



A meta-analysis of benthic rotifer community structure as a function of lake trophic state

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Abstract Our understanding of the ecological drivers that control community structure of benthic rotifers is poorly known. By reviewing 21 papers on freshwater benthic rotifers we compiled an inventory of an additional 258 species, 27 genera, and six families not previously listed in the review of benthic, lotic rotifers by Ricci and Balsamo (Freshw Biol 44:15–28, 2000). This raises the number of reported benthic species to 416, ~ 23% of all rotifers. Using selected papers within our dataset we tested two hypotheses: (1) Within lakes of different trophic state benthic rotifer communities differ in their species composition and (2) because rotifer trophic types reflect

strong specificity for certain foods, there is a difference in the distribution of trophic types in lakes of different trophic state. We found that the trophic state of water bodies influences species composition of benthic rotifers, but there was no significant difference in the distribution of their trophic types. To aid in understanding community assembly of benthic rotifers, we provide a list of knowledge gaps that future studies could address.

Keywords Benthos · Ecology · Interstitial · Diversity · Species composition

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Preface

This paper celebrates the research of the late Ramesh Gulati, a guide and mentor to us and many others. During his long, distinguished career he significantly extended our understanding of the ecology of trophic interactions in the plankton, lake biomanipulation, and lake restoration. In this short communication we extend his vision of understanding rotifer trophic dynamics into the realm of community structure of benthic rotifers.

Introduction

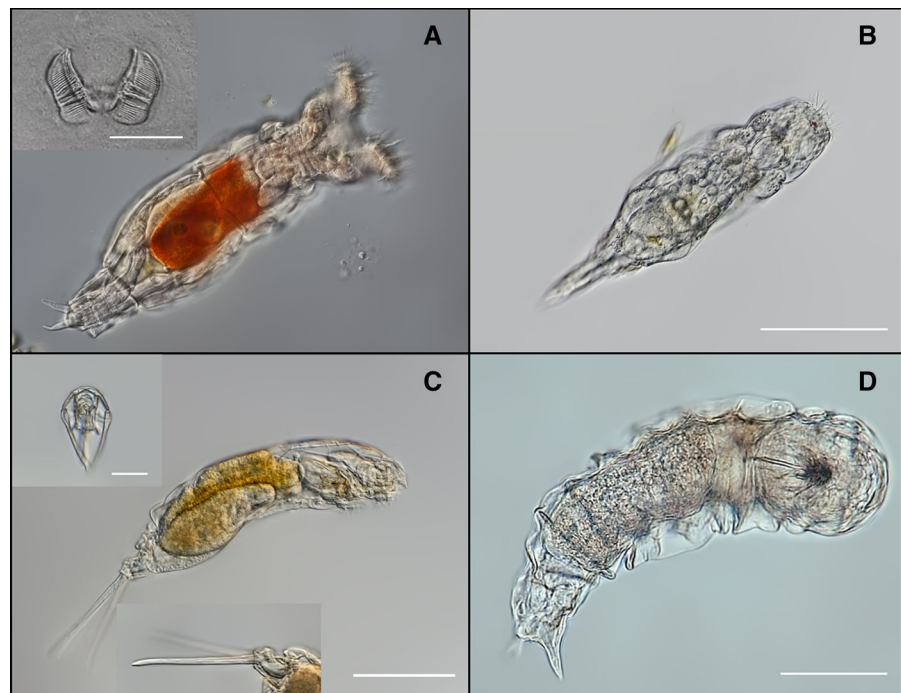
Rotifera (sensu stricto) is a diverse, moderately sized phylum of ~ 2000 species comprising small (~ 50–2000 µm), bilaterally symmetrical, metazoans, which exhibits a global distribution (Wallace et al. 2015). Although the community of benthic rotifers that reside in interstitial spaces of sediments has been known for a long time (Wiszniewski 1934; Pennak 1940), we still do not completely understand this distinctive community (Majdi et al. 2017) (Fig. 1).

