

Taxonomic composition of zoopsammon in fresh and brackish waters of Estonia, a Baltic province ecoregion of Europe

Küllli Lokko^{a,b}✉, Taavi Virro^a, and Jonne Kotta^b

^a Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia

^b Estonian Marine Institute, University of Tartu, Mäealuse 10a, 12618 Tallinn, Estonia

✉ Corresponding author, kulli.lokko@ut.ee

Received 21 July 2014, revised 26 September 2014, accepted 26 September 2011

Abstract. Zoopsammon communities, i.e. fauna dwelling in the interstitial sandy habitat at the water's edge, are largely understudied. The aim of the present study was to provide an overview of the taxonomic structure of zoopsammon in Estonian waters. The study is based on samples collected from four lakes across Estonia and from three sandy beaches on the Estonian coast of the Gulf of Finland, Baltic Sea, in 2008–2014. Animals from 12 phyla were found, of which the majority of rotifers and testate amoebae were identified to species level. A total of 156 taxa were determined, including 84 rotifer species and 39 testate amoebae species. In addition to the 46 new taxa for the Estonian fauna already registered in our previous works, the present study reports further 11 new rotifer, 19 testate amoebae, and 6 nematode taxa. The psammic communities in lake beaches had higher species richness than in coastal beaches, and the communities were more similar in coastal beaches than in lake beaches. The mesotrophic Lake Saadjärv had the highest taxon richness with 80 taxa from 10 phyla. Similarly, the number of testate amoebae species was higher in lake beaches than in coastal beaches. The number of taxa, especially the number of rotifer species, was lower in sampling sites with an elevated trophic state and/or human population density. The number of testate amoebae species was the highest in the hypertrophic Lake Verevi. As compared to testate amoebae, rotifer communities had a higher taxonomic richness at landscape scale characterized by variable communities both in time and space.

Key words: psammon, meiofauna, rotifers, testate amoebae, Baltic Sea, lake beach, Estonia.

INTRODUCTION

Zoopsammon is a diverse group of organisms living in the interstitial spaces between sand grains at the shoreline. The term *psammon* is nowadays mainly used to characterize freshwater sandy beach habitats, although it was originally defined as ‘a transitional zone between aquatic and soil habitats’ (Schmid-Araya, 1998), and is also applicable to brackish and marine beach habitats, where the intertidal zone can be considered as psammon habitat if the sediment consists of sand and is regularly exposed (e.g. Tzschaschel, 1983; Golemansky, 1998; De

Smet and Chernyshev, 2006; Alekperov et al., 2007). However, in the marine literature psammic communities are more often referred to as meiofauna.

Psammon communities have received very little attention compared to lower littoral and sublittoral meiobenthos, and psammon has been rarely treated as a single entity. Despite its unstable and very fluctuating environment, the arenal zone hosts a large variety of species (Pejler, 1995; Golemansky, 1998; Gheskiere et al., 2005). Protists, nematodes, rotifers, small crustaceans, tardigrades, gastrotrichs, turbellarians, oligochaetes, and insect larvae are regularly found from psammon habitats (Thane-Fenchel, 1968; Whitman and Clark, 1984; Schmid-Araya, 1998; Kotwicki et al., 2005a, 2005b). From psammic taxa, rotifers have received relatively much attention in freshwater habitats (e.g. Pejler, 1995; Bielańska-Grajner, 2001; Segers and Chittapun, 2001). In marine beach habitats, nematodes tend to be the most thoroughly researched psammic taxa (e.g. Gheskiere et al., 2004, 2005; Liu et al., 2008; Maria et al., 2012, 2013).

From the Baltic Sea area some information is available on psammic ciliates (Czapik and Fyda, 1992), testate amoebae (Golemansky, 1998), rotifers (Thane-Fenchel, 1968; Sørensen, 2001), and nematodes (Gheskiere et al., 2005). In Europe, freshwater zoopsammon has received more attention in Poland (e.g. Bielańska-Grajner, 2001; Ejsmont-Karabin, 2003; Nesteruk, 2007; Kalinowska, 2008, 2013; Bielańska-Grajner and Poznańska, 2010).

At the Estonian water bodies, the coastal zone was sampled already in the 19th century. In these studies, some beach invertebrates were recorded (Eichwald, 1849, 1852; Levander, 1894). However, it is not known where exactly the samples were taken (water or sediment, at waterline/beach or deeper water). First true reports on the interstitial fauna, i.e. zoopsammon, of sandy beach in Estonia date from the 1980s. In these sampling campaigns, Golemansky (1983) investigated psammic testate amoebae from the Estonian coast of the Gulf of Finland, and Kutikova and Haberman (1986) determined the taxonomic composition of rotifers from the arenal zone of Lake Võrtsjärv. Recently, some information has been provided about the taxonomic composition and density of zoopsammon communities, their temporal and spatial distribution, and relation with various environmental variables in some Estonian coastal beaches (Lokko et al., 2014) and in two lakes (Lokko et al., 2013; Lokko and Virro, 2014).

