

Seasonal variability in the structure and functional diversity of psammic rotifer communities: role of environmental parameters

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Abstract Data on the variability in structure and functioning of interstitial rotifer assemblages are rare; however, this knowledge is essential for understanding their role in the interstitial food web. In the present study, we characterized psammic rotifer communities in terms of dominance structure, trophic traits, taxonomic and functional diversity at a seasonal scale in freshwater lakes across Estonia and coastal beaches of the Baltic Sea. A total of 42 rotifer species were found from the coastal beaches and 66 species from the lakes. Functional indices did not exhibit smaller seasonal variability and neither did they respond better to changes in the environment compared to taxonomic indices. However, there were differences how environmental variables affected these two broad groups of response variables. The taxonomy-based

indices of rotifer communities were primarily driven by seasonal temperature regime, sediment characteristics and anthropogenic stressors, whereas the trait-based indices were a function of ecosystem types (freshwater or brackish water). The functional indices of the psammic rotifer communities strongly distinguished between freshwater and brackish habitats indicating that rotifers have different functional roles in food webs in fresh and brackish water environments.

Keywords Psammon · Rotifers · Spatial patterns · Seasonal dynamics · Traits · Functional diversity

Introduction

Conservation of biodiversity, ecosystem functions and ecosystem services is central to sustain the planetary resources and to protect the interests of future generations. When implementing various conservation policies, it becomes very important to understand the factors that influence biodiversity patterns (Mouillot, 2007). Biodiversity's association with ecosystem functioning depends on species densities along environmental niche space and traits that each species possesses (Cadotte et al., 2011).

In community ecology, trait-based research is quite common. As trait-based research is focusing on species' ecological functions, it enables enhanced understanding and improved prediction of the

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community structure and functioning in relation to environmental conditions (McGill et al., 2006; Smith et al., 2009; Cadotte et al., 2011; Litchman et al., 2010, 2013). The types of feeding mode, locomotion, and body size are widely used traits in community analyses (a few recent examples: Obertegger & Flaim, 2015; Nordström et al., 2015; Pomerleau et al., 2015). In zooplankton, food acquisition is one of the fundamental activities that determines fitness of an organism and is related to a diverse range of traits (Litchman et al., 2013), including morphological traits.

Rotifers are microscopic aquatic metazoans that are one of the main components of freshwater zooplankton and meiobenthos, where they contribute significantly to the total biomass and play a key role in energy transfer (Nogrady et al., 1993; Wallace, 2002). Moreover, rotifers can reach high numbers and have an important role in thalassic food webs (Mallin & Paerl, 1994; Saunders-Davies, 1998; Ikauniece, 2001). Rotifers are ideal test organisms for analysing relationships between habitat, community structure and trait-based functioning because it is known that they are abundant, diverse, and cosmopolitan to a large extent as well as they are sensitive to changes in the environment (Pejler, 1995; Segers, 2008). Although there exists a considerable overlap in the taxonomic composition of rotifer communities along a salinity gradient from freshwater to marine ecosystems (Thane-Fenchel, 1968; Lokko et al., 2014a), differences in size and dominance structure indicate different roles of rotifers in saltwater and freshwater environments (Paturej & Gutkowska, 2015).

Trait-based approaches, where species have been grouped into functional guilds according to their feeding types, have been used in a number of studies focusing on plankton communities, including planktonic rotifers (e.g., Špoljar et al., 2005, 2011; Virro et al., 2009; Litchman et al., 2010, 2013; Obertegger & Manca, 2011; Obertegger & Flaim, 2015). However, trait-based studies on interstitial meiofauna are almost lacking (e.g., Lokko & Virro, 2014; Ristau et al., 2015). Based on rotifer feeding strategies, Smith et al. (2009) introduced the Guild Ratio as the ratio of raptorial rotifers to microphagous species. The standardized Guild Ratio or Guild Ratio Index (GRI) (Obertegger et al., 2011) provides valuable insights into relationships between the environment, community structure, and ecosystem processes. GRI values range from -1 to $+1$ with positive values indicating

dominance of raptorial rotifers and negative values dominance of microphagous rotifers, respectively (Obertegger et al., 2011). GRI has several advantages over traditional diversity indices: it requires lower taxonomic resolution, focuses on functional aspects and the domination pattern can be captured even with lower sampling resolution (Obertegger et al., 2011).

Sandy beaches are dynamic environments that host considerably variegated biota. The psammic habitat (often referred to as *arenal* or *psammolittoral zone* in lakes) includes only narrow beach zones, most of which are regularly exposed to air for a longer or shorter period of time; only the hydroarenal zone is permanently covered with a thin water layer. In general, rotifers are very abundant in psammic habitats (Pejler, 1995; Schmid-Araya, 1998; Fontaneto et al., 2006; Covazzi Harriague et al., 2013; Lokko et al., 2014a, b) where they significantly contribute to the transfer of energy and matter between terrestrial and aquatic ecosystems. The psammon has received little attention compared to lower littoral and sublittoral meiobenthos, and thus we know very little on the structure and functioning of rotifer communities in these habitats (Pejler, 1995).

Seasonal variability is considered one of the most important factors for psammic organisms. The abundances of psammon rotifer communities are temporally very variable (e.g., Ejsmont-Karabin, 2001, 2005), driven by changes in water temperature, life cycles and/or feeding conditions (Lokko et al., 2013). Such seasonality varies among sites (Lokko et al., 2014b) and between years (Jordan et al., 1999). Community indices, especially trait-based indices, are expected to reasonably buffer the randomness of temporal variability component and thus give a generic view on rotifers' seasonality (e.g., Lokko & Virro, 2014). In general, due to considerable workload, multi-annual studies focusing on seasonality are rare for interstitial rotifers, and thus it is difficult to generalize their seasonal patterns in taxonomic composition, dominance and functioning. As the taxonomic composition may vary between years and sites, trait-based indices can reveal patterns and shifts in community functioning better than taxon-related metrics (e.g., Obertegger et al., 2011).

The objective of this study was to compare the dominance structure, taxonomic diversity and functional indicators of rotifer communities and explore seasonal changes in these parameters. We also

assessed the roles of different environmental forcing and anthropogenic pressures on patterns of taxonomic diversity and functioning of the psammic rotifer communities within the studied ecosystems. We expected that trait-based indices are seasonally less variable, compared to taxonomy-based composition or dominance assessment. Thereby, trait-based indices would be more robust to capture seasonal dynamics of rotifers as well as to link environmental change to the patterns of rotifers. This study was performed in fresh and brackish water psammic habitats to give a generic overview on the roles of psammic rotifers across different ecosystems.

Materials and methods

Study area

The study area encompasses three lakes with different trophic statuses, sand grain structures and anthropogenic impacts and three sandy beaches with different salinities, sand grain structures, and anthropogenic impacts along the Estonian coast of the Gulf of Finland, Baltic Sea (Fig. 1). The studied lakes belong to the same East Estonian drainage basin and are all characterized by moderately alkaline waters. The mesotrophic Lake Saadjärv is characterized by high water transparency, high hardness and slightly alkaline water (Ott, 2007). It is the deepest (maximum depth 25 m, surface area 707.6 ha; Mäemets, 1977) and has the lowest trophic status of the studied lakes. The sampling site was located at a relatively popular beach nearby a motorway. The eutrophic Lake Võrtsjärv is a large shallow lake (second largest in Estonia—surface area 27,000 ha; maximum depth 6 m) with its water exchanging completely every year (Tuvikene et al., 2004). The sampling site at Lake Võrtsjärv was located in a remote locality at the eastern coast of the lake. The hypertrophic Lake Verevi is the smallest of the studied lakes and relatively deep (maximum 11 m, average 3.6 m; surface area 12.6 ha) with a lower water exchange rate (water exchange 0.63-times per year; Loopmann, 1984; Ott et al., 2005). It is located in the small town of Elva and is very much used by swimmers. The lake was sampled at the edge of the popular beach.

The Gulf of Finland has a relatively large freshwater inflow; therefore, the gulf has a strong horizontal

salinity gradient. The surface salinity in the gulf varies from 0 at its eastern end to 7 ppt in the western areas (Pitkänen et al., 2008). Also the nutrients input and trophic state increase from west to east, and the gulf is considered one of the most eutrophicated basins in the Baltic Sea area (HELCOM, 2003; Pitkänen et al., 2007). The coastal sampling sites were located at Keibu Bay near Nõva village (Nõva Beach), at Pirita Beach within Tallinn City and at Narva Bay adjacent to the small town of Narva-Jõesuu (Narva-Jõesuu Beach). The most remote beach among the studied coastal beaches is Nõva Beach, located within a landscape protection area, and only occasionally used by swimmers. The anthropogenic impact is greatest at Pirita Beach as it is a very popular beach, located nearby a harbour within the capital city of Estonia. The flat Narva-Jõesuu Beach is also popular among swimmers.

Sampling

The sampling was conducted during 2011–2012. At each sampling site, the samples were taken monthly, during the vegetation period from April until October, with a sharp-edged corer with a 4.75 cm inner diameter and to a depth of 5 cm in the sand. The samples were collected along transects across the waterline up to 50 cm from the waterline in both directions. Each transect was divided into three zones: hydroarenal—permanently submerged sediment; hygroarenal—wet sand strip at the edge of the waterline; euarenal—beach sands upward the latter. Two samples were collected from each zone. Altogether 231 samples were collected. We missed some samples from lakes Võrtsjärv and Verevi, as the water level fluctuated greatly during the vegetation period and occasionally a sandy beach became too narrow or contained too much coarse sediment to be quantitatively sampled.

Animals were extracted by decantation. Each sample was transferred to a plastic container, and immediately rinsed three times with carbonated drinking water. After each rinse, the supernatant was poured off into a plastic bottle. Then the samples were fixed with Lugol's solution. Next, the samples were filtered through a 42- μ m plankton net to remove fine detritus particles and the samples were taken to 100 ml.



Fig. 1 Study area and location of the sampling stations (*blue dots*—coastal beaches; *red dots*—lake beaches)

From each sample, five 2 ml subsamples were taken to count all organisms under a microscope in a Bogorov chamber. For identification, the specimens were slide mounted in glycerol and determined to the lowest possible taxon using an Olympus BX 50 microscope. Illoricate rotifers were identified by their trophi which were dissolved out using household disinfectant Domestos® containing sodium hypochlorite (NaClO <5%).

For each sampling, additional samples for grain size, chlorophyll *a* and organic content of the sediment were collected. Care was taken that only samples without macrofauna were further analysed. Air, water and sand temperature, pH, salinity (in coastal beaches) and conductivity were measured. Wave activity was estimated to 10 points scale with 1 being weakest and 10 strongest waves, respectively. Vegetation cover was visually evaluated along a transect by means of 25-cm-edged square. In addition, the number of people at the beach segment was evaluated.

