Response of meiobenthos to migrating ripples in sandy lowland streams

Mariia Kryvokhyzhyna · Nabil Majdi · Anna Oprei · Michael Mutz · Ute Risse-Buhl

Abstract Stream sediments move at low flow forming migrating ripples. These ripples can cover substantial areas where benthic communities experience erosion-resting cycles of sand grains. Sediment surface and interstitial space is colonized by meiobenthos, an assemblage of microscopic invertebrates. Here we describe how sediment migration influences the structure of the meiobenthic community. We sampled migrating and stationary sediment patches in five streams. Sediments in migrating ripple patches were characterized by coarser grain size and higher oxygen concentration, but less organic matter and chlorophyll than stationary patches. Meiobenthos was more abundant in the superficial layer of stationary sediment compared to the underlying layer, whereas comparable abundances were observed in both layers of migrating patches. This suggests that ripple migration enhances the vertical mixing of interstitial communities. Among the environmental drivers measured, meiobenthos community structure was most related to sediment transport regime: Rotatoria were more abundant in migrating patches, whereas Chironomidae, Ceratopogonidae, Copepoda and Hydrachnidia were more abundant in stationary patches. Body-size structure was affected by sediment migration, with fewer larger organisms in migrating ripples. By modifying the distribution of benthic resources and of meiobenthic consumers, ripple migration likely affects energy flow paths through benthic food webs.

Keywords Sediment transport · Community structure · Benthic invertebrates · Morphofunctional traits

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Introduction

The bed of lowland streams and rivers is composed of fine-grained sediments that are easily mobilized and transported as bedload. Fine to medium sand (grain size $\sim 0.1$–$0.7$ mm) is mobilized at low flow velocities of $< 0.2$–$0.6$ m s$^{-1}$ and transported as migrating ripples (Verdonschot, 2001; Uehlinger et al., 2002; Baas, 2003). Ripples are triangular bedforms with a length of 8 to 20 cm and a height of less than 2 cm (Raudkivi, 1997). They are a common hydromorphological element of sandy stream- and riverbeds in lowland alluvial and glacial landscapes all over the world. Migrating ripples may cover between 20 and 50% of the streambed of undisturbed reaches and up to 100% of the streambed where reaches are prone to catchment erosion (Mutz et al., 2001; Wallbrink, 2004; Rabení et al., 2005; Marcarelli et al., 2015).

During ripple migration, sand grains (and organic particles) are eroded at the stoss- (upstream) side by shear stress and roll or saltate toward the crest, where they avalanche and deposit downstream in the trough of the ripple. There, sand grains and small organic particles are buried by subsequent grains and remain at rest until the eroding upstream face of the ripple approaches the grain’s position and the grain erodes again. This erosion-resting process is dynamic: The erosion scales in the range of seconds, whereas the resting phase ranges from several minutes to a few hours according to ripple size and flow velocity (Baas, 1999; Bridge, 2003; Harvey et al., 2012). Migrating ripples are well oxygenated, but bacterial abundance and phototrophic biomass are lower than in stationary sediments (Zlatanović et al., 2017; Wolke et al., 2020; Scheidweiler et al., 2021). Nevertheless, suspended particulate matter is trapped by migrating ripples, accumulates in the zone below the migrating layer (Harvey et al., 2012) and can serve as a potential food source for benthic invertebrates.

Meiobenthos (or meiofauna) is a diverse assemblage of microscopic metazoans colonizing marine and freshwater sediments. The meiobenthos is primarily defined by a size-criterion: passing through a 1-mm sieve, but retained on a 42-μm sieve (Higgins & Thiel, 1988), although a lower limit of 20 μm is recommended to avoid the loss of the smallest species and juvenile stages (Ptatscheck et al., 2020). In freshwater ecosystems, meiobenthos comprise representatives of species-rich animal groups like Arthropoda, Nematoda, Annelida, Rotatoria and Platyhelminthes (Majdi et al., 2020a). Freshwater meiobenthos can attain very high densities both in epibenthic and interstitial habitats ($10^5$–$10^7$ individuals per m$^2$). Some taxa appear to be especially resistant and resilient to habitat disturbances like floods (Gaudes et al., 2010; Majdi et al., 2012), droughts (Caramujo et al., 2008; Majdi et al., 2020b) and pollution (López-Doval et al., 2010; Ristau et al., 2012; Bighiu et al., 2020), likely aided by their short population turnover rates (Schmid-Araya et al., 2020), flexible morphofunctional traits (Neury-Ormanni et al., 2020), effective dispersal strategies (Ptatscheck & Traunspurger, 2020) and physiological resistance to environmental extremes (Rebecchi et al., 2020). These microscopic animals play an important ecological role, especially by stimulating microbially mediated processes such as primary production (Mathieu et al., 2007; D’Hondt et al., 2018) and organic matter and nutrient remineralization (Nascimento et al., 2012; Bonaglia et al., 2014), and by being intermediaries in the energy flow between microscopic and macroscopic organisms (Schmid-Araya et al., 2016).