The aim of this study is to provide an overview and sum up the current knowledge on the taxonomic structure of zoopsammon in Estonian waters. This summarized information serves as a basis of the current status of psammic communities both in freshwater and marine habitats and potentially allows assessing the current status and conservation value of Estonian interstitial beach habitats.

MATERIALS AND METHODS

The present study is based on two previous studies (Lokko et al., 2013, 2014) and an additional sampling campaign carried out in 2011–2014. Samples were taken

from three sandy beaches along the Estonian coast of the Gulf of Finland, Baltic Sea, and from four lakes across Estonia (Fig. 1). The coastal sampling sites were located at Keibu Bay near Nõva village (Nõva Beach, the westernmost sampling site), at Pirita Beach within Tallinn City, and at a popular beach of Narva Bay adjacent to a small town of Narva-Jõesuu (the easternmost site). The Gulf of Finland has a strong horizontal salinity gradient: the surface salinity varies from 0 in its eastern end to 7 ppt in the western areas (Pitkänen et al., 2008). Also 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 sampling sites from lakes were located at the eastern coast of Lake Võrtsjärv, at two beaches of Lake Saadjärv, at Lake Verevi, and at Lake Männiku. Võrtsjärv is the second largest lake in Estonia (surface area 27 000 ha). It is a shallow (max depth 6 m, average 2.8 m) eutrophic lake with a short water residence time (Timm, 1973; Tuvikene et al., 2004). Saadjärv is smaller (surface area 707.6–723.2 ha), but much deeper (max depth 25 m, average 8 m) (Mäemets, 1977; http://register.keskkonnainfo.ee/envreg/main?reg_kood=VEE2065300&mount=view, accessed 29.06.2014). Saadjärv has the lowest trophic status of the studied lakes. The mesotrophic Saadjärv is characterized by slow water exchange rates, high water transparency, high hardness, and alkaline water (Ott, 2007). The smallest of the studied lakes is Verevi, which is located in



Fig. 1. Study area and the location of the sampling stations. Blue dots represent sampled coastal beaches and red dots beaches of the studied lakes.

a small town of Elva and is very popular among swimmers. It is a hypertrophic and relatively deep (max 11 m, average 3.6 m, surface area 12.6 ha) lake with a low water exchange rate (Loopmann, 1984; Ott et al., 2005). The fourth of the studied lakes, Männiku, is located at the edge of Tallinn City. It is a moderately deep (max depth 9 m, average 5 m, surface area 118.7 ha) eutrophic lake of anthropogenic origin (Tamre, 2006; <http://register.keskkonnainfo.ee/envreg/main#HTTPb8aODzH81I2Zv8PJCBXuHAhsXWViIR>, accessed 29.06.2014) with steep slopes. It belongs to a complex of several lakes/water bodies within a sand quarry, which was established in the early 20th century. The main characteristics of the studied beaches, coordinates, and sampling times are presented in Table 1.

In each sampling site, samples of psammon were collected along transects across the waterline (up to 50 cm from the waterline in both directions). The samples were collected with sharp-edged corers with diameters of 2.9 and 4.75 cm down to a depth of 3–5 cm in the sand. The samples were transferred to a plastic container and rinsed three times with carbonated drinking water. After each rinse the supernatant was poured off into a plastic bottle and fixed with Lugol's solution. Then the samples were condensed to 100 mL by sedimentation for at least four days and siphoning off excess water. From each sample, five 2-mL subsamples were taken wherein all organisms were counted in a Bogorov chamber under a microscope. For the identification, specimens were slide-mounted in glycerol and determined to the lowest possible taxon. Illoricate rotifers were identified by their trophi, which were dissolved out using the household disinfectant Domestos[®], which contains sodium hypochlorite ($\text{NaClO} < 5\%$). At each sampling time various environmental parameters such as sand grain size, vegetation coverage, sand organic content, pH, temperature, and salinity were estimated. The details of measuring and estimating environmental parameters are described in Lokko et al. (2013, 2014).

The nomenclature of higher taxonomic units is based on the classifications in Halanych (2004), the Catalogue of Life (Roskov et al., 2014), and the World Register of Marine Species (WoRMS Editorial Board, 2014), and those of rotifers on Melone et al. (1998) and Sørensen and Giribet (2006). The classification of protists is based on Mazei and Tsyganov (2006) and Cavalier-Smith (2010). The nomenclature of rotifer species follows Jersabek et al. (2012). For testaceans, Mazei and Tsyganov (2006) was used. In other cases, the Catalogue of Life (Roskov et al., 2014) was consulted.