Sediment grain size was determined using sieving techniques. The following sieves were used: 2, 1, 0.5,

0.25 and 0.125 mm. The software Gradistat, version 8 (Blott & Pye, 2001) was used to calculate sorting and to obtain the mean percentages of different sediment fractions. The content of sediment organic matter was measured as a loss of ignition at 500 °C during 3 h. Chlorophyll *a* samples were extracted in 96% ethanol overnight. Chlorophyll *a* was quantified fluorometrically correcting for phaeopigments (Strickland & Parsons, 1972).

Data analysis

We used total abundance, taxonomic richness (total number of individuals found from sampling site and number of taxa per sample), and Shannon index to describe the patterns of dominance and taxonomic diversity of rotifer communities. Shannon index has been widely used in community ecology including psammic rotifer studies (e.g., Bielańska-Grajner, 2001, 2005; Ejsmont-Karabin, 2005).

In addition to the structural indices described above and following Obertegger & Flaim (2015), we focused

on the following functional traits associated with rotifers feeding and locomotion: body size, corona type, trophi type and general feeding mode. These traits were used to calculate Rao's quadratic entropy to assess the functional diversity in different sampling sites and seasons. The rotifers were assigned to three size classes according to their body size (biovolume). These estimates were based on direct measurements and mid-range sizes obtained from taxonomical keys (Kutikova, 1970; Segers, 1995; Nogrady et al., 1995; De Smet, 1996; De Smet & Pourriot, 1997). In small aquatic organisms, body size is an important trait related to feeding and predation pressure (Hansen et al., 1997; Lapesa et al., 2002). As for rotifers it determines the size of preferred food (Rothhaupt, 1990), maximum particle range that a rotifer can ingest (Bogdan & Gilbert, 1984) and is also related to the swimming speed (Salt, 1987). The biomasses of rotifers were estimated by using biovolume equations developed by Ruttner-Kolisko (1977) based on the mid-range size estimates as reported in the different guides (Segers, 1995; Nogrady et al., 1995; De Smet, 1996; De Smet & Pourriot, 1997) for taxa of *Cephalodella*, *Dicranophorus*, *Encentrum*, *Gastropus*, *Lecane*, *Polyarthra*, *Wierzejskiella*, Kutikova (1970) for *Colurella*, *Keratella*, *Lepadella*, *Notholca*, *Trichocerca*, and unpublished data (T. Virro) for bdelloids. The nomenclature of rotifer species follows Jersabek et al. (2015). The species found in the present study were divided into three size classes based on their body mass: small ($<0.08 \mu\text{g}$), medium ($0.08\text{--}0.34 \mu\text{g}$), and large ($>0.34 \mu\text{g}$). The 33rd and 66th percentiles of the rotifers' size distribution were used to define borderlines between classes.

Another trait associated with feeding and locomotion is the corona type. The corona is a ciliary apparatus that a rotifer uses for gathering food and in locomotion (Koste & Shiel, 1987). The corona is also related to the size of the perceptual field (Salt, 1987). Altogether seven types of corona are distinguished: *Notommata* type, *Philodina* type, *Asplanchna* type, *Euchlanis-Brachionus* type, *Conochilus* type, *Hexarthra* type, *Collotheca* type (Koste & Shiel, 1987).

The structure of trophi (jaws) determines how and which food items rotifers can handle. While trophi have species-specific features (and thus play an important role in identification), some generic types can be distinguished. Rotifers with virgate and cardate trophi actively pierce and/or pump out a food item,

whereas forcipate trophi are used to seize and grasp (Koste & Shiel, 1987). Rotifers with malleate and ramate trophi collect multiple small food items and use the trophi to cut and chew (Koste & Shiel, 1987; Nogrady et al., 1993).

A general feeding mode is the strategy how a rotifer gathers food. Two main feeding strategies have been distinguished: catching and handling larger food (prey) items individually or collecting several small food items at the same time (Smith et al., 2009; Obertegger et al., 2011).

The guild ratio index (GRI) (Obertegger et al., 2011) was employed to analyse the trophic structure of rotifer communities as it reflects the general feeding mode. The biomasses of rotifer taxa were pooled into functional feeding groups (guilds) of microphagous sedimentators and raptorial feeders according to their trophi types (based on Kutikova, 1970; Hillbricht-Ilkowska, 1983; Nogrady et al., 1993; Špoljar et al., 2005; Obertegger et al., 2011; Table 1). The genera with malleate or ramate trophi were assigned to microphagous sedimentators. The genera with virgate, cardate or forcipate trophi were classified as raptorial rotifers. In Proalidae, the trophi type varies also within genera, e.g., *Proales* species may fall into the types of malleate, virgate or anything in between whereas *Proalopsis* species may include virgate or intermediate types of malleate and virgate trophi (De Smet, 1996). Thus, species from these genera were classified based on their actual trophi type and known food objects. *Proales theodora* and *P. globulifera* were classified as microphagous species. The former has malleate trophi and consumes detritus, bacteria, diatoms and dinoflagellates (De Smet, 1996), the latter is known to feed on small diatoms (De Smet, 1996; Jersabek & Leitner, 2013). *Proales halophila* and *P. reinhardti* have similar trophi of the modified malleate-virgate type and have been observed to feed on large food items, e.g., diatoms up to $150 \mu\text{m}$ (Jansson, 1967; Thane-Fenchel, 1968; Litton, 1983; Lokko, personal observations) and were thus classified as raptors.

Rao's quadratic entropy (Q) has been suggested as one of the most promising measures of community functional diversity as it includes species abundances and more than one trait (Botta-Dukát, 2005; Lepš et al., 2006). Q expresses the mean distance between two randomly selected individuals and allows to estimate functional diversity of a community by

Table 1 Psammic rotifers from the studied lake and coastal beaches

	Lake Saadjärv	Lake Verevi	Lake Võrtsjärv	Nõva beach	Pirita beach	Narva-Jõesuu beach	Feeding type	Body size class	Corona type	Trophi type
<i>Bdelloidea</i> gen. et spp. indet.	x	x	x	x	x	x	Microphagous	M	Philodina	Ramate
<i>Cephalodella catellina</i> (Müller, 1786)	x						Raptorial	M	Notommata	Virgate
<i>Cephalodella delicata</i> (Wulfert, 1937)		x					Raptorial	M	Notommata	Virgate
<i>Cephalodella forficula</i> (Ehrenberg, 1838)			x				Raptorial	L	Notommata	Virgate
<i>Cephalodella gibba</i> (Ehrenberg, 1830)	x	x	x				Raptorial	L	Notommata	Virgate
<i>Cephalodella gracilis</i> (Ehrenberg, 1830)	x						Raptorial	M	Notommata	Virgate
<i>Cephalodella labiosa</i> (Wulfert, 1940)	x						Raptorial	M	Notommata	Virgate
<i>Cephalodella limosa</i> (Wulfert, 1937)		x					Raptorial	M	Notommata	Virgate
<i>Cephalodella megaloccephala</i> (Glascock, 1893)		x	x				Raptorial	M	Notommata	Virgate
<i>Cephalodella</i> spp.	x	x	x			x	Raptorial	L	Notommata	Virgate
<i>Cephalodella stercora</i> (Gosse, 1887)		x	x				Raptorial	L	Notommata	Virgate
<i>Cephalodella tinca</i> (Wulfert, 1937)		x	x			x	Raptorial	L	Notommata	Virgate
<i>Cephalodella ventripes</i> (Dixon-Nuttall, 1901)		x					Raptorial	M	Notommata	Virgate
<i>Colurella adriatica</i> (Ehrenberg, 1831)	x		x				Raptorial	M	Notommata	Virgate
<i>Colurella colurus</i> (Ehrenberg, 1830)	x		x	x			Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Colurella dicentra</i> (Gosse, 1887)			x	x			Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Colurella geophila</i> (Donner, 1951)				x			Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Colurella hindenburgi</i> (Steinecke, 1916)				x			Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Colurella marinovi</i> (Althaus, 1957)				x		x	Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Colurella</i> spp.	x	x	x				Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Colurella uncinata</i> (Müller, 1773)		x					Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Dicranophorus capucinus</i> (Harring & Myers, 1928)	x		x				Raptorial	L	Notommata	Forcipate
<i>Dicranophorus grandis</i> (Ehrenberg, 1832)		x					Raptorial	L	Notommata	Forcipate
<i>Dicranophorus hercules</i> (Wiszniewski, 1932)	x		x				Raptorial	L	Notommata	Forcipate
<i>Dicranophorus leptodon</i> (Wiszniewski, 1934)			x				Raptorial	M	Notommata	Forcipate
<i>Dicranophorus</i> cf. <i>luetkeni</i> (Bergendal, 1892)			x				Raptorial	L	Notommata	Forcipate
<i>Disostrocha aculeata</i> (Ehrenberg, 1832)		x					Microphagous	M	Philodina	Ramate
<i>Enicentrum</i> cf. <i>belluinum</i> (Harring & Myers, 1928)				x	x	x	Raptorial	M	Notommata	Forcipate
<i>Enicentrum</i> cf. <i>boreale</i> (Harring & Myers, 1928)				x			Raptorial	L	Notommata	Forcipate
<i>Enicentrum</i> cf. <i>fluviatile</i> (Wulfert, 1939)		x					Raptorial	S	Notommata	Forcipate
<i>Enicentrum graingeri</i> (Chengalath, 1985)						x	Raptorial	L	Notommata	Forcipate
<i>Enicentrum limicola</i> (Otto, 1936)				x			Raptorial	L	Notommata	Forcipate
<i>Enicentrum</i> cf. <i>limicola</i> (Otto, 1936)				x	x	x	Raptorial	M	Notommata	Forcipate