The quintessential feature of benthic rotifers is that they lie on the surface of aquatic sediments or inhabit the space between small particles in aquatic and terrestrial sediments and also between the debris of decaying *Sphagnum* in bogs and peatlands (Błędzki and Ellison 2003; Bielańska-Grajner et al. 2011, 2017; Dražina et al. 2017). In these realms, rotifers are generally within one or two orders of magnitude of the size of the particles (Pennak 1940). When sand is the dominant material comprising the matrix, the organisms of this habitat are termed psammion (*G. psammus*, sand). Psammobiotic species are present only in the sand, and psammophilic species may also be found swimming in the water. On the other hand, psammoxene species seem alien to the benthos; they may have

been washed into the sand as adults or perhaps as neonates (Pennak 1940; Ejsmont-Karabin 2004). For example, Bērziņš (1951) reported sessile species on the surface of sediments of lakes in Sweden (see also Ejsmont-Karabin 2003). The fate of an individual considered to be a psammoxene is unknown. No equivalent terms are available for systems dominated by high organic content (i.e., benthic muds or peat). In lentic systems, the interstitial habitat extends from above the water's edge (euarenal), into the wave-washed zone (hygroarenal), down into the littoral of lakes (hydroarenal) (Ejsmont-Karabin 2003; Kalinowska and Ejsmont-Karabin 2012). Some species are found deeper still, in the profundal zone (Moore 1939). In lotic systems, rotifers are present at or near the benthos and within the sediments of the riparian and hyporheic zones (Pacioglu 2009). In soils they tend to occupy the upper levels (Pourriot 1979; Devetter 2010; Devetter and Frouz 2011; Devetter et al. 2017). A few species have been found in subterranean habitats (Pejler 1995).

While abiotic factors of the interstitial realm may differ from other habitats, the biotic challenges for species in all habitats are essentially the same: besting competitors, avoiding parasites and predators, securing sufficient food for survival and reproduction, and

Fig. 1 Four representatives the rotifers reported in the literature as present in the benthos (consult Supplemental Table S1). Representative bdelloid: **a** *Philodina roseola*. Representative monogononts: **b** *Proales halophila*, **c** *Dicranophorus sigmoides*, and **d** *Taphrocampa annulosa*. Insets are the corresponding trophi. All photomicrographs courtesy of Michael Plewka: www.plingfactory.de. Scale bars: Animals, 50 µm; trophi, 20 µm



finding mates. Because benthic habitats vary spatially and temporally and the rotifers that inhabit them are diverse, it is difficult to make meaningful generalization about their communities. While we have known for many years that lake productivity accounts for the abundance of planktonic rotifers (Yoshida et al. 2003), we have gained relatively little understanding of how lake productivity affects the community structure of benthic species. Ejsmont-Karabin (2003) addressed this by examining the hypothesis that lakes with higher trophic states would have psammon rotifer communities with higher diversity. However, she found no support for this hypothesis and noted that the hypertrophic lakes examined had lower species richness (S). Ejsmont-Karabin (2003) concluded that there are several factors that govern the structure of benthic rotifer communities, with lake trophic status being only one.

Rotifers use their trophi to process food, with some species exhibiting strong specificity for certain food types (Edmondson 1965). Chang et al. (2010) used this knowledge to assign taxa to specific feeding groups and Obertegger et al. (2011), Špoljar et al. (2011), and Schöll et al. (2012) employed it to track changes in rotifer community structure. The purpose of this short communication was twofold: (1) We expanded the inventory of species that researchers have reported in benthic samples. That dataset should be useful in assessing the composition of feeding groups in different regions of aquatic habitats. (2) We re-examine the dataset from Ejsmont-Karabin (2003) to re-examine her conclusion that higher trophic state has a negative impact on the community structure of benthic rotifers. Specifically, we tested the simple hypotheses that (1) the community structure of benthic rotifers and (2) the array of trophi possessed by these species vary among lakes of different trophic states from a selected group of studies.

Review of case studies

Inventory of benthic species

This analysis of 21 studies adds an additional 258 species belonging to a total of 54 genera in 24 families that were not reported in the review by Ricci and Balsamo (2000) of rotifers reported from interstitial lotic habitats. Our compilation adds seven additional

families to the list of taxa identified from benthic samples: Asplanchnidae, Collothecidae, Conochilidae, Epiphanidae, Flosculariidae, Microcodidae, and Trochosphaeridae (Supplemental Table S1). Thus, including data from Ricci and Balsamo (2000), the total number of benthic taxa is > 415 species—~ 23% of all rotifers—most of these are in order Ploima. We note from this list that there is still a lack of information on bdelloid rotifers.