The Sørensen index (Krebs, 1989) was used to evaluate similarity between zoopsammonic communities of the sampling sites. In order to identify clusters of stations that are statistically dissimilar, a similarity profile (SIMPROF) test was used (Clarke et al., 2008) in the R environment and package clustsig (R Core Team, 2014; Whitaker and Christman, 2014).

Table 1. Sampling site coordinates, sampling time, and general environmental characteristics in the sampling sites. Variable mean (continuous variables) or most common value (categorical variables); minimum and maximum value or variable range is shown in brackets

	Võrtsjärv	Saadjärv	Verevi	Männiku	Nõva	Pirita	Narva-Jõesuu
Sampling site coordinates	58°13'45"N; 26°07'17"E	58°31'59"N; 26°38'46"E and 58°31'41"N; 26°41'45"E	58°13'44"N; 26°24'21"E	59°21'35"N; 24°42'59"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
Sampling time	Mar–Nov 2008; May–Oct 2011, Apr 2012	Apr–Oct 2008; May–Oct 2011, Apr 2012	May–Oct 2011, Apr 2012	May 2014	May–Oct 2011, Apr 2012	May–Oct 2011, Apr 2012	May–Oct 2011, Apr 2012
Sand type	Fine (fine–coarse)	Medium (medium– coarse)	Medium (fine– medium)	Medium–coarse	Medium (medium– coarse)	Medium (fine– coarse)	Fine (fine– medium)
Vegetation cover	15% (0–50%)	11% (0–60%)	19% (2–40%)	0%	0% (0–12%)	0%	0% (0–100%)
pH (littoral/ interstitial)	7.73 (6.77–9.5)	7.84 (6.92–9.4)	7.48 (6.63–7.98)	7.99 littoral	8.19 (6.68–9.11) interstitial	7.86 (7.67–8.34) interstitial	8.18 (7.57–8.7) interstitial
Porewater conductivity, mS ppt	0.579 (0.446–0.775)	0.626 (0.399–0.942)	0.629 (0.513–0.711)	NA	11.05 (9.09–12.43)	11.19 (7.19– 12.80)	5.46 (0.72–9.09)
Porewater salinity, ppt	NA	NA	NA	NA	5.41 (4–6.2)	5.46 (3–6.6)	2.4 (0–4)
Sand temperature, °C	19.9 (8.7–30.2)	16.6 (5.1–28.3)	20.1 (7.7–32)	15.8	15.67 (6.2–23.2)	15.16 (6–22.6)	14.99 (5.2–23.6)
Sand organic content	1.06 (0.22–7.39)	0.72 (0.33–3.18)	0.85 (0.22–4.77)	NA	0.53 (0.07–4.09)	0.59 (0.06–2.87)	0.48 (0.04–2.43)

NA – not analysed.

RESULTS AND DISCUSSION

A total of 156 non-overlapping taxa belonging to 12 phyla were found in the Estonian psammon communities, 69 taxa occurring in the Gulf of Finland and 123 taxa in lakes (Table 2). In our preceding studies (Lokko et al., 2013, 2014), 46 new zoopsammon taxa for the Estonian fauna were registered, including 25 rotifers, 17 testate amoebae, 1 cercozoan, 1 clitellate, 1 tardigrade, and 1 harpacticoid. The present study further adds new records of 11 rotifer, 19 amoebozoan, and 6 nematode taxa for Estonia (Table 2). Of all the taxa found, 90 occurred only in lake beaches and 39 in beaches of the Baltic Sea. The number of taxa per sample was higher in lake beaches than in coastal areas. Areal taxonomic richness was related to sample taxonomic richness in coastal areas but not in the lake ecosystems (Fig. 2). The most common taxa were nematodes, rotifers, ciliates, testate amoebae, and harpacticoids. Individuals from these taxa were found from all studied beaches. No oligochaetes were found from the beach of Lake Verevi. The most taxon-rich season was summer, whereas diversity peaked later in lake (in August) than in coastal beaches (June or July).