Table 1 continued

	Lake Saadjärv	Lake Verevi	Lake Võrtsjärv	Nõva beach	Pirita beach	Narva-Jõesuu beach	Feeding type	Body size class	Corona type	Troph type
<i>Encentrum marinum</i> (Dujardin, 1841)				x	x	x	Raptorial	M	Notommata	Forcipate
<i>Encentrum martoides</i> (Fott, 1960)					x		Raptorial	M	Notommata	Forcipate
<i>Encentrum mathesi</i> (Remane, 1949)				x		x	Raptorial	M	Notommata	Forcipate
<i>Encentrum</i> sp. 1						x	Raptorial	L	Notommata	Forcipate
<i>Encentrum villosum</i> (Harring & Myers, 1928)						x	Raptorial	L	Notommata	Forcipate
<i>Euchlanis dilatata</i> (Ehrenberg, 1832)	x						Microphagous	L	Euchlanis-Brachionus	Sub-Malleate
<i>Keratella cochlearis</i> (Gosse, 1851)	x	x	x		x	x	Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Keratella cruciformis</i> (Thompson, 1892)				x			Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Keratella quadrata</i> (Müller, 1786)				x	x		Microphagous	L	Euchlanis-Brachionus	Malleate
<i>Lecane bulla</i> (Gosse, 1851)		x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane closteroerca</i> (Schmarda, 1859)		x	x				Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane doryssa</i> (Harring, 1914)	x	x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane elongata</i> (Harring & Myers, 1926)		x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane flexilis</i> (Gosse, 1886)							Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane furcata</i> (Murray, 1913)	x	x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane hamata</i> (Stokes, 1896)	x	x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane luna</i> (Müller, 1776)	x	x		x			Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Lecane lunaris</i> (Ehrenberg, 1832)		x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane nana</i> (Murray, 1913)						x	Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane perpusilla</i> (Hauer, 1929)		x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane psammophila</i> (Wisniewski, 1932)	x		x			x	Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane punctata</i> (Murray, 1913)		x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane pusilla</i> (Harring, 1914)		x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane scutata</i> (Harring & Myers, 1926)	x	x	x				Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane stenroosi</i> (Meisner, 1908)		x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lecane tenuiseta</i> (Harring, 1914)		x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lepadella ovalis</i> (Müller, 1786)			x				Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lepadella patella</i> (Müller, 1773)		x	x				Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lepadella</i> spp.	x	x	x	x			Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Lindia janickii</i> (Wisniewski, 1934)				x			Raptorial	L	Notommata	Cardate
<i>Lindia torulosa</i> (Dujardin, 1841)		x		x		x	Raptorial	L	Notommata	Cardate
<i>Lophocharis oxyteron</i> (Gosse, 1851)		x					Microphagous	S	Euchlanis-Brachionus	Malleate
<i>Monommata</i> sp.		x					Raptorial	S	Notommata	Virgate/Virgate-Forcipate

Table 1 continued

	Lake Saadjärv	Lake Verevi	Lake Võrtsjärv	Nõva beach	Pirita beach	Narva-Jõesuu beach	Feeding type	Body size class	Corona type	Trophi type
<i>Mytilina mucronata</i> (Müller, 1773)	x						Microphagous	L	Euchlanis-Brachionus	Malleate
<i>Mytilina ventralis</i> (Ehrenberg, 1832)		x					Microphagous	L	Euchlanis-Brachionus	Malleate
<i>Notholea squamula</i> (Müller, 1786)				x			Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Notommata aurita</i> (Müller, 1786)		x					Raptorial	L	Notommata	Virgate
<i>Notommata cyrtopus</i> (Gosse, 1886)	x						Raptorial	L	Notommata	Virgate
<i>Notommata</i> cf. <i>doneta</i> (Harring & Myers, 1924)				x			Raptorial	M	Notommata	Virgate
<i>Philodina roseola</i> (Ehrenberg, 1832)		x					Microphagous	M	Philodina	Ramate
<i>Proales globulifera</i> (Hauer, 1921)				x	x	x	Microphagous	L	Notommata	Malleate- Virgate
<i>Proales halophila</i> (Remane, 1929)				x	x		Raptorial	L	Notommata	Malleate- Virgate
<i>Proales reinhardtii</i> (Ehrenberg, 1834)				x	x	x	Raptorial	L	Notommata	Malleate- Virgate
<i>Proales theodora</i> (Gosse, 1887)				x	x		Microphagous	L	Notommata	Malleate
<i>Proalinopsis caudatus</i> (Collins, 1872)				x	x		Raptorial	L	Notommata	Virgate
<i>Synchaeta cecilia</i> (Rousselet, 1902)				x		x	Raptorial	L	Asplanchna	Virgate
<i>Synchaeta</i> spp.		x					Raptorial	L	Asplanchna	Virgate
<i>Synchaeta tremula</i> (Müller, 1786)						x	Raptorial	L	Asplanchna	Virgate
<i>Trichocerca dixomutalli</i> (Jennings, 1903)	x		x	x	x		Raptorial	S	Asplanchna	Virgate
<i>Trichocerca obtusidens</i> (Olofsson, 1918)	x		x				Raptorial	M	Asplanchna	Virgate
<i>Trichocerca porcellus</i> (Gosse, 1851)		x					Raptorial	M	Asplanchna	Virgate
<i>Trichocerca similis</i> (Wierzejski, 1893)				x		x	Raptorial	M	Asplanchna	Virgate
<i>Trichocerca tenuidens</i> (Hauer, 1931)	x						Raptorial	M	Asplanchna	Virgate
<i>Trichocerca tenuior</i> (Gosse, 1886)	x		x	x	x		Raptorial	M	Asplanchna	Virgate
<i>Trichotria pocillum</i> (Müller, 1776)	x	x					Raptorial	M	Asplanchna	Virgate
<i>Trichotria truncata</i> (Whitelegge, 1889)							Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Wierzejskiella sabulosa</i> (Wiszniewski, 1932)			x		x		Microphagous	M	Euchlanis-Brachionus	Malleate
<i>Wierzejskiella velox</i> (Wiszniewski, 1932)	x		x				Raptorial	L	Notommata	Forcipate
<i>Wigrella depressa</i> (Wiszniewski, 1932)	x		x				Raptorial	L	Notommata	Forcipate
Total	29	40	27	28	16	26				

The code of the body size class is as follows: *S* small rotifers, *M* medium-sized rotifers, *L* large rotifers. The species found in the present study were divided into three size classes based on their body mass: small (<0.08 µg), medium (0.08–0.34 µg), and large (>0.34 µg)

combining the dispersion of species in trait space and the relative abundances of species (Botta-Dukát, 2005; Laliberté & Legendre, 2010). Q was calculated based on the following traits: body size (size class), corona type, trophi type, general feeding mode. As a measure of dissimilarity among the trait composition present in a community, the square root of the one-complement of Gowers similarity index was calculated, which is equivalent to a dissimilarity matrix with Euclidean metric properties. Package FD (Laliberté & Legendre, 2010; Laliberté et al., 2014) in the statistical software R (The R Foundation for Statistical Computing, 2014) was used to calculate Q .

Boosted Regression Trees (BRT) modelling (Elith et al., 2008) in R was used to assess relationships between environmental parameters and taxonomic and functional diversity of rotifer communities. In the R environment, packages gbm and dismo were used for BRT (Hijmans et al., 2014; Ridgeway et al., 2015). BRT is a modelling tool that incorporates algorithms of machine learning and properties of traditional statistics. BRT is capable of handling different types of predictor variables, it is not sensitive to outliers or missing data and yet the results are relatively easy to interpret. Another advantage of the BRT models is their superior predictive performance compared to most traditional modelling methods, making it possible to not only explain the relations between the biota and the environment, but also to predict the patterns (Elith et al., 2006, 2008). The BRT iteratively develops a large ensemble of small regression trees constructed from random subsets of the data. Each successive tree predicts the residuals from the previous tree to gradually boost the predictive performance of the overall model. In fitting a BRT, the learning rate and the tree complexity must be specified. The learning rate determines the contribution of each successive tree to the final model, as it proceeds through the iterations. The tree complexity fixes whether only main effects (tree complexity = 1) or interactions are also included (tree complexity > 1). Ultimately, the learning rate and tree complexity combined determine the total number of trees in the final model.

For BRT modelling, the independent variables were sampling site, distance from waterline, chlorophyll *a*, organic content, vegetation coverage, porewater conductivity, porewater salinity, pH, sand temperature, wave activity, trampling intensity (levels: deserted,

few, tens, hundreds of people), sand coarseness (levels: fine, medium, coarse), sand sorting (levels: poorly sorted, medium sorted, medium well sorted, well sorted, very well sorted), mean particle size, percentage of silt, coarse, medium and fine sand. Multiple models were run at the model learning rate 0.01 and 0.001 with an interaction depth (tree complexity) of 5 and a bag fraction of 0.5. The optimum model was selected based on model performance. Model performance was evaluated using the cross validation statistics calculated during model fitting (Hastie et al., 2001). A random 20 % of the data was assigned for testing model accuracy.

In order to supplement BRT analyses the repeated measures permutational two-way ANOVA was used to detect differences in the environmental parameters, GRI, Q and Shannon diversity index values between ecosystem types (coastal vs. lake beach) and study sites (nested in ecosystem types). The permutational analysis was used as the data did not follow the assumptions of traditional ANOVA. We used the package Primer Permanova version 7.0.10 (Anderson et al., 2008) and the analyses were based on Euclidean distances.

Results

Environmental variables

In the sampled coastal beaches, mean sediment particle size decreased from west to east and varied during vegetation period (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} = 0.001$ and $p_{\text{Month}} = 0.001$). There were significant differences in sediment sorting between coastal beaches, but this pattern did not follow the longitudinal gradient as in sediment grain size. Instead, the highest values were found in the easternmost beach and the lowest sorting in the central beach, respectively (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} = 0.001$; Table 2). Salinity and conductivity were similar on Nõva and Pirita beaches, but substantially lower on Narva-Jõesuu Beach (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} = 0.001$). Sand chlorophyll *a* also differed among beaches with the lowest values found in the Narva-Jõesuu Beach (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} = 0.001$). Porewater pH and sand organic

Table 2 The timing of sampling and general characteristics of the sampling sites. Variable mean (continuous variables) or most common value (categorical variables); minimum and maximum value or variable range is shown in brackets

	Vörtsjärv	Saadjärv	Verevi	Növa	Pirita	Narva-Jõesuu
Sampling time	May–Oct 2011, Apr 2012	May–Oct 2011, Apr 2012	May–Oct 2011, Apr 2012	May–Oct 2011, Apr 2012	May–Oct 2011, Apr 2012	May–Oct 2011, Apr 2012
Sampling site coordinates	58°13'45"N; 26°07'17"E	58°31'41"N; 26°41'45"E	58°13'44"N; 26°24'21"E	59°13'45"N; 23°42'8"E	59°28'11"N; 24°49'38"E	59°27'8"N; 28°1'18"E
Median diameter of sand grains (µm)	596 (202–1796)	618 (386–1679)	309 (222–907)	619 (196–1790)	402 (176–876)	189 (173–219)
Vegetation cover (%)	15 (0–50)	11 (0–60)	19 (2–40)	0 (0–12)	0	0 (0–100)
pH range (interstitial)	7.64 (6.77–9.5)	7.80 (6.92–9.4)	7.42 (6.63–7.98)	8.19 (6.68–9.11)	7.86 (7.67–8.34)	8.18 (7.57–8.7)
Porewater conductivity (mS)	0.579 (0.446–0.775)	0.626 (0.399–0.942)	0.629 (0.513–0.711)	11.05 (9.09–12.43)	11.19 (7.19–12.80)	5.46 (0.72–9.09)
Porewater salinity (ppt)	NA	NA	NA	5.41 (4–6.2)	5.46 (3–6.6)	2.4 (0–4)
Sand temperature range (°C)	19.9 (8.7–30.2)	16.6 (5.1–28.3)	20.1 (7.7–32)	15.67 (6.2–23.2)	15.16 (6–22.6)	14.99 (5.2–23.6)
Sand chlorophyll <i>a</i> content	2.86 (0–10.20)	3.18 (0–21.27)	3.08 (0.58–13.11)	3.58 (0–20.69)	2.91 (0.29–13.99)	1.08 (0–3.79)
Sand organic content (%)	1.06 (0.22–7.39)	0.72 (0.33–3.18)	0.85 (0.22–4.77)	0.53 (0.07–4.09)	0.59 (0.06–2.87)	0.48 (0.04–2.43)

content were not significantly different among beaches (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} > 0.05$).

