012; Kazemi-Dinan et al., 2014; Ptatscheck & Traunspurger, 2014) and therefore tend to appear during later phases of colonization. Accordingly, in their study of colonization using artificial tree-holes Ptatscheck & Traunspurger (2014) detected predatory nematode species solely in the treatments with added leaf litter, while Peters et al. (2007) described an increase in species number from 1 to 4 nematode species on artificial hard substrates during the first 10 days of colonization. Not only the availability of food resources but also their exploitation by different nematode species influences the population growth rate and the possibility of becoming established in a habitat, as shown by Ilieva-Makulec (2001) and Gansfort et al. (2018). Furthermore, top-down effects caused by predators or bioturbators can

also significantly shape the nematode community (e.g., Weber & Traunspurger, 2016). These examples show that the sequence in which species immigrate to a habitat and the resulting priority effects, in the form of biological interactions with already established communities (e.g., Incagnone et al., 2015), contribute to defining nematode community structure (Derycke et al., 2013). However, much remains to be learned about the establishment processes of nematodes, as there is still a lack of studies on the succession of new habitats that consider nematodes at the species level.

Further approaches

The studies presented in our review describe the emigration and transport of nematodes and the different spatial levels at which the spread of these organisms occurs. While the short distances covered by active movement can be adequately investigated in laboratory tests, accurately tracing the long-range transfer of nematodes is much more difficult. The migration routes of larger transporting animals (e.g., birds) can be tracked, water flow or wind direction can be taken into account, the effect of hydrodynamics on small organisms in the water column can be calculated and the next possible neighboring populations can be localized. However, none of these approaches has thus far led to a clear understanding of the spread of nematodes and other small organisms. For example, the extent to which nematodes within a river network are connected through dispersal is not known. Studying the genetic diversity of certain nematode species (e.g., Derycke et al., 2013; Ristau et al., 2013; Schenk et al., 2016) can provide insights into the gene flow between species at different locations and thus the extent and range of their dispersal. Furthermore, “sophisticated experimental experiments” are another key for the detailed understanding of meiofauna dispersal processes (Cerca et al., 2018).

Conclusion

The dispersal modes of nematodes have been investigated in the laboratory and in the field. In some of those studies, collections of nematodes obtained during the transfer phase (e.g., in the water column or on larger organisms) were assessed with respect to a single dispersal mode. In others, the ability of

nematodes to colonize disturbed or azoic substrates was the focus. Taken together, the results provide further evidence that nematodes are well-equipped pioneer organisms and often one of the first metazoans to establish populations at new, disturbed or even isolated habitats. However, less is known about the importance of long-range dispersal modes, such as zoochory or transport in ship water tanks, for local population structures and even less about the impact of immigrating nematodes on existing or emerging communities. Both translocation and subsequent settlement processes must be taken into account to answer the question whether, for nematodes, getting everywhere means staying everywhere and thus whether nematodes are successful dispersers.

Acknowledgements Open Access funding provided by Projekt DEAL. We would like to thank the anonymous reviewers for their very helpful and constructive remarks.

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