Table 2. Zoopsammon taxa from beaches of lakes Võrtsjärv, Saadjärv (two sites), Verevi, and Männiku, and coastal beaches Nõva, Pirita, and Narva-Jõesuu. Summarized information from previous studies (Lokko et al., 2013, 2014) and recent supplementary material. Asterisked (*) taxa are new records for Estonia

Taxon	Võrtsjärv	Saadjärv	Verevi	Männiku	Nõva	Pirita	Narva-Jõesuu
Phylum Amoebozoa							
Class Lobosea							
Order Arcellinida							
<i>Arcella</i> sp.					x	x	
<i>Arcella artocrea</i> Leidy, 1876*			x				
<i>Arcella catinus</i> Penard, 1890*			x				
<i>Arcella crenulata</i> Deflandre, 1928*	x		x				
<i>Arcella discoides</i> Ehrenberg, 1843	x	x	x				
<i>Arcella hemisphaerica</i> Perty, 1852		x			x	x	
<i>Centropyxis aerophila</i> Deflandre, 1929	x	x	x		x		x
<i>Centropyxis aculeata</i> (Ehrenberg, 1838)	x	x	x	x			
<i>Centropyxis cassis</i> (Wallich, 1864)	x	x					
<i>Centropyxis constricta</i> (Ehrenberg, 1841)	x	x	x				
<i>Centropyxis discoides</i> Penard, 1902					x		

Continued overleaf

Table 2. Continued

Taxon	Võrtsjärv	Saadjärv	Verevi	Männiku	Nõva	Pirita	Narva-Jõesuu
<i>Centropyxis delicatula</i> Penard, 1902*	x	x	x				
<i>Centropyxis ecornis</i> (Ehrenberg, 1841)*	x		x				
<i>Centropyxis hirsuta</i> Deflandre, 1929*			x				
<i>Centropyxis</i> cf. <i>laevigata</i> Penard, 1890*			x				
<i>Centropyxis orbicularis</i> Deflandre, 1929*			x	x			
<i>Centropyxis platystoma</i> Penard, 1890	x	x					
<i>Cyclopyxis</i> spp.					x	x	x
<i>Cyclopyxis arcelloides</i> (Penard, 1902)	x	x					
<i>Cyclopyxis eurystoma</i> Deflandre, 1929*			x				
<i>Cyclopyxis kahli</i> (Deflandre, 1929)*	x		x				
<i>Diffflugia amphora</i> (Leidy, 1874) Penard, 1902							x
<i>Diffflugia bidens</i> Penard, 1902		x					
<i>Diffflugia brevicolla</i> Cash et Hopkinson, 1909*		x					
<i>Diffflugia elegans</i> Penard, 1890	x		x		x		
<i>Diffflugia globulosa</i> (Dujardin, 1837) Penard, 1902*			x				
<i>Diffflugia gramen</i> Penard, 1902	x	x					
<i>Diffflugia lacustris</i> (Penard, 1899)					x	x	x
<i>Diffflugia lithophila</i> (Penard, 1902) Gauthier-Lièvre et Thomas, 1958	x		x				
<i>Diffflugia lobostoma</i> Leidy 1879	x		x				
<i>Diffflugia penardi</i> Hopkinson, 1909	x	x	x		x		
<i>Diffflugia</i> cf. <i>pulex</i> Penard, 1902*			x				
<i>Diffflugia urceolata</i> Carter, 1864		x			x		x
<i>Lesquereusia modesta</i> Rhumbler, 1895*	x						
<i>Netzelia tuberculata</i> (Wallich, 1864)*	x		x				
<i>Phryganella acropodia</i> (Hertwig et Lesser, 1874) Hopkinson, 1909*			x		x		
cf. <i>Trigonopyxis</i> sp.*			x				
<i>Zivkovicia</i> cf. <i>spectabilis</i> (Penard, 1902)*					x		
Phylum Ciliophora							
Ciliophora indet.	x	x	x	x	x	x	x

Taxonomic composition of zoosammon in Estonian waters

Table 2. Continued

Taxon	Võrtsjärv	Saadjärv	Verevi	Männiku	Nõva	Pirita	Narva-Jõesuu
Phylum Cercozoa							
Class Imbricatea							
<i>Cyphoderia ampulla</i> (Ehrenberg, 1840) Leidy, 1879	x			x	x		x
<i>Psammonobiotus communis</i> Golemansky, 1967					x		
Phylum Foraminifera							
Class Monothalamea							
cf. <i>Allogromia</i> sp.*					x		
Phylum Platyhelminthes							
Class Rhabditophora							
Rhabditophora indet.	x	x		x	x	x	x
Phylum Gastrotricha							
Chaetonotidae gen. et spp. indet.		x			x	x	x
<i>Chaetonotus</i> sp.				x			
Phylum Rotifera							
Class Bdelloidea							
Bdelloidea gen. et spp. indet.	x	x	x		x	x	x
<i>Philodina roseola</i> Ehrenberg, 1832*			x				
Class Monogononta							
<i>Cephalodella catellina</i> (Müller, 1786)		x					
<i>Cephalodella elegans</i> Myers, 1924	x						
<i>Cephalodella forficula</i> (Ehrenberg, 1838)	x	x					
<i>Cephalodella gibba</i> (Ehrenberg, 1830)	x	x					
<i>Cephalodella gracilis</i> (Ehrenberg, 1830)		x					
<i>Cephalodella intuta</i> Myers, 1924	x	x					
<i>Cephalodella labiosa</i> Wulfert, 1940*		x					
<i>Cephalodella limosa</i> Wulfert, 1937		x					
<i>Cephalodella megaloccephala</i> (Glascott, 1893)	x	x					
<i>Cephalodella tenuiseta</i> (Burn, 1890)	x	x					
<i>Cephalodella</i> spp.	x						x
<i>Cohurella adriatica</i> Ehrenberg, 1831		x		x	x		