In the sampled lake beaches, mean sediment particle size was the smallest in Lake Verevi beach, where the sediment sorting was also the lowest (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} = 0.009$ for mean sediment particle size and $p_{\text{Study site}} = 0.002$ for sediment sorting). The mean porewater pH was similar in all sampled lake beaches, but the porewater pH varied considerably in Lake Saadjärv and in Lake Vörtsjärv during the vegetation period (two-way repeated measures permutational ANOVA, $p_{\text{Month}} = 0.006$). Sediment organic matter content varied during vegetation period and was the highest in Lake Verevi beach and the lowest at the Lake Saadjärv beach (two-way repeated measures permutational ANOVA, $p_{\text{Month}} = 0.013$ and $p_{\text{Study site}} = 0.007$).

Abundance and community composition of psammic rotifers

A total of 88 rotifer taxa were identified from the studied beaches: 42 taxa from coastal beaches and 66

taxa from lake beaches (Table 1). The dominating genera were different in coastal and lake beaches. The most abundant taxa in coastal beaches were *Colurella*, *Encentrum*, *Proales* and *Trichocerca* (mean abundances during the vegetation period were 0.52 ± 0.20 , 0.18 ± 0.04 , 0.28 ± 0.10 , 0.31 ± 0.16 ind. $\text{cm}^{-3} \pm \text{SE}$, respectively), whereas the predominant rotifer taxa in lakes were *Bdelloidea* and *Lecane* (mean abundances during the vegetation period were 0.36 ± 0.05 and 0.39 ± 0.06 ind. $\text{cm}^{-3} \pm \text{SE}$, respectively). We observed several infrequently reported species in our material (Supplementary Figs. S1–S7). *Colurella marinovi* and *E. matthesi* were represented only by a few specimens in coastal beaches. We found also several specimens resembling *Encentrum belluinum* (designated as *E. cf. belluinum* in Table 1). From the lake beaches, we found single specimen of *Dicranophorus leptodon*, and specimens close to *D. luetkeni* (*D. cf. luetkeni* in Table 1) and *Encentrum fluviatile*.

Seasonal patterns of abundance varied from beach to beach, but were low in early spring and late autumn (Fig. 2). Abundances were generally comparable in coastal beaches and lake beaches (two-way repeated measures permutational ANOVA, $p_{\text{Ecosystem type}} > 0.05$), only in Növa Beach the abundances were much

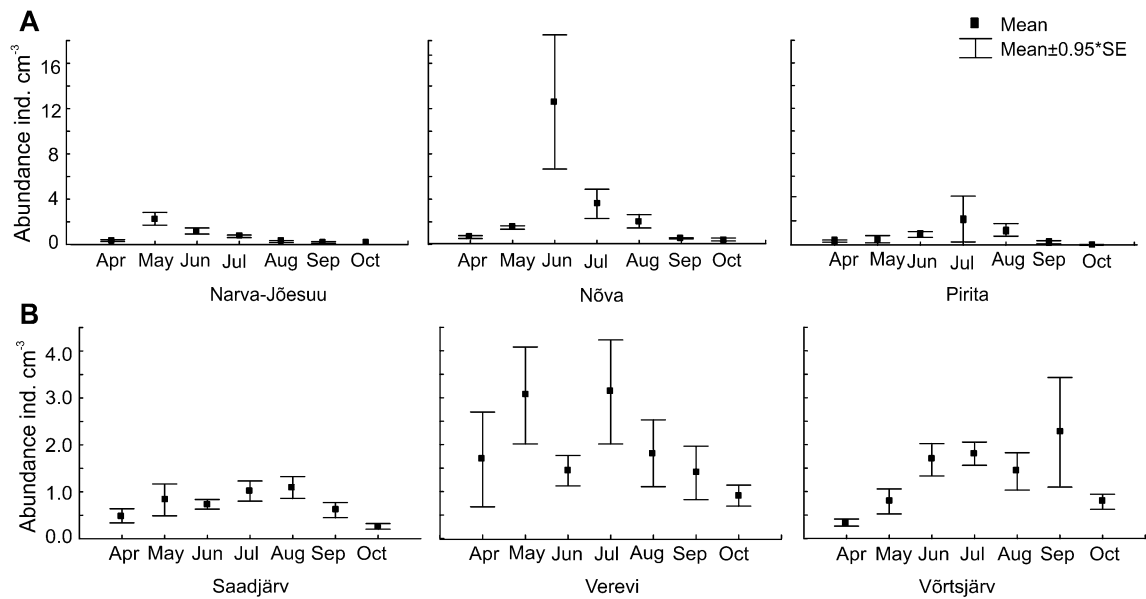


Fig. 2 Average density of psammic rotifers (\pm SE) in the studied beaches in 2011–2012 (A—coastal beaches; B—lake beaches)

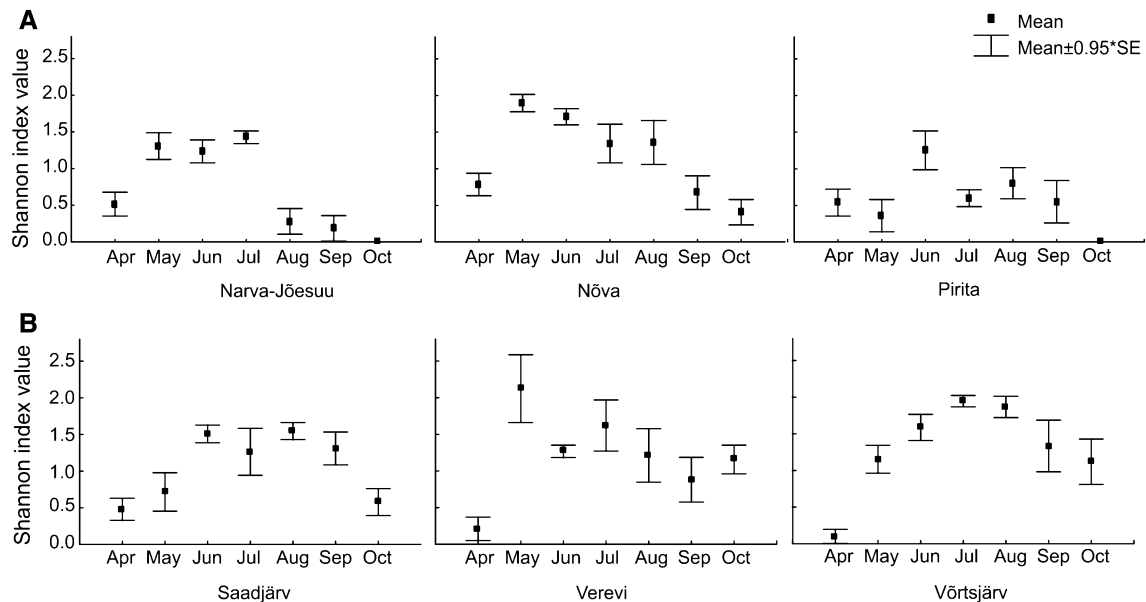


Fig. 3 Seasonal variability in the Shannon diversity index values (\pm SE) in 2011–2012 (A coastal beaches; B lake beaches)

higher (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} = 0.017$, difference between Nõva and other study sites at $p < 0.05$). Species abundances were highly variable with no clear patterns of seasonality.

Overall taxonomic richness and Shannon index values were similar both in coastal beaches and lake

beaches (two-way repeated measures permutational ANOVA, $p_{\text{Ecosystem type}} > 0.05$ for both), whereas Shannon index values peaked earlier than in lake beaches (Fig. 3). Shannon index values differed significantly among sampled beaches (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} = 0.023$), with highest values estimated at the remote

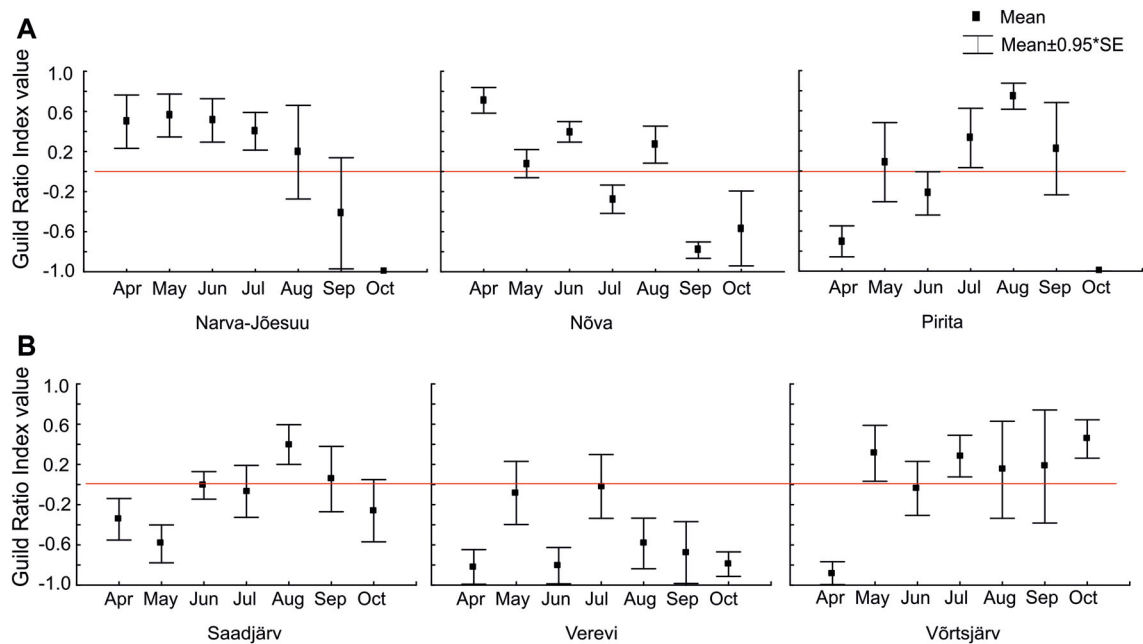


Fig. 4 Seasonal variability in the Guild Ratio index values (\pm SE) in 2011–2012. Positive values (above horizontal red line) indicate dominance of raptorial rotifers and negative values indicate microphagous dominance. (A coastal beaches; B lake beaches)

Nõva Beach and the lowest values at Pirita Beach among the coastal beaches. In lake beaches, Shannon index was the highest at Lake Võrtsjärv and lowest at

the mesotrophic Lake Saadjärv. In general, Shannon index values were highest in the warm season, but in Lake Verevi, it peaked already in May.