Influence of trophic state

Since its inception the trophic state index (TSI), with subsequent modifications, has been a useful proxy to assess lake trophic state (LTS) (Carlson 1991) and by extension to assess the trophic state of the lake on its biota. For example, Slugocki and Czerniawski (2018) found that an increase in TSI led to shifts in zooplankton taxonomy and had negative effect on zooplankton diversity in 79 temperate lakes. Ejsmont-Karabin (2003) used the TSI to examine benthic rotifers in 18 lakes ranging in trophic state from mesotrophic to hypertrophic. In our reanalysis of that dataset we found that S decreased as a function of a lake's TSI, but that S rose as a function of Secchi disk depth before leveling off in eu- and hypereutrophic lakes (Fig. 2).

To explore the distinctiveness of benthic taxa further, we re-examined data of rotifers from two other closely opposed and well-studied lakes located in the Great Masurian Lake District (northeastern Poland): one mesotrophic (Kuc) and one eutrophic

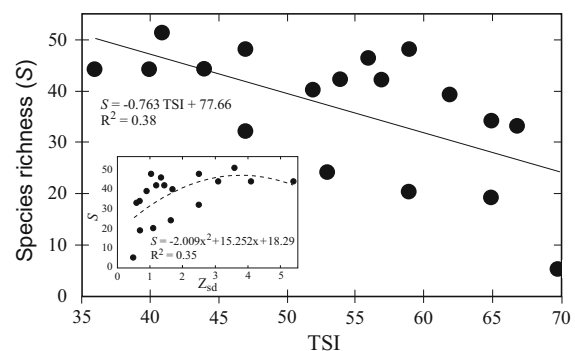


Fig. 2 Species richness (S) of rotifers from the benthos as a function of the trophic state. These data come from 18 lakes in the Great Masurian Lake District of northeastern Poland (Ejsmont-Karabin 2003). TSI trophic state index; insert = S as a function Secchi disk depth (Z_{sd})