Continued overleaf

Table 2. Continued

Taxon	Võrtsjärv	Saadjärv	Verevi	Männiku	Nõva	Pirita	Narva-Jõesuu
<i>Colurella colurus</i> (Ehrenberg, 1830)	x	x			x	x	
<i>Colurella dicentra</i> (Gosse, 1887)	x				x		
<i>Colurella geophila</i> Donner, 1951					x		
<i>Colurella hindenburgi</i> Steinecke, 1916					x		x
<i>Colurella marinovi</i> Althaus, 1957					x		x
<i>Dicranophorus capucinus</i> Harring et Myers, 1928	x	x					
<i>Dicranophorus hercules</i> Wiszniewski, 1932	x	x					
<i>Dicranophorus leptodon</i> Wiszniewski, 1934*	x						
<i>Dicranophorus semnus</i> Harring et Myers, 1928*	x						
<i>Dicranophorus sigmoides</i> Wulfert, 1950		x					
<i>Elosa spinifera</i> Wiszniewski, 1932				x			
<i>Elosa worrallii</i> Lord, 1891*				x			
<i>Encentrum belluinum</i> Harring et Myers, 1928					x	x	x
<i>Encentrum boreale</i> Harring et Myers, 1928					x	x	x
<i>Encentrum limicola</i> Otto, 1936					x		
<i>Encentrum marinum</i> (Dujardin, 1841)					x	x	x
<i>Encentrum matthesi</i> Remane, 1949					x		x
<i>Encentrum rousseleti</i> (Lie-Pettersen, 1905)	x						
<i>Encentrum uncinatum</i> (Milne, 1886)	x						
<i>Euchlanis dilatata</i> Ehrenberg, 1832		x					
<i>Gastropus stylifer</i> Imhof, 1891		x		x			
<i>Keratella cochlearis</i> (Gosse, 1851)		x	x	x		x	x
<i>Keratella cruciformis</i> (Thompson, 1892)					x		
<i>Keratella hiemalis</i> Carlin, 1943	x	x					
<i>Keratella quadrata</i> (Müller, 1786)					x	x	
<i>Lecane bulla</i> (Gosse, 1851)		x					
<i>Lecane closterocerca</i> (Schmarda, 1859)	x	x	x	x			
<i>Lecane doryssa</i> Harring, 1914*			x				
<i>Lecane flexilis</i> (Gosse, 1886)	x	x	x				
<i>Lecane galeata</i> (Bryce, 1892)	x	x					
<i>Lecane hamata</i> (Stokes, 1896)		x	x				