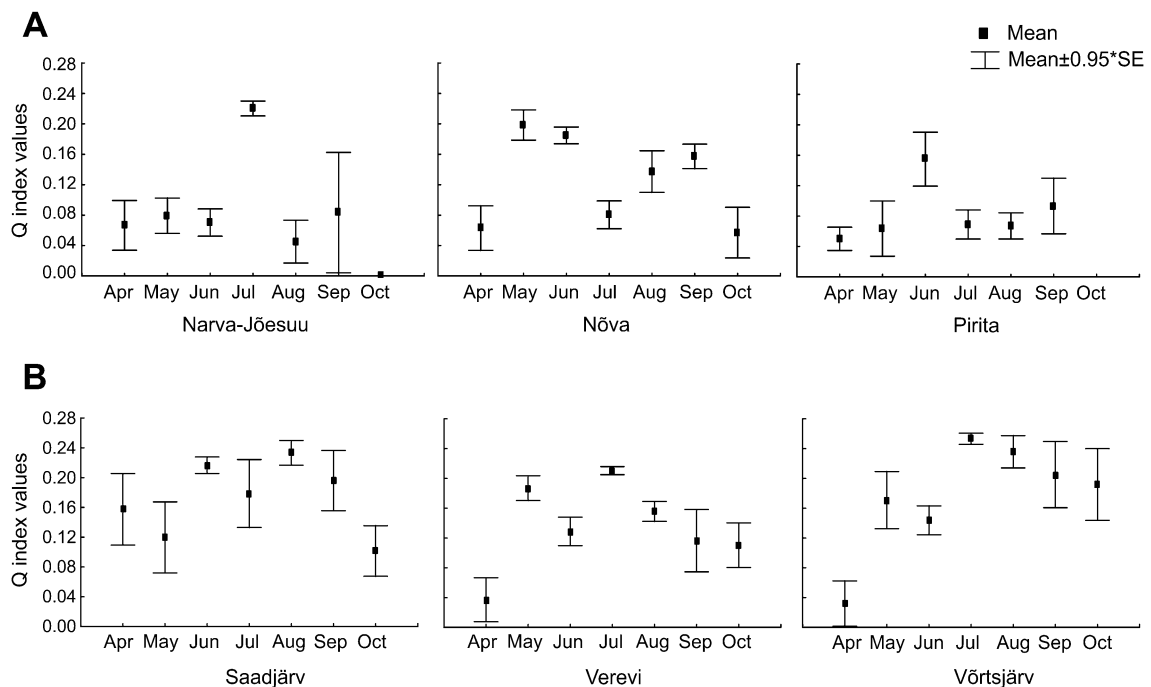


Fig. 5 Seasonal variability in the Rao's quadratic entropy values (Q) (\pm SE) in 2011–2012 (A coastal beaches; B lake beaches)

Table 3 Relative importance of environmental variables (%) describing variability in the taxonomic and functional community indices based on population densities/biomass (for GRI) (%), explained variance by model, *Trampl.* tramplingactivity, *Veg.* vegetation coverage, *Chl a* content of chlorophyll *a*, *Org.* content of sand organic matter, *Cond./Sal.* porewater conductivity and salinity)

	%	Sampled beach	Zone	Trampl.	Wave activity	Veg.	Chl a	Org.	Temp.	pH	Cond./Sal.	Sand structure
Lakes: abundance	50.07	1.068	5.082	0.616	1.399	1.349	8.406	7.481	13.851	2.661	2.778	55.309
Lakes: taxa per sample	51.70	0.721	4.698	1.198	1.707	2.961	5.772	9.099	22.646	3.800	4.498	42.899
Lakes: Shannon index	57.12	1.417	5.227	1.011	1.976	4.228	7.233	7.416	23.498	3.684	8.647	35.664
Lakes: GRI	49.53	8.742	8.544	1.637	4.649	2.884	12.026	5.950	5.782	3.822	5.911	40.053
Lakes: <i>Q</i> index	43.37	3.800	5.606	2.356	3.059	3.274	9.544	7.777	12.483	3.996	4.046	44.058
Coastal: abundance	53.88	0.054	0.932	0.069	0.908	0.003	2.068	11.235	11.552	12.112	26.953	34.115
Coastal: taxa per sample	70.04	1.674	2.193	1.656	1.854	0.085	4.298	11.745	12.373	15.013	12.921	36.189
Coastal: Shannon index	66.36	1.741	2.287	1.672	1.707	0.006	4.468	16.293	20.721	12.185	6.793	32.127
Coastal: GRI	44.54	1.360	2.104	6.517	2.414	0.217	4.258	8.380	9.841	18.426	9.963	36.521
Coastal: <i>Q</i> index	63.05	1.512	4.507	1.128	2.859	0.013	6.090	19.065	11.833	9.898	7.063	36.032

The GRI values were significantly higher in brackish water beaches than in fresh water beaches (two-way repeated measures permutational ANOVA, $p_{\text{Ecosystem type}} = 0.003$; Fig. 4). While raptorial rotifers dominated in coastal beaches during the most of the growing season (GRI values >0), microphagous rotifers prevailed (GRI values <0) in lake beaches. The dominating raptorial taxa differed in coastal and lake beaches, although the genus *Trichocerca* was abundant in both environments. Moreover, the GRI values varied significantly among beaches (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} = 0.002$). In freshwater environments, raptorial dominance was common only in Lake Vörtsjärv (in May and late summer and autumn) and did not occur in hypertrophic Lake Verevi.

The *Q* index was substantially higher in lake beaches compared to coastal beaches (two-way repeated measures permutational ANOVA, $p_{\text{Ecosystem type}} = 0.001$; Fig. 5) but within ecosystem types (lake/coastal) the community functional diversity significantly differed among beaches (two-way repeated measures permutational ANOVA, $p_{\text{Study site}} = 0.026$), being higher at lakes with lower trophic status and in coastal beaches with lower anthropogenic impact. There were no generic patterns of seasonality in community functional diversity shown by different seasonalities among the studied

beaches. However, in coastal beaches, the *Q* values were lower in early spring and late autumn.

Relationship with environmental variables

Temperature, sand structure and sand organic content defined the majority of variability in total abundance of rotifers both in fresh and brackish water ecosystems. In brackish water beaches, salinity and pH also contributed to the abundance model (Table 3). For total abundance, the BRT models accounted for 53.88 and 50.07 % of the overall variability in coastal and lake beaches, respectively.

The BRT models had a relatively good predictive performance for sample taxonomic richness and Shannon index, accounting for between 51.7 and 70.04 % of the overall variability (Figs. 6, 7). Variability in the richness and diversity values was primarily due to sand structure, sand temperature and content of sand organic matter. Sample taxonomic richness and Shannon index increased with elevated temperature, content of sand organic matter and reduced porewater conductivity both in lake beaches and in coastal beaches. However, in coastal beaches, the porewater pH and sediment grain size were also important variables associated with taxonomic richness, with higher taxonomic richness occurring at higher porewater pH values and higher share of coarse

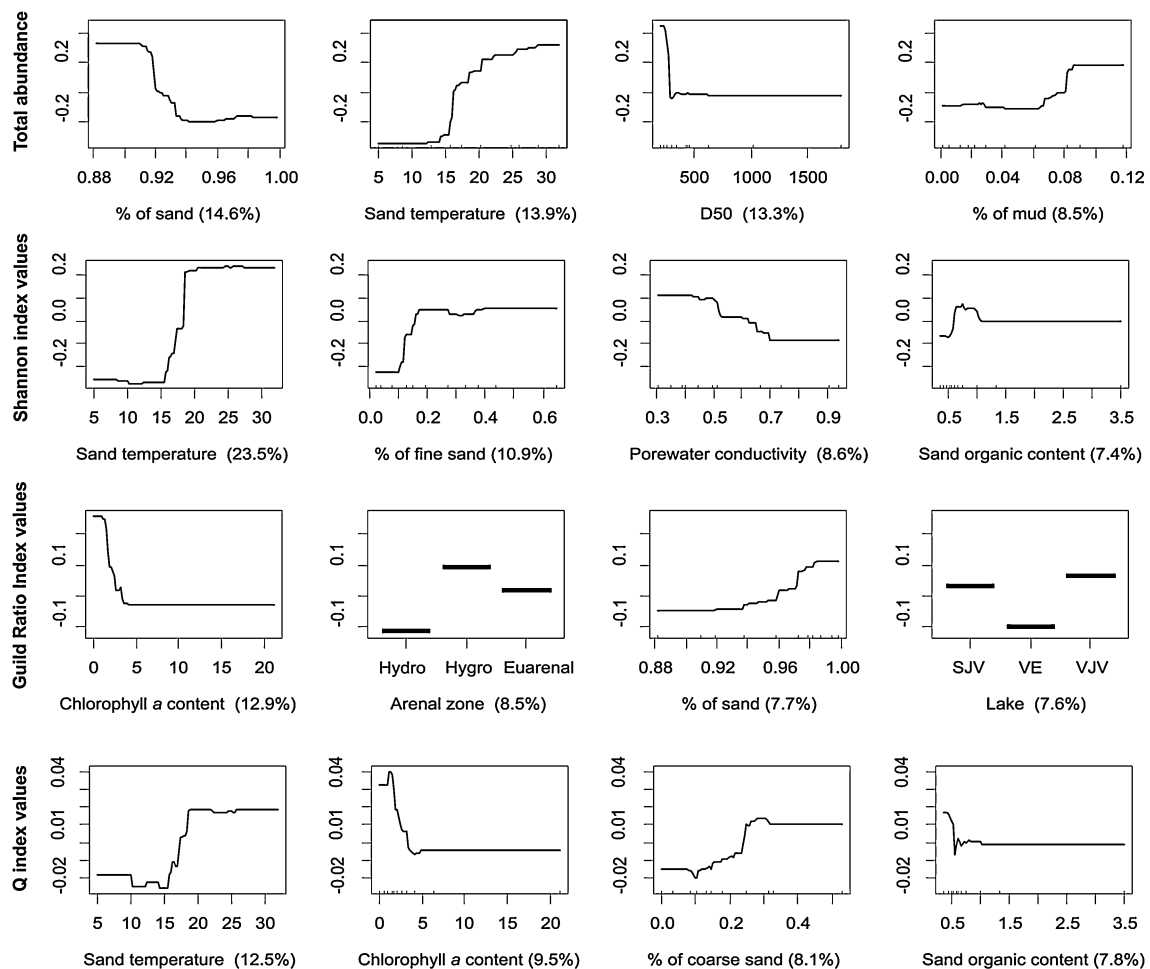


Fig. 6 Role of different environmental variables on GRI, Shannon diversity index, functional diversity and abundances of rotifers with different trophi types in lake beaches. The upward tickmarks on the *x*-axis show the frequency of distribution of data along this axis. The fitted function is a proxy for the change in the dependent variable. Fitted functions in a BRT model show the effect of a variable on the response

after accounting for the average effects of all other variables in the model. The relative contribution of environmental variable to the overall variability of model is shown in brackets. The code of abbreviations is as follows: *SJV* Lake Saadjärv, *VE* Lake Verevi, *VJV* Lake Võrtsjärv; *D50* mean particle size of the beach sand

sand. Shannon index increased from hydroarenal to euarenal in lake beaches.