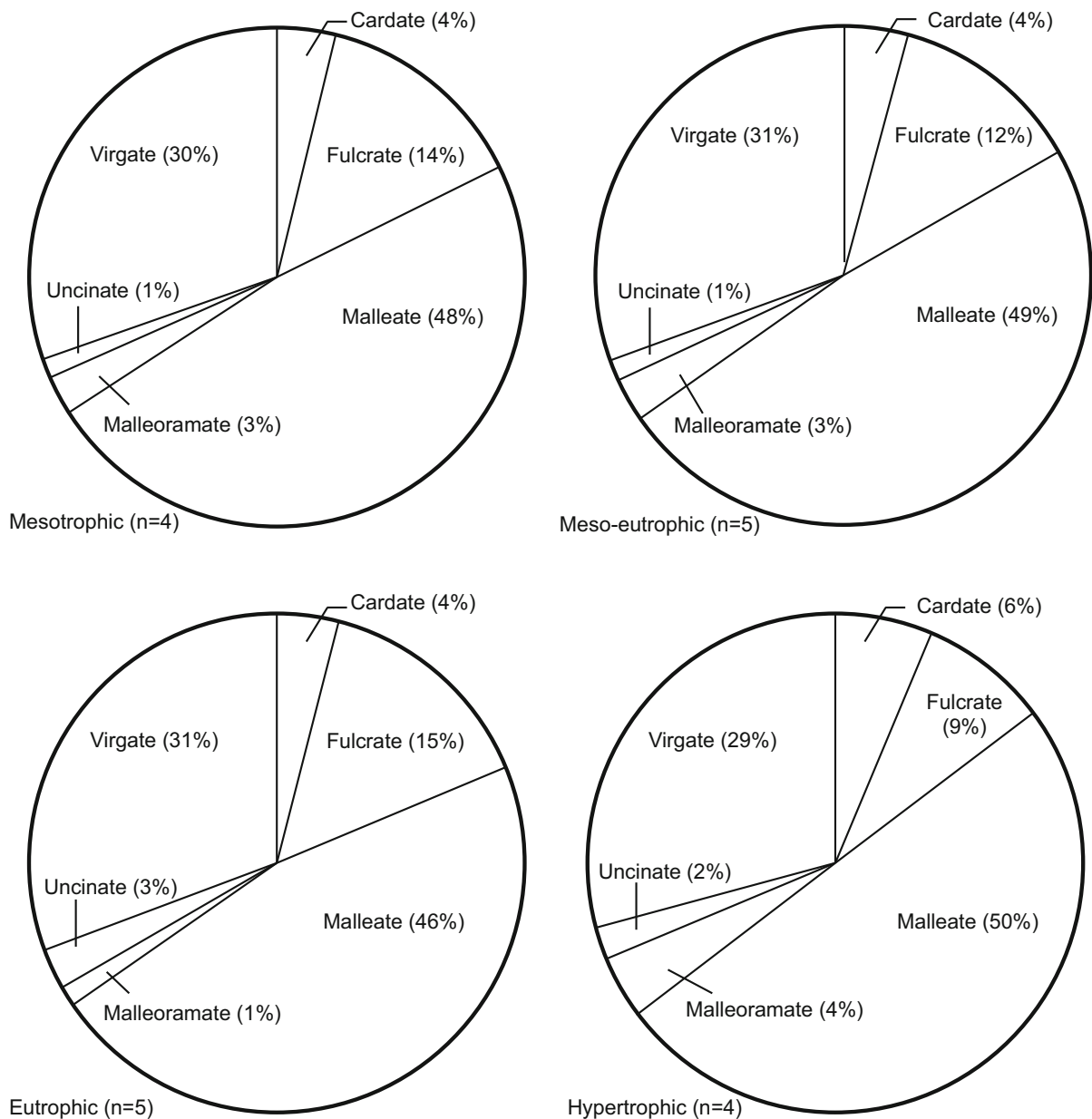


Fig. 3 Comparison of trophi types found in benthic, monogonont rotifers from 18 lakes categorized by their trophic state: mesotrophic ($n = 4$), meso-eutrophic ($n = 5$), eutrophic ($n = 5$), and hypertrophic ($n = 4$). Data from Table 7 of Ejsmont-Karabin (2003)

(Mikolajskie). These data include all taxa identified to species in the Appendix of Muirhead et al. (2006). We categorized these taxa as either (1) specimens collected from cores taken from the benthos or (2) specimens collected by 30- μ m net in open water pelagic sites and open water sites in the littoral, and also sessile species. In analyzing the rotifer species composition, we found that the frequency of benthic

taxa differed in these two lakes: 17.8% were present only in the benthos of Lake Kuc and 37.0% were present only in the benthos of Lake Mikolajskie. Using a 2×2 test of independence (G test, with Williams' correction; Sokal and Rohlf 1981) we rejected the null hypothesis that relative occurrence of rotifers in the benthos versus the other collection sites was independent of lake ($G_{adj} = 8.41$; $df = 1$; $p < 0.005$).

Table 1 Knowledge gaps in the community composition and function of benthic rotifers

Knowledge gap	Potential approaches	Selected references*
1. Too few studies include bdelloids in their analyses	Train more students in classical taxonomy, but in concert with modern techniques of molecular species identification	A
2. Do species of rotifers present in the benthos possess cosmopolitan distributions?	Use a combination of classical taxonomy and DNA bar coding and environmental DNA (eDNA) to assess the distributional patterns	B
3. Lack of experimental research limits our ability to test effects of sediment composition, e.g., depth, grain size, temperature, pH, water chemistry, toxins, and/or organic load on the assemblage of benthic rotifer communities	Establish mesocosms (with natural or artificial sediments), subjecting them to various environmental factors and/or to diverse disturbances (e.g., dose–response relationships)	C
4. We have not fully resolved the influence of the trophic state of a lake on benthic population levels or community structure	Undertake wide-ranging surveys of the benthos of lakes possessing varying trophic state from oligo- to hypertrophic, as well as lakes in desert, tropical, and tundra regions	D
5. Can the gut contents of invertebrate predators (e.g., protozoans, flatworms, insects) reveal the presence of rare rotifer taxa?	Use established microscopical techniques and emerging eDNA technology to analyze gut contents of predators that may prey on benthic rotifers	E
6. Are benthic rotifer communities (assemblages and population levels) controlled by bottom-up or top-down forces?	Initiate studies of systems with different trophic states to generate testable hypotheses about food web dynamics and the contribution of rotifers to benthic production	F
7. After disturbances (e.g., prolonged drought) are populations of benthic rotifers resupplied from adult colonists (pelagic–benthic coupling) or hatchlings from diapausing embryos?	Monitor the repopulation of systems after natural disturbance and develop mesocosm experiments	G
8. What is the relative importance of in situ reproduction versus population increase via immigration in the benthic rotifer community? Is there a seasonal reset to community structure?	Use mesocosms to perform controlled experiments pursuing conditions conducive to asexual reproduction. See also the potential approach noted in knowledge gap #2	H
9. Do psammoxene species (i.e., members of several genera: <i>Asplanchna</i> , <i>Collotheca</i> , <i>Limnias</i> , <i>Notholca</i> , and <i>Synchaeta</i>) reproduce and are they an important component to nutrient cycling?	Use mesocosms to perform controlled experiments using conditions favorable for survival and reproduction	I
10. Does mixis occur in monogononts that inhabit interstitial habitats?	Use mesocosms to perform controlled experiments under conditions favorable to mixis	J