Taxonomic composition of zoopsammon in Estonian waters

Table 2. Continued

Taxon	Võrtsjärv	Saadjärv	Verevi	Männiku	Nõva	Pirita	Narva-Jõesuu
<i>Lecane luna</i> (Müller, 1776)		x	x		x		
<i>Lecane nana</i> (Murray, 1913)							x
<i>Lecane perpusilla</i> (Hauer, 1929)		x					
<i>Lecane psammophila</i> (Wiszniewski, 1932)	x	x					x
<i>Lecane punctata</i> (Murray, 1913)	x	x					
<i>Lecane pusilla</i> Harring, 1914			x		x		
<i>Lecane scutata</i> (Harring et Myers, 1926)*	x	x		x			
<i>Lecane stenroosi</i> (Meissner, 1908)			x				
<i>Lecane subulata</i> (Harring et Myers, 1926)		x		x			
<i>Lepadella ovalis</i> (Müller, 1786)	x	x					
<i>Lepadella patella</i> (Müller, 1773)	x	x	x	x			
<i>Lindia torulosa</i> Dujardin, 1841			x		x		x
<i>Monommata</i> sp.*			x				
<i>Mytilina mucronata</i> (Müller, 1773)		x					
<i>Notholca squamula</i> (Müller, 1786)	x	x			x		
<i>Notommata cyrtopus</i> Gosse, 1886		x					
<i>Notommata</i> cf. <i>doneta</i> Harring et Myers, 1924						x	
<i>Notommata stitista</i> Myers, 1937	x						
<i>Pleurata vernalis</i> (Wulfert, 1935)*				x			
<i>Polyarthra dolichoptera</i> Idelson, 1925	x						
<i>Polyarthra luminosa</i> Kutikova, 1962				x			
<i>Polyarthra remata</i> Skorikov, 1896				x			
<i>Proales globulifera</i> (Hauer, 1921)					x	x	x
<i>Proales halophila</i> Remane, 1929					x	x	x
<i>Proales reinhardti</i> (Ehrenberg, 1834)					x	x	x
<i>Proales theodora</i> (Gosse, 1887)					x	x	x
<i>Proales</i> spp.	x					x	
<i>Proalinopsis caudatus</i> (Collins, 1872)						x	x
<i>Synchaeta cecilia</i> Rousselet, 1902					x		x
<i>Synchaeta tremula</i> (Müller, 1786)							x
<i>Trichocerca dixonuttalli</i> (Jennings, 1903)	x	x			x	x	x
<i>Trichocerca intermedia</i> (Stenroos, 1898)	x	x					
<i>Trichocerca obtusidens</i> (Olofsson, 1918)		x					
<i>Trichocerca rousseleti</i> (Voigt, 1902)		x					

Continued overleaf

Table 2. Continued

Taxon	Võrtsjärv	Saadjärv	Verevi	Männiku	Nõva	Pirita	Narva-Jõesuu
<i>Trichocerca similis</i> (Wierzejski, 1893)		x			x		x
<i>Trichocerca tenuidens</i> (Hauer, 1931)*		x					
<i>Trichocerca tenuior</i> (Gosse, 1886)	x	x			x		x
<i>Trichotria pocillum</i> (Müller, 1776)		x					
<i>Trichotria truncata</i> (Whitelegge, 1889)							x
<i>Wierzejskiella sabulosa</i> (Wiszniewski, 1932)	x						x
<i>Wierzejskiella velox</i> (Wiszniewski, 1932)	x	x					
<i>Wigrella depressa</i> Wiszniewski, 1932*	x	x					
Phylum Annelida							
Class Polychaeta							
<i>Hediste diversicolor</i> (Müller, 1776)					x		
Polychaeta juv.					x		x
Class Clitellata							
Clitellata indet.	x			x			
<i>Chaetogaster diastrophus</i> (Gruithuisen, 1828)		x					
<i>Chaetogaster setosus</i> (Svetlov, 1925)		x					
<i>Chaetogaster</i> sp.		x					
<i>Lumbricillus lineatus</i> (Müller, 1774)					x		
<i>Marionina</i> sp.					x	x	x
<i>Nais elinguis</i> Müller, 1774					x		x
<i>Paranais litoralis</i> (Müller, 1780)						x	
Tubificidae juv.		x					
Phylum Mollusca							
Class Bivalvia							
Bivalvia juv.		x					
Phylum Nematoda							
Nematoda indet.	x	x	x	x	x	x	x
Class Adenophorea							
Leptolaimidae indet.	x						
<i>Prochromadora</i> sp.*					x		
<i>Microlaimus</i> sp.					x		
Enoplida indet.		x					

Taxonomic composition of zoosammon in Estonian waters

Table 2. Continued

Taxon	Võrtsjärv	Saadjärv	Verevi	Männiku	Nõva	Pirita	Narva-Jõesuu
<i>Enoplolaimus</i> sp.*						x	
<i>Amphimonhystera</i> sp.*						x	
<i>Linhystera</i> sp.*					x	x	x
<i>Retrotheristus</i> sp.*					x		
<i>Valvaelaimus</i> sp.*					x		
Phylum Tardigrada							
Class Eutardigrada							
<i>Milnesium</i> sp.	x	x		x			
Class Heterotardigrada							
<i>Oreella</i> sp.					x		x
Phylum Arthropoda							
Subphylum Chelicerata							
Class Arachnida							
Arachnida indet.	x	x			x		
Subphylum Tetraconata							
Class Maxillopoda							
Harpacticoida gen. et spp. indet.	x	x		x	x	x	x
<i>Harpacticus uniremis</i> Krøyer, 1842		x			x		
<i>Parastenocaris brevipes</i> Kessler, 1913		x		x	x		
<i>Mesocyclops leukarti</i> (Claus, 1857)		x					
Cyclopidae juv.	x	x					
Nauplii indet.			x	x	x	x	x
Class Branchiopoda							
<i>Alona</i> sp.			x				
<i>Chydorus sphaericus</i> (Müller, 1776)	x	x					
<i>Peracantha truncata</i> (Müller, 1785)		x					
Class Ostracoda							
Ostracoda indet.		x	x	x		x	
Class Insecta							
Ephemeroptera indet.		x					
Diptera juv.	x	x	x		x	x	x
Number of taxa: 156	65	81	42	25	61	32	42