The key environmental variables that explained variability in Guild Ratio Index differed among lake and coastal beaches (Figs. 6, 7); however, in both ecosystems higher GRI values were associated with lower sand chlorophyll *a* content. In lake beaches, GRI values were highest at the waterline. Sediment characteristics were also important. In coastal beaches, the key variables for GRI were porewater pH, temperature and the share of coarse sand, with higher GRI values

estimated at higher pH and temperature, and lower share of coarse sand.

Sand temperature was one of the key variables for the community functional diversity (*Q*) in both habitat types with higher functional diversity occurring at higher temperatures. Moreover, in lake beaches, higher functional diversity was associated with higher share of coarse sand and lower chlorophyll *a* content. In coastal beaches sand organic content and porewater pH described a significant proportion of functional diversity and opposed to lake environment higher

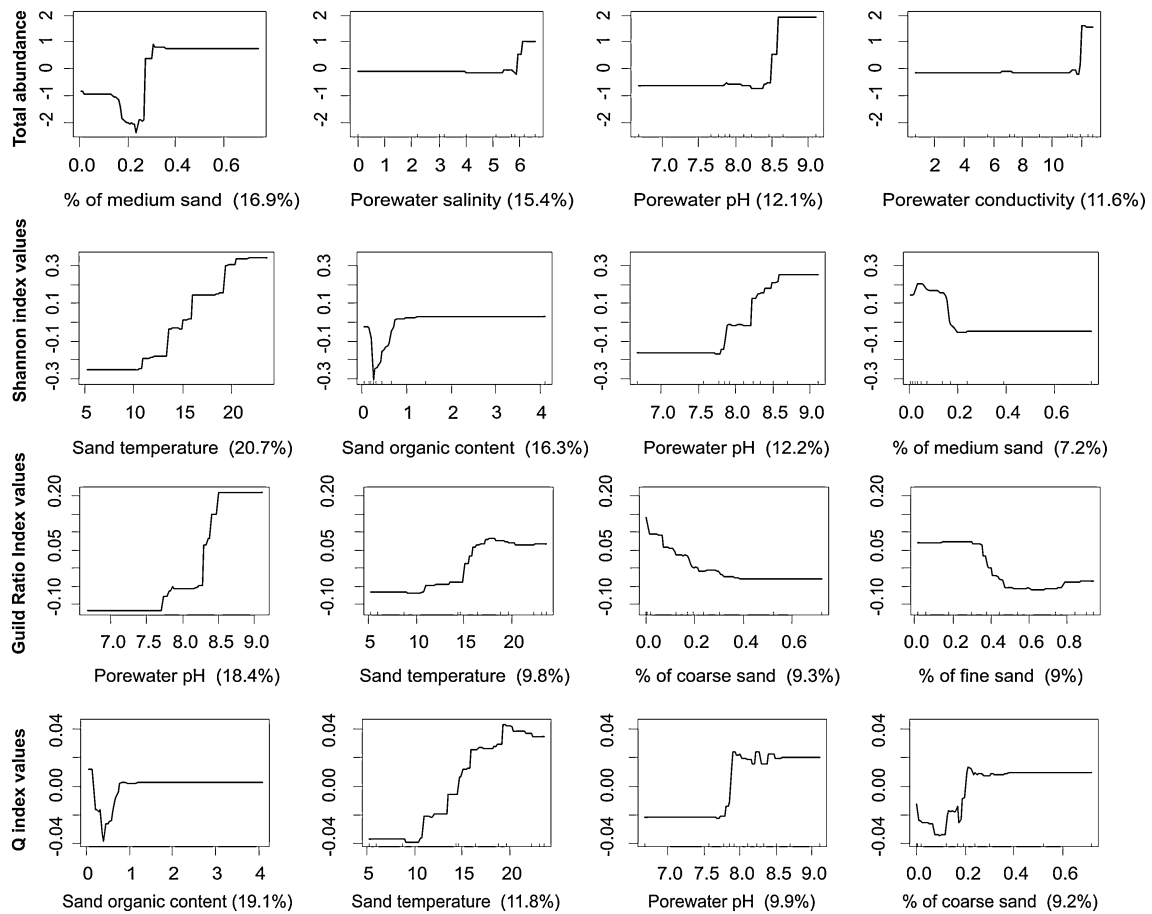


Fig. 7 Role of different environmental variables on GRI, Shannon diversity index, functional diversity and abundances of rotifers with different trophic types in coastal beaches. The upward tickmarks on the x-axis show the frequency of distribution of data along this axis. The fitted function is a

proxy for the change in the dependent variable. Fitted functions in a BRT model show the effect of a variable on the response after accounting for the average effects of all other variables in the model. The relative contribution of environmental variable to the overall variability of model is shown in brackets

functional diversity was associated to higher chlorophyll *a* content. In lake beaches, functional diversity increased from hydroarenal to euarenal, whereas in coastal beaches the hydroarenal zone had the highest functional diversity.

Discussion

The results of the present study indicate that in terms of functional indices, the psammic rotifer communities in freshwater and brackish habitats were distinctly different, although some rotifer species were found at the full range of salinity gradient and taxonomic richness among habitats was similar. More

specifically, raptorial rotifers dominated in coastal beaches, while microphagous rotifers generally prevailed in lake beaches during most of the sampled period. Such significant differences in main feeding modes indicate that rotifers have different functional roles in food webs in fresh and brackish water environments.

Contrary to expectation, functional indices did not exhibit smaller seasonal variability and neither did they respond better to changes in the environment compared to structural indices (taxonomic richness and Shannon index). However, the study also indicated that environmental variables responsible for the variability patterns of diversity and functioning of psammic rotifers were largely different. If the

diversity patterns were primarily driven by seasonal temperature regime, sediment characteristics and anthropogenic impact/trophic state then the trait-based functioning of psammic rotifer communities was a function of broad ecosystem types (freshwater or brackish water).

As this is the first study where interstitial rotifers from brackish waters have been grouped into functional guilds based on their feeding types, it is difficult to draw out the reasons for the raptorial rotifer domination in coastal beaches compared to lake beaches. However, many rotifers inhabiting brackish beaches have been shown to be euryhaline (Thane-Fenchel, 1968) and this was also confirmed in the present study with a number of species occurring both in lakes and coastal beaches. Thus, salinity is likely not the main determining factor for the dominance of raptorial or other rotifer feeding types.

In lakes, the higher GRI has been associated with lower trophic state of the water body (Obertegger & Manca, 2011; Lokko & Virro, 2014). However, in the present study no such clear pattern appeared. The content of sediment organic matter, that may also indicate the trophic state of a habitat, was among key variables only in the areas characterized by moderate values of sediment organic matter (i.e., coastal beaches). The observed bell-shaped response curve (not shown in figures as the content of sediment organic matter was not among the strongest predictors) indicated that raptorial rotifers benefit from moderate content of organic matter i.e., nutrient loads and above this level such trophic group is depressed.

In this study, we did not quantify the oxygen content of sediments, but earlier studies have shown that in areas with limited water exchange the content of sediment organic matter is inversely related to the concentration of oxygen in the sediment (Cowan et al., 1996; Giere, 2009; Almroth-Rosell et al., 2012). It is likely that the response of psammic rotifers to decreased oxygen concentration is non-linear and there exists a clear oxygen threshold above which oxygen concentration plays a minor role for psammic rotifers (Strayer et al., 1997). In hypoxic conditions, however, further decrease in oxygen concentration would yield to strong effects on the taxonomic composition, richness and abundance of rotifers.

It is plausible that differences in the GRI values between coastal and lake beaches were related to food composition and competition. Changes in raptorial-

microphagous ratio in plankton have been shown to reflect shifts in cladocerans community and the mean size of phytoplankton cells rather than changes in the trophic conditions of the lake (Obertegger & Manca, 2011). Thus, the size and type of available food as well as interspecific competition for food within meiofauna community might possibly drive the functionality of psammic rotifer communities. In coastal beaches, the very abundant and often underestimated ciliates (e.g., Lokko et al., 2014b) can be competitors for microphagous rotifers as well as a food source for raptorial rotifers (Arndt, 1993; Agasild et al., 2007). Both rotifers and ciliates are recognized as important grazers of bacteria related to detritus (Fenchel, 1969; Nogrady et al., 1993; Giere, 2009) and several rotifers from brackish interstitial habitats have been reported to feed on ciliates (and rotifers as well), e.g., *Encentrum marinum* (Thane-Fenchel, 1968), which was also common in our study area.

Another factor that might play a role in the functional structure of rotifer communities is the temporal stability and spatial heterogeneity of psammic habitats. It has been shown that shallow coastal sediments are very active on a daily basis, whereas in lakes bottom sediments can be inactive for months (Nordstrom & Jackson, 2012). Such temporal stability often results in an elevated small-scale patchiness with a high diversity of microhabitats allowing the coexistence of many selective fine-particle feeders in lake beaches. Although rotifer communities were mostly dominated by microphagous species in lakes, higher GRI values were systematically observed at the waterline that is the least stable arenal zone in lakes. Similarly, structurally more complex beaches were characterized by an elevated functional diversity of rotifer communities and vice versa. Such relationship between functional diversity and beach complexity has been shown earlier for intertidal nematode communities (Gingold et al., 2010). The functional diversity was also higher in lakes with lower trophic status and in coastal beaches with lower anthropogenic impact. However, in contrast to previous studies (Ejsmont-Karabin, 2003; Bielańska-Grajner, 2005), the Shannon diversity index and taxonomic richness did not show a clear relationship with the trophic state of the lake and was highest in the hypertrophic lake in the present study.