Many meiobenthic species are well adapted to life in interstices, showing morphological traits such as small-size and worm-shaped bodies, but other species may have more affinities with epibenthic habitats as they harbor appendages or ciliature enabling them to swim, cling or glide, or even stay firmly attached onto surfaces (Gaudes et al., 2010; Neury-Ormanni et al., 2020). The morphofunctional structure of meiobenthic communities has been found to respond to environmental constraints, such as seasonal fluctuations of micro-algae quantity (Neury-Ormanni et al., 2020). During ecological succession of surfaces, pioneering taxa are either active dispersers with potent swimming abilities (e.g., Copepoda) or able to reproduce fast and exploit alternative resources in the form of suspended food particles (e.g., Rotatoria) (Peters et al., 2007; Kathol et al., 2011; Majdi et al., 2012). Furthermore, taxa with a small body-size, worm-shaped bodies or active swimming structures were found to be the most resilient to hydrological changes (Gaudes et al., 2010).

For more than two decades, meiobenthologists have been assessing community structure patterns in relation to substrate type and sediment grain size (e.g., Schmid-Araya, 1998; Ward & Palmer, 1994; Beier & Traunspurger, 2003). Even in relatively
stable and homogeneous sandy beds (i.e., in laboratory ponds), meiofauna shows a patchy horizontal micro-distribution at centimeter scale (Gansfort et al., 2018), and a pronounced vertical zonation within the streambed as a result of hydrological constraints, heterogeneous distribution of resources, and gradient of oxygen concentration (e.g., Ward & Palmer, 1994; Marchant, 1995; Clinton et al., 1996; Teiwes et al., 2007; Traunspurger et al., 2015; Peralta-Maraver et al., 2019). How migrating ripples influence the abundance and composition of meiofauna has only been researched in marine systems: For example, densities of Nematoda oscillate in migrating ripples of an intertidal flat matching with ripple wavelength where the highest densities are found in ripple crests (Hogue & Miller, 1981). The latter authors hypothesize that Nematoda benefit from repeatedly deposited organic material in troughs during low tide, which subsequently is buried under crests at high tide. More recently, Schratzberger & Larcombe (2014) observe that, at larger spatial scales, zones in the marine subtidal with high sediment mobility show a more homogeneous landscape and, thus, a lower species diversity. On the contrary, the sediment in zones less frequently mobilized harbors a mosaic of habitat patches and, thus, a more taxonomically and functionally diverse nematofauna.

The cryptic nature, and tedious handling of the meiofauna has prevented their systematic inclusion into most stream ecology studies (Majdi et al., 2020a). While some evidence from marine environments suggests that the distribution of meiofauna is affected by the sediment transport regime, we lack knowledge of the effect of migrating ripples on meiofaunal communities in lotic ecosystems. As a first exploration, we hypothesized that (1) sediments migrating as ripples have lower meiofaunal abundance. (2) Migrating sediments have more meiofaunal taxa known for their resistance (like Tardigrada or Rotatoria) or active colonization abilities. While in stationary sediments a marked vertical distribution and a community composed of more interstitial specialists with characteristic worm-shaped bodies or larger sizes should be observed. (3) When placed in the context of multiple environmental effects, sediment migration should emerge as a significant driver of taxonomic and functional structure of the benthic community.

Material and methods

Study sites

We sampled the bed of five lowland streams in north-eastern Germany once between May and June 2020 (Table S1). Verlorenwasser, Plane, Pulsnitz and Spree are located in the Elbe catchment. Oker is part of the Weser catchment. All streams studied were shaped by the young and old ice drift of moraine landscape and had a sandy streambed. The stream hydrology was perennial and showed characteristic lowland pluvial regime, with low flow periods typically occurring in late spring and summer and high flow periods occurring in winter and early spring. Water level and discharge of the studied streams were below base flow between mid-March and June 2020 (Table S1). All streambeds were characterized by a mosaic of migrating ripples and stationary sediment patches (Fig. 1). Migrating ripples covered between 34 and 64% of the streambed across the sampled reach length of 220 to 3780 m (Table S1). All streams had low macrophyte vegetation (Fig. 1). Sampling sites at Verlorenwasser, Plane and Pulsnitz (mean reach width 4–6 m) were forested and characterized by numerous coarse in-stream woody structures (Fig. 1). Sampling sites at Spree and Oker (mean reach width 11–17 m) were open and without coarse in-stream woody structures (Fig. 1).

Sediment sampling

Sediment patches of two contrasting sediment transport regimes, migrating ripples and stationary sediment, were sampled at three independent sampling sites located at least 20-fold the stream width apart (Montgomery & Buffington, 1997) resulting in a reach length of 220 to 3780 m (Table S1). Sites at Spree were tenfold the stream width apart because water was deep and did not allow optical inspection of the streambed and localization of migrating ripple and stationary sediment patches. To avoid sampling bias due to the patchy distribution of the meiofauna, five sediment cores (3.4 cm diameter, 20 cm long) were taken at each sampling site. Another set of six cores were taken at each sampling site to determine environmental parameters such as sediment grain size, dry mass (DM), organic matter content, Chl a (as proxy for phototrophic biomass) and
Fig. 1 Examples of migrating ripples and stationary sediment patches in sandy beds of five lowland streams in north-eastern Germany. a Pulsnitz, b Verlorenwasser, c Plane, d Oker, and e Spree. Triangles show migrating ripple patches and squares show stationary sediment patches.
bacterial abundance. Samples from all three sites per stream were pooled to obtain a composite sample representative for the whole stream reach. We differentiated two depth layers: the superficial layer (0–1.5 cm depth) and the underlying layer (1.5–3 cm depth). This resulted in a total of 20 samples (2 transport regimes × 2 layers × 5 streams) for meiobenthos and environmental parameters that were processed directly in the field (see “Processing of sediment samples” section).