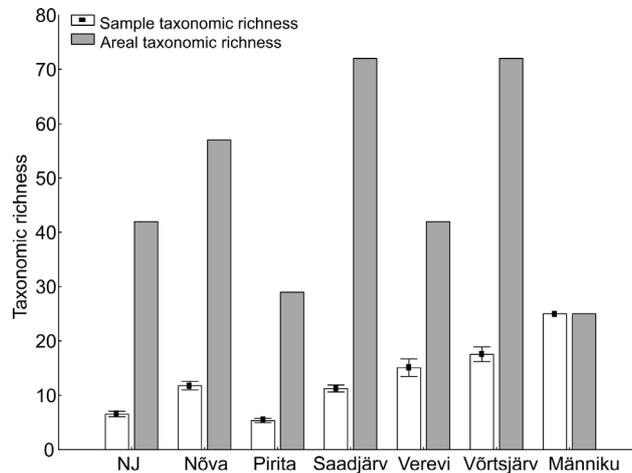


Fig. 2. Sample taxonomic richness (\pm SE) in the studied beaches in 2011–2012 and in Lake Männiku (represented by a single sample). NJ – Narva-Jõesuu.

Rotifers are one of the main groups of zoopsammon. As compared to other psammonic taxa, rotifers have received much more attention (e.g. Bielańska-Grajner, 2001, 2005; Ejsmont-Karabin, 2001, 2003, 2005; Thane-Fenchel, 1968), at least in freshwater habitats. This gives a possibility of comparing communities among different water bodies and making assumptions about the ecological status and overall taxonomic richness of a water body. Rotifers are ideal for analysing relationships between habitat and community as this group of invertebrates are very diverse, giving often the highest number of species to local diversity, and cosmopolitan to a large extent (Pejler, 1995; Segers, 2008). In our material, the majority of rotifer species belong to the families Dicranophoridae (18% of the 84 identified species), Notommatidae (18%), and Lecanidae (18%). The most diverse genus was *Lecane* (15 species), followed by *Cephalodella* (10) and *Encentrum* (7). Domination of these families and genera is typical of psammonic communities (Schmid-Araya, 1998). According to the present information on global distribution of rotifers (Segers, 2007; Jersabek and Leitner, 2013), of the rotifer species recorded in the psammon of the studied water bodies, 48 (58%) are cosmopolitan and other 22 (27%) have a wide distribution covering both Palaearctic and Nearctic, several of these are also known from some other biogeographic regions. Eleven (13%) species are restricted to Palaearctic. The occurrence of *Encentrum belluinum* in the samples from the Estonian coast of the Gulf of Finland and *Notommata stitista* in Lake Võrtsjärv is of interest. These two species are presently reported only from the Nearctic region. Probably *N. stitista* is a rare species, as it has not been found since its discovery (Nogrady et al., 1995). Our findings indicate a potential Holarctic distribution of these two species. *Cephalodella intuta*, *C. tenuiseta*, *Lecane doryssa*, *Notommata doneta*, and *Pleurata vernalis* are also regarded as rather rare (Nogrady et al., 1995; Segers, 1995). The presence of *L. doryssa* and *L. punctata* is noteworthy for their

known cosmotropical–cosmosubtropical distribution (Segers, 1995). The range of these warm-stenotherms appears to be wide, reaching the temperate zone where they can find suitable conditions during summer months. A peculiar female specimen of *Monommata* sp. was encountered in a sample from Lake Verevi. The rotifer has toes of equal length like *Monommata aequalis* (Ehrenberg, 1830), but differs from it having a smaller body and uniformly wide blade-like toes, which to our knowledge are dissimilar from the previously described *Monommata* taxa. However, further study based on sufficient material is needed for a formal description of a possible new taxon.

Testate amoebae are another key component of psammon, although much less information is available about this highly diverse group. Unfortunately, we currently lack the taxonomic competence of free-living nematodes in Estonia. Therefore nematodes have received very little attention in freshwater psammon and it is not possible to make any interregional comparisons.