Seasonal patterns of psammic rotifer communities have received great attention, especially in freshwater

ecosystems (e.g., Ejsmont-Karabin, 2001; Radwan & Bielanska-Grajner, 2001; Bielańska-Grajner, 2005; Lokko & Virro, 2014). In general, sandy beaches are very dynamic and unstable habitats with rotifer communities characterized by high within-season and site-to-site variability (e.g., Ejsmont-Karabin, 2001, 2005). In the present study, the seasonal patterns in taxonomic composition, dominance, and abundance of rotifers were also site-specific, but some commonalities such as low abundances in early spring and late autumn were found. These site-specific effects were likely driven by differences in food availability and intensity of anthropogenic impacts, as indicated by BRT models. In beaches with high trampling intensity (Lake Verevi and Narva-Jõesuu Beach) the rotifer abundances peaked before the beach season. However, in popular Piritä Beach the highest abundance was recorded in July, which is generally the high season for swimmers. In general, the functional characteristics of psammic communities such as the GRI and Q values had higher temporal variability and lower spatial variability compared to the studied structural indices. Thus, the functional diversity of psammic rotifers seems to be related more to the site-specific parameters, e.g., trophic state or anthropogenic impacts whereas the taxonomic diversity of psammic rotifers better reflects seasonal temperature dynamics. This also indicates that even if functional data are derived from structural data then patterns of variability of such structural and functional indices differ. Quite often functional traits can be shared by several species whereas taxonomic diversity retains the information on species composition (Botta-Dukát, 2005). This is true also for the present study: the overall taxonomic richness was the highest in Lake Verevi, whereas among the studied freshwater environments the functional diversity of this lake was the lowest. The most species-rich genus in Lake Verevi was *Lecane* represented by 15 species, however, all these species (except *L. luna*) share the same functional traits used in this study.

Temperature was an important variable for the Shannon index, which resulted in lower values in spring and autumn. The higher taxonomic diversity observed during the warm period is in compliance with previous findings (Muirhead et al., 2006; Lokko & Virro, 2014). Although we did not find any generic pattern of seasonality for GRI, Obertegger et al. (2011) reported a clear seasonal dynamics in GRI and this

dynamics persisted over several years. In our study, we observed very context (i.e., site)-specific seasonal patterns of GRI. For psammic rotifers, lower GRI have been found in spring and autumn and highest values in summer (Lokko & Virro, 2014). In the present study, somewhat similar dynamics were observed in Lake Saadjärv but not in Lake Võrtsjärv or coastal beaches. In the present study, temperature was among the key variables associated with GRI values only in coastal beaches. While temperature regulates the physiological and metabolic processes of rotifers (Nogrady et al., 1993), it is considered to have negligible effect on the overall dominance of microphagous or raptorial rotifers (Obertegger & Manca, 2011) as different species have different temperature optima (Bērziņš & Pejler, 1989). More likely the GRI index should follow changes in the abundance of their competitors e.g., cladocerans (Obertegger et al., 2011). However, temperature was the key variable for the Q index with higher, though variable values estimated at higher temperatures.

According to the present knowledge on global biogeographic distribution of rotifers (Segers, 2007; Jersabek & Leitner, 2013), several rare species or species with limited distribution were encountered in the studied beaches. The occurrence of *Colurella marinovi* in the samples from the Estonian coast of the Gulf of Finland is of interest. *C. marinovi* is probably a rare species, as it has not been recorded since its discovery from the psammolittoral of the Bulgarian coast of the Black Sea (Kutikova, 1970; Jersabek & Leitner, 2013). From coastal beaches, we found also a number of specimens we have designated as *Encentrum* cf. *belluinum*. These resembled *E. belluinum* which was originally described from a freshwater pond and presumably has Nearctic distribution, as stated by Segers (2007). The status of *E. cf. belluinum* and also the possible occurrence of *E. belluinum* in the brackish Baltic Sea and its wider distribution needs further study. *Encentrum limicola*, *E. matthesi* and *Dicranophorus leptodon* are not frequently reported; however, the occurrence of *E. limicola* and *E. matthesi* in coastal beach sand, and *D. leptodon* in lake arenal zone is in line with previous findings (De Smet & Pourriot, 1997). In addition to specimens clearly identifiable as *E. limicola*, we found a few specimens resembling more *E. boreale* by their outer shape, size and shape of trophi (especially the shape of intra-malleus; trophi length 37.5 μ m). The specimens were

identified as *E. cf. boreale*. Some specimens had trophi similar to *E. limicola*, but with distinctly smaller measurements (trophi 22–25 µm, toes 10–15 µm). As our specimens had features more close to *E. limicola* (longer club-shaped intramallei, fulcrum length slightly less than rami length, shape of preuncinal tooth), we excluded *E. marinum*, otherwise also quite similar to *E. limicola* in trophi appearance. We designated these forms as *E. cf. limicola*. We also found a specimen (*Dicranophorus cf. luetkeni*) somewhat similar to *D. luetkeni* from the beach of Lake Võrtsjärv. This is possibly a new species, as the rami are relatively longer (as compared to the length of fulcrum) than in *D. luetkeni*, and the lateral caudally pointing projection at the tip of the rami is absent.

To conclude, the studied freshwater and brackish ecosystems had structurally relatively similar psammic rotifer communities whereas the rotifer functional diversity largely differed among these broad ecosystems. The taxonomic diversity of psammic rotifers reflected better temporal variability of environment (lower between-site variability) whereas the functional diversity of psammic rotifers was more related to the site-specific parameters (lower between-month variability). The structural variability of rotifer communities was primarily driven by seasonal temperature regime, sediment characteristics and anthropogenic impact/trophic state, whereas the trait-based functional diversity was due to differences in freshwater and coastal beaches. This suggests that rotifers have different functional roles in fresh and brackish water environments. Likewise the results advocate for the usage of trait-based functional indices in order to gain deeper knowledge of common groups of microscopic animals such as psammic rotifers that are difficult to handle in controlled experiments.

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References

- Agasild, H., P. Zingel, I. Tõnno, J. Haberman & T. Nõges, 2007. Contribution of different zooplankton groups in grazing on phytoplankton in shallow eutrophic Lake Võrtsjärv (Estonia). *Hydrobiologia* 584: 167–177.
- Almroth-Rosell, E., A. Tengberg, S. Andersson, A. Apler & P. O. J. Hall, 2012. Effects of simulated natural and massive resuspension on benthic oxygen, nutrient and dissolved inorganic carbon fluxes in Loch Creran, Scotland. *Journal of Sea Research* 72: 38–48.
- Anderson, M. J., R. N. Gorley & K. R. Clarke, 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E Ltd., Plymouth.
- Arndt, H., 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. *Hydrobiologia* 255: 231–246.
- Bērziņš, B. & B. Pejler, 1989. Rotifer occurrence in relation to temperature. *Hydrobiologia* 175: 223–231.
- Bielańska-Grajner, I., 2001. The psammic rotifer structure in three Lobelian Polish lakes differing in pH. *Hydrobiologia* 446(447): 149–153.
- Bielańska-Grajner, I., 2005. The influence of biotic and abiotic factors on psammic rotifers in artificial and natural lakes. *Hydrobiologia* 546: 431–440.
- Blott, S. J. & K. Pye, 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms* 26: 1237–1248.
- Bogdan, K. G. & J. J. Gilbert, 1984. Body size and food size in freshwater zooplankton. *Proceedings of the National Academy of Science of the United States of America* 81: 6427–6431.
- Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* 16: 533–540.
- Cadotte, M. W., K. Carscadden & N. Mirotchnick, 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48: 1079–1087.
- Covazzi Harriague, A., C. Misic, I. Valentini, E. Polidori, G. Albertelli & A. Pusceddu, 2013. Meio- and macrofauna communities in three sandy beaches of the northern Adriatic Sea protected by artificial reefs. *Chemistry and Ecology* 29: 181–195.
- Cowan, J. W., J. R. Pennock & W. R. Boynton, 1996. Seasonal and interannual patterns of sediment-water nutrient and oxygen fluxes in Mobile Bay, Alabama (USA): regulating factors and ecological significance. *Marine Ecology Progress Series* 141: 229–245.
- De Smet, W. H., 1996. Rotifera 4: The Proalidae (Monogononta). *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World* 9. SPB Academic Publishing bv, Amsterdam.
- De Smet, W. H. & R. Pourriot, 1997. Vol. 5: Rotifera. The Dicranophoridae (Monogononta) and the Ituridae (Monogononta): *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World* 12. SPB Academic Publishing bv, Amsterdam.
- Ejsmont-Karabin, J., 2001. Psammic rotifers in two lakes of different trophy – their abundance, species structure and role in phosphorous cycling. *Verhandlungen des Internationalen Verein Limnologie* 27: 3856–3859.
- Ejsmont-Karabin, J., 2003. Rotifera of lake psammic: community structure versus trophic state of lake waters. *Polish Journal of Ecology* 51: 5–35.