Oxygen concentration of the interstitial water was measured directly at sampling in superficial (0.1 and 1 cm depth) and underlying layer (2 and 3 cm depth) of three random migrating ripple and stationary sediment patches using an oxygen microsensor (0.9 mm diameter; Microx TX 3, PreSense Precision Sensing GmbH, Regensburg, Germany; Gerull et al., 2011).

Environmental parameters in-stream water

Flow velocity was measured approximately 2 cm above the streambed at 5 to 10 spots per sediment patch and sampling site (Mini Air 20, Schiltknecht, Zürich, Switzerland). Stream water temperature, oxygen concentration, pH, and conductivity were measured using a portable probe (WTW Multi 3630 IDS). The mean leaf area index of the reach (in %), as measure of canopy coverage was estimated from a skyward image taken at each sampling site approximately 15 cm above the water surface with a reflex camera (EOS 60D, Canon). Images were binarized, and the area of dark pixels was quantified using imaging software (ImageJ version 2.0.0). Water samples were taken at each sampling site to analyze the concentration of soluble reactive phosphorous (SRP), NH₄-N, NO₃-N (filtered through 0.2 µm membranes), and dissolved organic carbon (DOC, filtered through 0.45 µm membranes). Samples for dissolved nutrients and DOC were kept at 4°C and measured the next day. Dissolved nutrients and DOC in water were analyzed as described in Risse-Buhl et al. (2017).

Processing of sediment samples

Fresh sediment for grain size and organic matter analysis was stored at –20°C. Grain size distribution was determined by passing dried sediment (124.5 ± 36.3 g DM) through a series of 8 nested sieves (mesh sizes ranging from 0.112 mm to 3.55 mm) on a sieve shaker. The obtained D₂₅ and D₇₅ values were used to calculate Trask’s sorting coefficient as (D₇₅/D₂₅)⁰.⁵. Sediment organic matter content (%) was determined as difference of dry mass (48 h at 60°C) and ash free dry mass (4 h at 550°C).

A total of 10.6 ± 2 g DM from fresh sediment was stored at –20°C for Chl a determination. Chl a concentration was measured by high performance liquid chromatography (Ultimate3000, Thermo Fisher Scientific Corporation, Waltham, MA, USA) after extraction with 90% ethanol and several freezing/thawing cycles (Scheidweiler et al., 2021).

For bacterial abundance, 2.5 ml of fresh sediment (4.2 g DM) were fixed with formaldehyde (3.7% final concentration). Bacteria were detached from sediment grains by ultrasonic treatment (1 min at 20% amplitude, HTU SONI I 30, G. Heinemann Ultraschall- und Labortechnik, Schwäbisch Gmünd, Germany). Bacteria in a subsample of 0.1–0.5 ml were filtered onto black polycarbonate membranes (pore size 0.2 µm), stained with acridine orange and counted using an epifluorescence microscope at 1000-times magnification (Axioskop2, Zeiss, Jena, Germany) (Kamjunke et al., 2015).

Fresh sediment for meiobenthos quantification (217.5 ± 34.6 g DM) was fixed with formaldehyde (3.7% final concentration) and stored at 4°C. Meiobenthos were extracted from sediments following the protocol of Traunspurger et al. (2015). In short, the whole sample was processed in the way that half of it was transferred into a 50 ml centrifuge tube, filled with water and centrifuged at 1500 ×g for 10 min to remove formaldehyde and excess water. The supernatant was poured through a 20 µm sieve. Afterwards, the sediments were suspended in a colloidal silica solution (Ludox-HS40, gravity set at 1.14 g cm⁻³, Sigma-Aldrich) and centrifuged at 800×g for 5 min to separate particles with specific gravity < 1.14 (including meiobenthos) from heavier sediment particles. The supernatant was poured through the same sieve. The extraction procedure was repeated with the other half of the sample. All fractions retained on the sieve were collected, preserved in formaldehyde (3% final concentration) and stained with a few drops of Rose Bengal for at least 48 h before counting. Extracted samples were observed at 10 to 80-times magnification (S8APO, Leica, Wetzlar, Germany) and invertebrates were counted, identified and assigned
to morphofunctional categories (see next section). Between 44 and 1295 individuals were counted from each sample, with only three out of twenty samples containing less than 100 individuals.

**Meiobenthos taxonomic and trait classification**

Meiobenthos was identified to the lowest practical taxonomic-level (see Table 1). Furthermore, we assigned individuals counted to five morphofunctional categories based on basic traits such as locomotion, body shape and size. These categories were slightly adapted following the morphofunctional classifications proposed by Gaudes et al. (2010) and Townsend & Hildrew (1994). We differentiated species with cilia, worm-shaped body, and appendages. We could further breakdown “worm-shaped” and “with appendages” categories into two body-size classes: small and large, with a threshold set at 1.5-mm body length. This was based on the assumption that size would dictate population turnover rates (Brown et al., 2004) as well as the ability to reach and actively spread through newly formed habitats.

**Statistical analysis**

All analyses were performed under R computational framework (v4.0.4; R Development Core Team, 2018), using packages ‘ImPerm’ (Wheeler & Torchio, 2010), ‘vegan’ (Oksanen et al., 2013), and ‘ggplot2’ for visualization (Wickham, 2011).