We do not consider this list to be exhaustive, either in identifying knowledge gaps nor in presenting potential approaches that may lead to their solutions. Selected references represent studies that partially address the gaps: See also Majdi et al. (2020)

*A—Fontaneto et al. (2007). B—Curini-Galletti et al. (2012), Fontaneto (2019), Fontaneto et al. (2015) and Gansfort et al. (2020). C—Friedrich et al. (2017). D—Ejsmont-Karabin (2012). E—Nandini et al. (2011); Schmid-Araya and Schmid (2000). F—Nandini and Sarma (2005); Schmid-Araya and Schmid (1995); Schmid-Araya and Schmid (2000). G—Górski et al. (2013); Maazouzi et al. (2017). H—Ejsmont-Karabin (2005). I—Ejsmont-Karabin (2005). J—Walsh et al. (2017)

To further investigate the construct that LTS has an influence on the rotifer benthic community, we examined the distribution of the trophi types of benthic rotifers in lakes of the four trophic states defined by Ejsmont-Karabin (2003): mesotrophic, meso-eutrophic, eutrophic, and hypertrophic. While they appear similar (Fig. 3), we tested the null hypothesis that frequency occurrence of rotifer trophi

types is independent of LTS. To do this we categorized benthic rotifers according to their trophi types, i.e., cardate, forcipate, malleate + malleoramate, incudate + uncinata, and virgate. We combined the trophi types (malleate + malleoramate and incudate + uncinata) to assure that all cells in the matrix were > 0. While recognizing that collapsing trophi types may introduce taxonomic and/or phylogenetic biases, our

purpose was not to look for these signatures in the data. The purpose of this analysis was simply to determine whether rotifers with different types of trophi were present in lakes differing in trophic status. Thus, we used a RxC test of independence (G test, with Williams' correction), and we found that rotifer trophi type was independent of LTS ($G_{\text{adj}} = 3.12$; $df = 15$; $p > 0.05$). Thus, trophic state does not affect the composition of rotifer trophi types present in the benthos, at least in these systems.

Remarks and conclusions

Although application of the trophic state index has been criticized (Megard et al. 1980), it has proven to be useful in explaining the abundance of rotifers as a function of lake trophic state (Macêdo et al. 2020). As illustrated in Fig. 2, our simple analysis supports Ejsmont-Karabin's (2003) conclusion that species richness decreased as a function of increasing trophic state index. We also determined that a trait-based characteristic (trophi type) did not vary depending on lake trophic state, i.e., trophi type was similar across LTS. These results may seem incongruous as researchers such as Yoshida et al. (2003) have shown that rotifer abundance and biomass are related to food supply. However, the factors that drive zooplankton richness are more complex than simply lake productivity. In their study of 41 lakes Hoffmann and Dodson (2005) found that zooplankton species richness exhibited a positive linear relationship with productivity in pristine lakes ($n = 15$), but in developed lakes ($n = 26$) the relationship was negative.

In the studies of temperate lakes that we reviewed here, we found that lake trophic state shows a negative relationship with species richness of benthic rotifers. However, this analysis is disadvantaged by a lack of data from oligotrophic lakes. We also found that rotifer trophi types are not influenced by lake trophic state. While many factors probably influence species richness in benthic rotifers, we suggest that a missing component is food diversity (Edmondson 1965). Overall, we conclude that our current understanding of the community assembly of benthic rotifers is still inadequate and a number of knowledge gaps remain (Gansfort et al. 2020). To fill these gaps, we need questions that can develop into testable hypotheses that inform both general ecological and evolutionary

theories. In Table 1 we detail ten specific challenges and offer potential approaches that should help clarify our understanding of benthic rotifers.

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Authors' contributions Conceptualization: EJW, SSSS, SN, RLW; Methodology: SSSS, SN, RLW; Analysis: RLW, SSSS, SN; Original draft: RLW; Revisions: EJW, SSSS, SN, RLW; Funding acquisition: EJW, SSSS, SN, RLW.

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Availability of data and material The expanded list of benthic species is available in Supplemental Table S1.

Compliance with ethical standards

Conflict of interest Not applicable.

Consent to participate Each author consented to participate in the research.

Consent for publication Each author consents to publish this MS.

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