- Ejsmont-Karabin, J., 2005. Short time-response of psammic communities of Rotifera to abiotic changes in their habitat. *Hydrobiologia* 546: 423–430.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huetmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. Mc C Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz & N. E. Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.
- Elith, J., J. R. Leathwick & T. Hastie, 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802–881.
- Fenchel, T., 1969. The ecology of marine microbenthos IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa. *Ophelia* 6: 1–182.
- Fontaneto, D., W. H. De Smet & C. Ricci, 2006. Rotifers in saltwater environments, re-evaluation of an inconspicuous taxon. *Journal of the Marine Biological Association of the United Kingdom* 86: 623–656.
- Giere, O., 2009. *Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments*, 2nd ed. Springer-Verlag, Berlin-Heidelberg.
- Gingold, R., M. Mundo-Ocampo, O. Holovachov & A. Rocha-Olivares, 2010. The role of habitat heterogeneity in structuring the community of intertidal free-living marine nematodes. *Marine Biology* 157: 1741–1753.
- Hansen, P. J., P. K. Bjørnsen & B. W. Hansen, 1997. Zooplankton grazing and growth: scaling within the 2–2000- μ m body size range. *Limnology and Oceanography* 42: 687–704.
- Hastie, T. J., R. J. Tibshirani & J. H. Friedman, 2001. *The Elements of Statistical Learning*. Springer-Verlag, New-York.
- HELCOM, 2003. *The Baltic marine environment 1999–2002*. Baltic Sea Environment Proceedings 87: 46 pp.
- Hijmans, R. J., S. Phillips, J. Leathwick & J. Elith, 2014. *dismo: species distribution modeling*. R package version 1.0-5. <http://CRAN.R-project.org/package=dismo>
- Hillbricht-Ilkowska, A., 1983. Response of planktonic rotifers to the eutrophication process and to the autumnal shift of blooms in lake Biwa, Japan. I. Changes in abundance and composition of rotifers. *Japanese Journal of Limnology* 44: 93–106.
- Ikauniece, A., 2001. Long-term abundance dynamics of coastal zooplankton in the Gulf of Riga. *Environment International* 26: 175–181.
- Jansson, A.-M., 1967. The food-web of the Cladophora-belt fauna. *Helgoländer wissenschaftliche Meeresuntersuchungen* 15: 574–588.
- Jersabek, C. D. & M. F. Leitner, 2013. *The Rotifer World Catalog*. World Wide Web electronic publication. <http://www.rotifera.hausdernetur.at/>
- Jersabek, C. D., W. H. De Smet, C. Hinz, D. Fontaneto, C. G. Hussey, E. Michaloudi, R. L. Wallace & H. Segers, 2015. List of available names in zoology, candidate part Phylum Rotifera, species-group names established before 1 January 2000. (1) Completely defined names (A-list), and (2) incompletely defined names, with no types known (B-list): 335 pp. http://rotifera.hausdernetur.at/Rotifer_data/files/LAN_CandidatePart-SpeciesRotifera-2015-12-04.pdf. Accessed 27 June 2016.
- Jordan, S., D. K. Shiozawa & J. M. Schmid-Araya, 1999. Benthic invertebrates of a large, sandy river system: the Green and Colorado Rivers of Canyonlands National Park, Utah. *Archiv Fur Hydrobiologie* 147: 91–127.
- Koste, W. & R. J. Shiel, 1987. Rotifera from Australian inland waters. II. Epiphanidae and Brachionidae (Rotifera: Monogononta). *Invertebrate Taxonomy* 7: 949–1021.
- Kutikova, L. A., 1970. Rotifers (Rotatoria) of the Fauna of the USSR. Eurotatoria (Ploimida, Monimotrochida, Paedotrochida). Nauka, Leningrad. (in Russian).
- Laliberté, E., P. Legendre & B. Shipley, 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.
- Laliberté, E. & P. Legendre, 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.
- Lapesa, S., T. W. Snell, D. M. Fields & M. Serra, 2002. Predatory interactions between a cyclopoid copepod and three sibling rotifer species. *Freshwater Biology* 47: 1685–1695.
- Lepš, J., F. De Bello, S. Lavorel & S. Berman, 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* 78: 481–501.
- Litchman, E., P. de Tezanos Pinto, C. A. Klausmeier, M. K. Thomas & K. Yoshiyama, 2010. Linking traits to species diversity and community structure in phytoplankton. *Hydrobiologia* 653: 15–28.
- Litchman, E., M. D. Ohman & T. Kiorboe, 2013. Trait-based approaches to zooplankton communities. *Journal of Plankton Research* 35: 473–484.
- Litton Jr., J. R., 1983. Collections on Planktonic and Interstitial Marine Rotifers from Puerto Rico. *Proceedings of the Indiana Academy of Science* 93: 475–478.
- Lokko, K. & T. Virro, 2014. The structure of psammic rotifer communities in two boreal lakes with different trophic conditions: Lake Võrtsjärv and Lake Saadjärv (Estonia). *Oceanological and Hydrobiological Studies* 43: 49–55.
- Lokko, K., T. Virro & J. Kotta, 2014a. Taxonomic composition of zoopsammon in the fresh and brackish waters of Estonia, the Baltic province ecoregion of Europe. *Estonian Journal of Ecology* 63: 242–261.
- Lokko, K., J. Kotta & T. Virro, 2014b. Seasonal trends in horizontal and vertical patterns of zoopsammon in the brackish Baltic Sea in relation to key environmental variables. *Proceedings of the Biological Society of Washington* 127: 58–77.
- Loopmann, A., 1984. Suuremate Eesti järvede morfomeetriselised andmed ja veevahetus (Morphometrical data and water exchange of larger Estonian lakes). Eesti NSV teaduste Akadeemia, Tallinn: 150 pp (in Estonian).
- Mäemets, A., 1977. Eesti NSV järved ja nende kaitse (Lakes of the Estonian S.S.R. and their protection). Valgus, Tallinn: 264 pp (in Estonian).
- Mallin, M. A. & H. W. Paelel, 1994. Planktonic trophic transfer in an estuary: seasonal, diel and community structure effects. *Ecology* 75: 2168–2184.
- McGill, B. J., B. J. Enquist, E. Weiher & M. Westoby, 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178–185.

- Mouillot, D., 2007. Niche-assembly vs. dispersal-assembly rules in coastal fish metacommunities: implications for management of biodiversity in brackish lagoons. *Journal of Applied Ecology* 44: 760–767.
- Muirhead, J. R., J. Ejsmont-Karabin & H. J. Macisaac, 2006. Quantifying rotifer species richness in temperate lakes. *Freshwater Biology* 51: 1696–1709.
- Nogrady, T., R. L. Wallace & T. W. Snell, 1993. Rotifera. : Volume 1: Biology, Ecology and Systematics: Guides to the Identification of the Microinvertebrates of the Continental Waters of the World 4. SPB Academic Publishing bv, The Hague.
- Nogrady, T., R. Pourriot & H. Segers, 1995. Rotifera. Vol. 3: The Notommatidae and the Scardiidae. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World 8. SPB Academic Publishing bv, Amsterdam.
- Nordstrom, K. F. & N. L. Jackson, 2012. Physical processes and landforms on beaches in short fetch environments in estuaries, small lakes and reservoirs: a review. *Earth-Science Reviews* 111: 232–247.
- Nordström, M. C., K. Aarnio, A. Törnroos & E. Bonsdorff, 2015. Nestedness of trophic links and biological traits in a marine food web. *Ecosphere* 6: 1–14.
- Obertegger, U. & G. Flaim, 2015. Community assembly of rotifers based on morphological traits. *Hydrobiologia* 753: 31–45.
- Obertegger, U. & M. Manca, 2011. Response of rotifer functional groups to changing trophic state and crustacean community. *Journal of Limnology* 70: 231–238.
- Obertegger, U., H. A. Smith, G. Flaim & R. L. Wallace, 2011. Using the guild ratio to characterize pelagic rotifer communities. *Hydrobiologia* 662: 157–162.
- Ott, I., T. Kõiv, P. Nõges, A. Kisand, A. Järvalt & E. Kirt, 2005. General description of partly meromictic hypertrophic Lake Verevi, its ecological status, changes during the past eight decades and restoration problems. *Hydrobiologia* 547: 1–20.
- Ott, I. (ed.), 2007. Saadjärve limnoloogilised uurimused II [Limnological studies of Lake Saadjärv]. Eesti Maaülikooli Põllumajandus-ja Keskonnainstituudi Limnoloogiakeskus (in Estonian).
- Paturej, E. & A. Gutkowska, 2015. The effect of salinity levels on the structure of zooplankton communities. *Archives of Biological Science Belgrade* 67: 483–492.
- Pejler, B., 1995. Relation to habitat in rotifers. *Hydrobiologia* 313(314): 267–278.
- Pitkänen, H., M. Kiirikki, O. Savchuk, A. Rääke, P. Korpinen & F. Wulff, 2007. Searching efficient protection strategies for the eutrophicated Gulf of Finland: the combined use of 1D and 3D modeling in assessing long-term state scenarios with high spatial resolution. *Ambio* 36: 272–279.
- Pitkänen, H., J. Lehtoranta & H. Peltonen, 2008. The Gulf of Finland. In Schiewer, U. (ed.), *Ecology of Baltic Coastal Waters*. Springer, Berlin: 285–308.
- Pomerleau, C., A. R. Sastri & B. E. Beisner, 2015. Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean. *Journal of Plankton Research* 37: 712–726.
- R Core Team 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Radwan, S. & I. Bielańska-Grajner, 2001. Ecological structure of psammic rotifers in the ecotonal zone of Lake Piaseczno (eastern Poland). *Hydrobiologia* 446(447): 221–228.
- Ridgeway, G., D. Edwards, B. Kriegler, S. Schroedl & H. Southworth, 2015. gbm: Generalized Boosted Regression Models. R package version 2.1.1. <http://CRAN.R-project.org/package=gbm>
- Ristau, K., N. Spann & W. Traunspurger, 2015. Species and trait compositions of freshwater nematodes as indicative descriptors of lake eutrophication. *Ecological Indicators* 53: 196–205.
- Rothhaupt, K. O., 1990. Differences in particle size-dependent feeding efficiencies of closely related rotifer species. *Limnology and Oceanography* 35: 16–23.
- Ruttner-Kolisko, A., 1977. Suggestions for biomass calculations of planktonic rotifers. *Archiv für Hydrobiologie* 8: 71–76.
- Salt, G. W., 1987. The components of feeding behavior in rotifers. *Hydrobiologia* 147: 271–281.
- Saunders-Davies, A., 1998. Differences in rotifer populations of the littoral and sub-littoral pools of a large marine lagoon. *Hydrobiologia* 387(388): 225–230.
- Schmid-Araya, J. M., 1998. Rotifers in interstitial sediments. *Hydrobiologia* 387(388): 231–240.
- Segers, H., 1995. Rotifera. Vol. 2: The Lecanidae (Monogononta). Guides to the Identification of the Microinvertebrates of the Continental Waters of the World 6. SPB Academic Publishing bv, The Hague.
- Segers, H., 2007. Annotated checklist of the rotifers (Phylum Rotifera), with notes on nomenclature, taxonomy and distribution. *Zootaxa* 1564: 1–104.
- Segers, H., 2008. Global diversity of rotifers (Rotifera) in freshwater. *Hydrobiologia* 595: 49–59.
- Smith, H. A., J. Ejsmont-Karabin, T. M. Hess & R. L. Wallace, 2009. Paradox of planktonic rotifers: similar structure but unique trajectories in communities of the Great Masurian Lakes (Poland). *Verhandlungen des Internationalen Verein Limnologie* 30: 951–956.
- Špoljar, M., I. Habdija, B. Primc-Habdija & L. Sipos, 2005. Impact of environmental variables and food availability on rotifer assemblage in the karstic barrage Lake Visovac (Krka River, Croatia). *International Review of Hydrobiology* 90: 555–579.
- Špoljar, M., T. Tomljanović & I. Lalić, 2011. Eutrophication impact on zooplankton community: a shallow lake approach. the Holistic Approach to. *Environment* 4: 131–142.
- Strayer, D. L., S. E. May, P. Nielsen, W. Wollheim & S. Hausam, 1997. Oxygen, organic matter, and sediment granulometry as controls on hyporheic animal communities. *Archiv für Hydrobiologie* 140: 131–144.
- Strickland, J. D. H. & T. R. Parsons, 1972. A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board of Canada* 167: 1–310.
- Thane-Fenchel, A., 1968. Distribution and ecology of non-planktonic brackish-water rotifers from Scandinavian waters. *Ophelia* 5: 273–297.

- Tuvikene, L., A. Kisand, I. Tõnno & P. Nõges, 2004. Chemistry of lake water and bottom sediments. In Haberman, J., E. Pihu & A. Raukas (eds.), Lake Võrtsjärv. Estonian Encyclopaedia Publishers, Tallinn: 89–102.
- Virro, T., J. Haberman, M. Haldna & K. Blank, 2009. Diversity and structure of the winter rotifer assemblage in a shallow eutrophic northern temperate Lake Võrtsjärv. *Aquatic Ecology*, 43: 755–764.
- Wallace, R. L., 2002. Rotifers: exquisite metazoans. *Integrative and Comparative Biology* 42: 660–667.