To test hypothesis 1, we used an ANOVA performing permutation tests (pANOVA, aovp function in ‘lmPerm’, 9999 permutations, further referred to as PERMANOVA). This test was based on Hellinger-transformed abundance data of taxonomic groups and morphofunctional traits. Multivariate homoscedasticity was tested using Anderson’s PERMDISP2 procedure (betadisper function), which is a multivariate analogue of Levene’s test. Multivariate homoscedasticity was met for both taxonomic groups (transport \( P = 0.42 \), layer \( P = 0.38 \)) and morphofunctional traits (transport \( P = 0.37 \), layer \( P = 0.78 \)). In addition, we used similarity percentage (SIMPER) to perform pairwise comparisons of groups of samples based on their taxonomic and morphofunctional community structure. SIMPER was used to highlight the taxa (or traits) that contributed the most to dissimilarities observed among groups of samples.

To test hypothesis 3, we used non-metric multidimensional scaling (nMDS) based on Hellinger-transformed data and Kulczinsky’s distance matrix to ordinate sites and species scores in a biplot (metaMDS function). Kulczinsky’s distance was chosen over other dissimilarity indices as it returned the best gradient separation in our case (tested after rankindex function). Ordinations summarized the observed differences in community structure relatively well, as the goodness-of-fit (GOF) of stressplots was high (GOF-taxa = 0.96, GOF-trait = 0.99) and stress-values were acceptable (stress-taxa = 0.20, stress-trait = 0.09).

**Table 1** Morphofunctional trait classification and corresponding taxonomic groups

| Morphofunctional trait | Taxonomic group                                                                 |
|------------------------|---------------------------------------------------------------------------------|
| Small & cilia           | Rotatoria, Gastrotricha                                                          |
| Small & worm-shaped     | Nematoda, Annelida (Aeolosomatidae), Arthropoda (Insecta: Chironomidae)       |
| Large & worm-shaped     | Annelida (Tubificidae, Aeolosomatidae, Haplotaxidae), Arthropoda (Insecta: Chi-|
|                         | ronomidae, Ceratopogonidae)                                                   |
| Small & appendages      | Arthropoda (Hydrachnidia; Crustaceae: copepoda, Ostracoda, Cladocera), Tardigrada |
| Large & appendages      | Arthropoda (Crustaceae: Amphipoda, Insecta: Ephemeroptera, Trichoptera, Odonata)|

These taxonomic groups (except Trichoptera and Odonata) are also illustrated in Fig. 4.
(Kruskal & Wish, 1978). To distinguish the most important environmental factors describing the variability in taxonomic and morphofunctional community structure of meiobenthos, we fitted vectors of five continuous factors (sorting coefficient, organic matter content, oxygen concentration, bacterial abundance, Chl a) and centroids of levels of categorical factors (transport and layer) to the nMDS (envfit function, 999 permutations). The significance of factors (vectors) fitted to the ordination plot was assessed using a goodness-of-fit statistic ($R^2$) and a $P$-value being based on a permutation test. All environmental factors were centered before the analyses. The direction of a vector showed the direction of the gradient, and the length of the vector was proportional to the correlation strength between the variable score and the ordination space.

**Results**

**Environmental background**

The three forested streams Pulsnitz, Verlorenwasser and Plane had a larger leaf area index (more shade by riparian vegetation cover) than the two wider and more open streams Oker and Spree (Table S1). Water temperature of all streams ranged between 11 and 19°C. Oxygen concentration in the stream water was close to saturation and comparable among streams, as was pH. Conductivity was highest in Oker compared to all other streams. Dissolved carbon and nutrients (DOC, DIN, SRP) were lowest in Verlorenwasser compared to all other streams. SRP concentration at both Verlorenwasser and Spree ranged between 3 and 12 µg l$^{-1}$ which was approximately one order of magnitude lower than that of the other streams. These low SRP concentrations resulted in higher C:P (173 and 223, respectively) and N:P (34 and 41, respectively) ratios indicating that Verlorenwasser and Spree were likely more P-limited (Table S1).

Flow velocity was on average 2.3× higher above migrating ripple patches than above stationary sediment patches at 0.24 m s$^{-1}$ (ranging 0.18–0.31 m s$^{-1}$) above migrating against 0.14 m s$^{-1}$ (0.03–0.28 m s$^{-1}$) above stationary (Table 2). The sorting coefficient of streambed sediments was also significantly higher in migrating ripples than in stationary sediments ($p$ANOVA: $SS_{1,16} = 0.1$, $P = 0.012$), indicating that migrating ripple sediments were coarser and with more uniform grain size than stationary sediments (Table 2). Oxygen concentration in interstitial water was also significantly higher in migrating ripples than in stationary sediments ($SS_{1,16} = 35.9$, $P < 0.001$). Oxygen concentration in superficial sediment layer was significantly higher than in the underlying sediment layer ($SS_{1,16} = 28.1$, $P = 0.002$), with lowest concentration reaching hypoxia (< 2 mg l$^{-1}$) in the underlying layer of stationary sediments (Table 2). Stationary sediments had 2.8× to 3.7× more organic matter than migrating ripple sediments ($SS_{1,16} = 2.5$, $P < 0.001$). The bacterial abundance averaged 7.8×10$^7$ g$^{-1}$ DM (ranging from 3.5×10$^7$ up to 14.3×10$^7$ cells g$^{-1}$ DM) and was neither affected by transport ($SS_{1,16} = 2.2×10^{15}$, $P = 0.18$)

| Environmental factors                          | Migrating ripple | Stationary sediment | pANOVA                  |
|-----------------------------------------------|------------------|---------------------|-------------------------|
|                                               | Superficial      | Underlying          | Superficial            | Underlying |                |
| Flow velocity                                 | 0.24 (0.05)      | 0.14 (0.07)         |                         |            | mig > stat     |
| Sorting coefficient [(D$_{75}$/D$_{25}$)$^{0.5}$] | 1.8 (0.1)        | 1.6 (0.2)           | 1.8 (0.1)              | 1.6 (0.2)  | mig > stat     |
| Organic matter content (%)                    | 0.4 (0.1)        | 0.3 (0.1)           | 0.4 (0.1)              | 0.3 (0.1)  | mig < stat     |
| Dissolved oxygen in sediment pore water (mg O$_2$ l$^{-1}$) | 7.3 (0.6)        | 5.1 (1.2)           | 5.4 (0.8)              | 2.3 (2.0)  | mig > stat sf > ul |
| Bacteria (10$^7$ cells g$^{-1}$ DM)           | 6.9 (2.4)        | 9.0 (3.3)           | 6.5 (3.3)              | 8.6 (4.0)  | ns             |
| Chl a (µg g$^{-1}$ DM)                        | 34.7 (62.5)      | 92.1 (56.6)         | 26.4 (40.4)            | 72.0 (23.9)| mig < stat     |

Values represent spatial mean (standard deviation) of five German streams. Significant results of the permutation-based analysis of variance (pANOVA) between mig and stat as well as between sf and ul are represented. ns, not significant. Chl a, Chlorophyll a, DM, dry mass. (D$_{75}$/D$_{25}$)$^{0.5}$, sorting coefficient.
nor by layer \((SS_{1,16} = 7.7 \times 10^{13}, P = 0.80)\). Chl \(a\) averaged 56.3 µg g\(^{-1}\) DM (ranging 1.2–158.8 µg g\(^{-1}\) DM) and was on average 2.7× higher in stationary sediments than in migrating ripples (Table 2, \(SS_{1,16} = 1.3 \times 10^4, P = 0.03\)).

### Meiobenthos abundance

The total abundance of sediment-dwelling meiobenthos roughly spanned over one order of magnitude ranging from minimum value of 0.24 ind. g\(^{-1}\) DM to a maximum value of 6.65 ind. g\(^{-1}\) DM (Table 3). Total abundances were not significantly different across migrating ripples and stationary sediments (pANOVA: \(SS_{1,16} = 0.04, P = 0.94\)). The relatively low p-value of the interaction term \((SS_{1,16} = 8.8, P = 0.07)\) and pairwise treatment comparison suggested that total abundances tended to be different between layers depending on the transport regime. In other words, meiobenthos was 6× more abundant in the superficial layer compared to the underlying layer of the stationary sediment patches, while both layers of migrating ripple patches had comparable abundances (Table 3).

### Structure of the meiobenthic community

The meiofauna taxa were clustered into 17 taxonomic groups belonging to the six phyla: Nematoda, Rotatoria, Tardigrada, Gastrotricha, Annelida (Haplotaxidae, Tubificidae, and Aeolosomatidae) and Arthropoda (Cladocera, Copepoda, Ostracoda, Gammaridae, Hydrachnidia, Chironomidae, Ceratopogonidae, Ephemeroptera, Trichoptera, and Odonata). Generally, the community was dominated by Rotatoria with on average 26.9% (range 2.8–69.3%) of individuals counted, Nematoda with on average 21.6% (range 1.1–70.5%), and Annelida (especially Aeolosomatidae) with on average 20.3% (range 1.3–73.6%) (see Fig. 2, Table 3). Smaller individuals (≤1.5 mm) were more commonly found than larger individuals (>1.5 mm) (Fig. 2, Table 3).

Both, the taxonomic and morphofunctional structure of the meiobenthic community were significantly different between migrating ripple and stationary sediment patches (PERMANOVA: taxa \(F_{1,16} = 4.78, P < 0.001\), traits \(F_{1,16} = 7.69, P = 0.002\)), but not between superficial and underlying sediment layers (taxa \(F_{1,16} = 0.80, P = 0.60\), traits \(F_{1,16} = 0.57, P = 0.61\)).

### Table 3 Absolute abundance of benthic invertebrate taxa and morphofunctional traits dwelling in superficial and underlying layers of sandy sediments in migrating ripple and stationary sediment patches

| Group       | Migrating ripples |           | Stationary sediment |          |
|-------------|-------------------|-----------|---------------------|----------|
|             | Total Superficial | Underlying | Total Superficial   | Underlying |
| Taxonomic   |                   |           |                     |          |
| Rotatoria   | 0.92 (0.99)       | 0.76 (0.83)| 1.08 (1.21)         | 0.28 (0.38)| 0.48 (0.47)| 0.09 (0.09) |
| Nematoda    | 0.18 (0.15)       | 0.25 (0.18)| 0.11 (0.09)         | 0.59 (0.90)| 1.00 (1.18)| 0.19 (0.17) |
| Annelida    | 0.64 (0.68)       | 0.81 (0.93)| 0.48 (0.32)         | 0.46 (0.65)| 0.75 (0.86)| 0.17 (0.10) |
| Insecta     | 0.03 (0.03)       | 0.04 (0.04)| 0.02 (0.01)         | 0.28 (0.35)| 0.51 (0.38)| 0.06 (0.04) |
| Tardigrada  | 0.15 (0.19)       | 0.11 (0.17)| 0.19 (0.22)         | 0.11 (0.21)| 0.20 (0.28)| 0.02 (0.02) |
| Crustacea   | 0.10 (0.17)       | 0.15 (0.23)| 0.04 (0.05)         | 0.23 (0.41)| 0.42 (0.53)| 0.03 (0.03) |
| Gastrotricha| 0.03 (0.03)       | 0.03 (0.02)| 0.04 (0.04)         | 0.01 (0.01)| 0.01 (0.01)| 0.01 (0.01) |
| Hydrachnidia| 0.00 (0.01)       | 0.01 (0.01)| 0.00 (0.00)         | 0.01 (0.01)| 0.02 (0.02)| 0.00 (0.00) |
| Morphofunctional traits |            |           |                     |          |
| Small & cilia| 0.95 (0.82)       | 0.79 (0.84)| 1.12 (1.25)         | 0.29 (0.24)| 0.49 (0.46)| 0.09 (0.09) |
| Small & worm-shaped| 0.75 (0.39)       | 0.96 (0.80)| 0.53 (0.35)         | 1.07 (0.74)| 1.84 (1.43)| 0.30 (0.19) |
| Small & appendages| 0.25 (0.29)       | 0.26 (0.40)| 0.23 (0.21)         | 0.34 (0.32)| 0.62 (0.64)| 0.05 (0.03) |
| Large & worm-shaped| 0.11 (0.12)       | 0.13 (0.15)| 0.08 (0.09)         | 0.26 (0.11)| 0.41 (0.17)| 0.11 (0.07) |
| Large & appendages| 0.00 (0.00)       | 0.00 (0.00)| 0.00 (0.00)         | 0.02 (0.01)| 0.03 (0.02)| 0.00 (0.00) |
| Total invertebrates| 2.05 (1.31)       | 2.14 (1.36)| 1.96 (1.68)         | 1.97 (2.00)| 3.39 (3.21)| 0.56 (0.28) |

Values represent spatial mean (standard deviation) of five German streams as number of individuals per gram sediment dry mass.

(modified table and text from the original source)
On the one hand, Rotatoria were relatively more abundant in migrating ripples (Fig. 3a) and found to be significant contributors to the difference with the stationary community (SIMPER, \( P = 0.003 \), see Table S2 for SIMPER scores). On the other hand, Chironomidae (SIMPER, \( P = 0.002 \)) and Copepoda (\( P = 0.011 \)) were relatively more abundant and significantly associated with stationary sediment patches. Hydrachnidia (\( P < 0.001 \)) and Ceratopogonidae (\( P = 0.001 \)), although generally rare, were never found in samples from migrating ripple patches (Fig. 3a). No significant association of taxon with layer was detected.

Small individuals with cilia were relatively more abundant in migrating ripple patches (SIMPER: \( P = 0.002 \)), whereas large, worm-shaped individuals (\( P = 0.003 \)) and large individuals with appendages (\( P = 0.020 \)) were more abundant in stationary sediment patches (Fig. 3b, Table S2). Again, no significant association of trait with layer was detected.

Testing effects of environmental factors on the distribution of taxa and traits

Based on taxonomic community structure, the nMDS ordination plot distinguished samples based on transport regime (migrating vs stationary) but the differentiation based on layer did not stand out as clearly (Fig. 3a). Among the seven environmental factors fitted to the ordination, transport regime (\( R^2 = 0.67, P = 0.001 \)), organic matter content (\( R^2 = 0.47, P = 0.006 \)), sorting coefficient (\( R^2 = 0.38, P = 0.01 \)) and Chl \( \alpha \) (\( R^2 = 0.38, P = 0.02 \)) significantly explained the variability in taxonomic community structure of the meiobenthos (Fig. 3a). Oxygen concentration of the interstitial pore water (\( R^2 = 0.25, P = 0.08 \)) tended to be important but was not significant for the distribution of meiobenthos. The distribution of taxa corroborated well with SIMPER results (Table S2). Rotatoria scored towards the lower-left panel of the biplot (affinities with migrating ripples, sorting coefficient and oxygen concentration in the sediment) (Fig. 3a, Table S3). Chironomidae, Copepoda, Ceratopogonidae and Hydrachnidia scored towards the upper-right panel of the biplot (affinities with stationary patches, Chl \( \alpha \) and organic matter content in the sediment). Other relevant meiobenthic taxa such as Nematoda and Aelosomatidae tended to distinguish along the first nMDS axis: Nematoda scored towards the right-side of the ordination plot together with the factors bacteria and layer. Aelosomatidae scored towards the left-side of the ordination (Fig. 4a, Table S3).

Considering morphofunctional trait structure, again, the nMDS ordination displayed a clearer differentiation between transport rather than layer, with the migrating ripple samples scoring generally towards the left-side of the ordination, while the stationary samples scored towards the right-side.
Fig. 3 Non-metric multidimensional scaling (nMDS) of the Kulczinsky’s distances of the meiobenthos community structure in superficial and underlying sediment layers of migrating ripple and stationary sediment patches of five German streams. a Taxonomic abundance (scores are represented in Table S3) and b morphofunctional trait abundance (scores are represented in Table S4). Environmental fitting was used to determine significant effects of environmental factors. Other abbreviations: transport (migrating vs. stationary sediment); layer (superficial vs. underneath layer); oxygen (oxygen concentration in sediment pore water); sort.c (sediment sorting coefficient); om (organic matter content); chl.a (sediment Chl a concentration); bac (bacterial abundance in sediment). Grey * indicate significant effect of environmental factors; black * indicate a significant contribution of a taxon, or trait, to community dissimilarity between migrating and stationary sediments (SIMPER analysis, see Table S2)
of the ordination plot (Fig. 3b). Among the seven included environmental factors, transport ($R^2 = 0.55, P = 0.001$), sorting coefficient ($R^2 = 0.40, P = 0.01$) and Chl $a$ ($R^2 = 0.35, P = 0.03$) significantly explained the variability in the morphofunctional trait structure (Fig. 3b). Oxygen concentration of the interstitial pore water ($R^2 = 0.29, P = 0.06$) and organic matter content ($R^2 = 0.29, P = 0.06$) tended to also explain the distribution of traits. Trait differentiation mostly occurred along nMDS axis 1 and corroborated with SIMPER results (Table S2). Small individuals with cilia had more affinities with samples collected from migrating ripples showing a higher sediment sorting coefficient. Large individuals with worm-shaped body or with appendages had more affinities with stationary patches showing a higher concentration of Chl $a$ and organic matter (Fig. 3b, Table S4).

**Discussion**

**Originality of the study**

The migration of sand ripples is a typical morphological element of sandy streambeds occurring at various time scales and flow velocities, depending on local hydrology, granulometry and streambed morphology (Montgomery & Buffington, 1997; Garcia, 2008; Andreotti et al., 2012; Rinaldi et al., 2016). However, there is still little quantitative data about the commonness of bed form ripple distribution, except from case studies. Here we sampled five sand bed streams in Germany and we found a substantial coverage of migrating ripples (34–64%), which matches published data on coverage of migrating ripples in undisturbed (20–50%) and eroded reaches (up to 100%, see Mutz et al., 2001; Wallbrink, 2004; Rabení et al., 2005; Marcarelli et al., 2015). Given the wide distribution of sand bed streams and rivers in lowland alluvial and glacial landscapes all over the world (e.g., Mississippi River, Colorado River) our data underline the significance of this phenomenon and its consequences for river ecology and water management.

To the best of our knowledge, our study is the first to investigate the distribution of meio- benthos in migrating ripples vs. stationary sediments at small spatial scales in sandy streams. Although some studies already tackled this process in marine systems: For example, Hogue & Miller (1981) carefully investigated the micro-distribution of meiobenthic organisms like Nematoda in tidal ripples that move alternatively in multiple directions. Here we argue that stream ripples generally migrate continuously in the same direction (downstream) adding an original and distinctive feature in comparison to Hogue & Miller’s study investigating distribution of meio-benthos in tidal ripples.
Hypothesis 1: Meiobenthos abundance should be lower in migrating ripples

In our study, meiobenthic abundance was comparable in migrating ripples (2.1 ind. g⁻¹ DM, corresponding to ca. 1.0 x 10⁶ ind. m⁻², after sediment dry-weight to area correction) and stationary sediments (2.0 ind. g⁻¹ DM, corresponding to ca. 8.4 x 10⁵ ind. m⁻²) contradicting our first hypothesis that sediment migrating as ripples would negatively affect meiobenthos abundance. More generally, our abundances are fairly comparable to meiobenthos abundance in the order of 10⁵–10⁶ individuals per m² sediment that have been reported in several other temperate sandy streams (e.g., Beier & Traunspurger, 2003; Reiss & Schmid-Araya, 2008; Majdi et al., 2015).

However, our results contrast with the marked changes of abundance observed in Nematoda populations experiencing cyclic migration or larger scale sediment transport in marine systems (Hogue & Miller, 1981; Schratzberger & Larcombe, 2014). We expected that total meiobenthic abundances would differ between migrating ripples and stationary sediments as moving sediments tend to homogenize the interstitial habitat. In an intertidal flat, Hogue & Miller (1981) found a correlation between the wavelength of sand ripples and the abundance of Nematoda. These authors further hypothesized that particles of organic matter and fecal pellets accumulating in ripple troughs at low tide would be buried by avalanching sand at high tide. The described organic matter distribution in response to sediment dynamics would explain a more abundant Nematoda community in ripple crests at the time of their sampling. However, in our study we did not find significant differences in total meiobenthic abundance, nor abundances of Nematoda between migrating ripples and stationary sediments, whereas organic matter and Chl a appeared more concentrated in stationary sediments. There is ample evidence in the literature that stream meiobenthos reacts positively to the availability and quality of organic matter and microphytobenthos (reviewed in Swan & Palmer, 2000; Majdi & Traunspurger, 2015). We were thus surprised that total meiobenthic abundance was not different despite lower organic matter and Chl a content in migrating ripples compared to stationary sediments. There is room for further investigations of causalities involved in this process, but we may evoke here that total meiobenthos abundance might not be the best measurement to detect significant changes in a complex community where individual taxa or morpho-functional groups probably play different ecological roles. Total biomass, secondary production, body-size distribution spectrum or taxonomic and trait-based composition are all more likely to be more accurate proxies when it comes to detect effects structuring stream meiobenthic communities (e.g., Peralta-Maraver et al., 2019; Neury-Ormanni et al., 2020; Schmid-Araya et al., 2020). Rotatoria were more abundant in migrating ripples, but they are minor contributors in terms of biomass (ca. 0.01 to 1 µgDM ind⁻¹). Hence, we may speculate that standing biomass of invertebrates was lower in migrating ripples in comparison to stationary sediments where relatively large taxa such as insect larvae were more abundant.

Interestingly, in our abundance model, the interaction term between transport and layer was marginally significant suggesting the existence of a pattern in which the meiobenthos could be more abundant in the superficial layer of stationary sediments, while in migrating ripples abundances were similar regardless of sediment depth. This matches with a general consensus in the literature stating that conditions in deeper sediment layers are less favorable for the establishment of an abundant meiobenthic community in comparison to superficial layers, mainly because of anoxia (e.g., Beier & Traunspurger, 2003; Omesová & Helešic, 2010; Traunspurger et al., 2015). Thus, although we lacked strong evidence to support this pattern, further studies may investigate whether sediment migration has the potential to create beneficial conditions for the establishment of a more abundant fauna in deeper layers, as vertical constraints (like oxygen depletion) would be more likely to be offset by the dynamic sediment mixing process.

Hypothesis 2: Migrating ripples should favor more resistant or more resilient taxa

Based on the assumption that sediment transport regime imposes spatio-temporal constraints on sediment texture and resource distribution (e.g., Harvey et al., 2012; Schratzerer & Lacombe, 2014), we hypothesized that sediment migrating as ripples would affect the taxonomic and morphofunctional structure of the meiobenthic community, in the sense that small and particularly resistant taxa such as
Rotatoria, Nematoda or Tardigrada would be favored in migrating ripples. This hypothesis was confirmed by our results at both taxonomic and morphofunctional levels, as we found significant structural differences when comparing communities found in migrating ripples with the seemingly more diverse communities found in stationary sediments (summarized in Fig. 4).

More specifically, our results showed that migrating ripples mostly supported Rotatoria. Rotatoria are among the smallest meiofaunal representatives, they are parthenogenetic animals with extremely short population turn-over rates (hours to a few days), some taxa have a soft-body and can actively move through interstices (Bdelloidea), but Monogononta are also known to actively swim in the water column (Ricci & Balsamo, 2000). These features allow Rotatoria to be one of the most ecologically relevant and abundant meio-benthic group in freshwater sediments and hard-substrates (e.g., Schmid-Araya, 1998; Duggan, 2001), and to be among the very first metazoans to settle and colonize newly formed epibenthic habitats in lakes and rivers (Peters et al., 2007; Majdi et al., 2012). Furthermore, Rotatoria can also exploit small particles and planktonic food items by settling onto surfaces and filtering the water column with their oral ciliature (Kathol et al., 2011). Given these abilities it is likely that Rotatoria can withstand the periodic sediment transport in migrating ripples and recolonize sand grains more easily than other meio-benthic groups. Rotatoria could further benefit from the absence of competitors (or predators) less adapted to the “ever-changing” life conditions in migrating ripples. In that case, migrating sediment would represent an ideal niche and refuge for Rotatoria, but we recommend further studies to better identify the causes leading to the effect that we observed and to identify which groups or species among Rotatoria benefit the most of a migrating sediment landscape.

Hypothesis 3: Sediment migration should be a significant driver of community structure

When considering the influences of several environmental variables on meio-benthos distribution, our results confirmed that sediment migration was a significant driver of community structure. This advocates that sediment transport regime is (1) specifically an important mechanical driver of meio-benthos distribution in addition to commonly regarded drivers (see Swan & Palmer, 2000). (2) More generally,
a useful addition to models linking the response of freshwater ecosystems to environmental constraints. And (3) an important environmental filter, at least for interstitial biota like meio-benthos. Hence, migrating patches should be increasingly considered as a specific type of benthic micro-habitat harboring a specialized fauna.

Nevertheless, the effects of migrating ripples are multifaceted and likely the result of complex modifications of environmental gradients that are vital for the distribution of benthic invertebrates. At microscopic scales, when the grains collide, biofilm cover and cohesion is limited to fissures and crevices providing protection against mechanical abrasion (Risse-Buhl, pers. com.). Moreover sand grains travel cyclically: they are mobilized (i.e., erosion period) then buried and immobile for a certain period of time (i.e., resting period) (Fig. 4). This erosion-resting cycle modifies the distribution of key abiotic gradients like the vertical penetration of oxygen and light, the stratification of grain-size categories, but also the distribution of resources available for consumers. For example, we found less organic matter and Chl a in migrating ripples. Thus, the process of sediment migration probably imposes a set of important constraints on the life-style or size of resident organisms. For example, we observed that larger organisms failed to thrive in migrating ripples. As a consequence we may argue that sediment migration has the potential to alter stream food web dynamics by modifying (1) bottom-up and (2) top-down effects. (1) Bottom-up: Migrating ripples showed lower concentrations of organic matter and Chl a in comparison to stationary sediment patches, meaning lower food availability for detritivores and algivores. Hence, these patches would be less likely to house wide trophic pyramids supporting more trophic levels and larger body-size classes. Future studies should also investigate whether lower concentrations of Chl a were a result of the miniaturization of local algal communities to withstand dislodgement and burial by moving sand grains. Miniaturization of micro-algal communities would constrain the ability of larger algivores to exploit algal biomass, but would favor smaller deposit- or filter-feeding organisms like Rotatoria. (2) Top-down: Sediment sorting coefficient was higher in migrating ripples meaning that interstitial organisms (even large burrowing ones) have a higher risk of being dislodged and then more exposed to predation by benthivorous fishes in the superficial sediment (Hicks, 1984; Posey, 1986; Weber et al., 2018). Such predation effects could further cascade and benefit the smallest members of the community (like Rotatoria) that would experience lower predation risk by fishes.

Future studies should incorporate these topics and examine especially whether and how the process of sediment migration can modify the patchiness of stream habitats, channel the quantity and quality of benthic resources, and modulate their flows through the benthic food web.

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