In the studied lakes the number of taxa decreased with increasing trophic state. The zoopsammon of the mesotrophic Lake Saadjärv had the highest taxonomic diversity among the studied beaches with a total of 81 taxa from 10 phyla. Altogether, 65 taxa were found from the eutrophic Lake Võrtsjärv. The zoopsammon of the hypertrophic Lake Verevi consisted only of 42 taxa. However, this pattern applied only to the overall number of taxa and the number of rotifer taxa. The number of testate amoebae species had a reversed pattern. Nevertheless, as the total number of samples varied from lake to lake, it may not reflect the true relationship between diversity and trophic state of the lake. Moreover, dominant ciliates, nematodes, and bdelloids were generally not identified to lower taxa, which may further bias the overall pattern of diversity. However, a similar relationship between the number of rotifer species and trophic state was found in a study carried out in Poland, where more rotifer species were found in lakes with a lower trophic status (Bielańska-Grajner, 2005). In another study in the same ecoregion the species richness was notably lower in hypertrophic lakes (Ejsmont-Karabin, 2003).

Taxonomic richness per sample was the highest in Lake Männiku, probably due to good environmental conditions for a large number of taxa at the time of sampling. Based on the sampling campaign carried out in 2011–2012, the highest average number of taxa per sample was recorded in Lake Võrtsjärv and lowest in Lake Saadjärv (Fig. 2). In 2008 the average number of taxa per sample in Lake Saadjärv was somewhat higher, yet lower than in the hypertrophic Lake Verevi in 2011–2012. While Saadjärv has a lower trophic status than the other studied lakes it is possible that the habitat can support a lower number of taxa in a small patch at a given time and the overall high number of taxa in the lake was provided by the high patchiness and complex seasonal dynamics.

In coastal areas the sample taxonomic richness was lower than in lake beaches. It followed the same pattern as sea-scape taxonomic richness, indicating that compared to lakes beach habitats in coastal areas were more homogeneous in space and time.

Our study also suggested a similar pattern between the trophic state and the number of psammic taxa in coastal beaches with the number of taxa decreasing with increasing anthropogenic impact. The lowest taxonomic richness (32 taxa, including 15 rotifer and 4 testate amoebae taxa) was recorded from Pirita Beach, which is located within Tallinn City adjacent to a yacht harbour and is a very popular beach. However, differently from lakes the number of testate amoebae taxa was likewise lower in coastal beaches with a higher anthropogenic impact.

Only 25 taxa were found from Lake Männiku. As this lake was represented by only one sample, the true biodiversity can be probably much higher. Moreover, the lake was sampled in May, which was not a season of high psammic taxonomic richness in any of the other studied lakes. Yet this sample represented the highest zoopsammon abundance recorded in Estonia (279 ind cm⁻³) so far.

The overall zoopsammon abundance was generally much higher in lake beaches than in coastal beaches. The maximum psammic abundance reached 203 ind cm⁻³ in Lake Võrtsjärv and 92.3 ind cm⁻³ in Lake Saadjärv (Lokko et al., 2013), whereas for coastal beaches the respective value was only 46.6 ind cm⁻³.

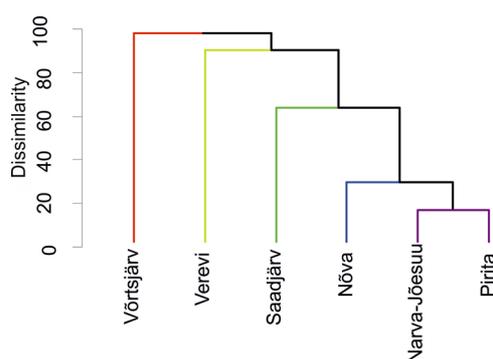
A total of 13 taxa of testate amoebae were recorded from the psammon of the Gulf of Finland in this study. Previously, Golemansky (1983) sampled beach sand from the Estonian coast of the Gulf of Finland and found 23 species of testate amoebae. Interestingly, the only overlapping taxa were *Cyphoderia ampulla*, *Psammonobiotus communis*, and *Cyclopyxis* sp. This is possibly caused by different sampling and analysing techniques and a wider habitat range (up to 16 m landwards from the waterline) compared to our study. Freshwater beaches had more testate amoebae species than coastal beaches. The testate amoebae community of Lake Verevi with 23 testate amoebae taxa seemed to have an especially high taxonomic richness.

The psammic rotifer community of the Gulf of Finland was represented by 35 taxa. This is similar to the numbers recorded from interstitial habitats in Scandinavia where Thane-Fenchel (1968) found 28 interstitial rotifer species from Askö Harbor. In Nõva Beach with similar salinities we recorded 26 rotifer taxa. The number of rotifer species found in the psammon from lakes Võrtsjärv and Saadjärv resembles the numbers previously recorded from some Polish lakes with a similar trophic level; moreover, quite a few species overlapped in the two countries (Radwan and Bielańska-Grajner, 2001; Ejsmont-Karabin, 2005).

The coefficients of Sørensen similarity between the studied areas are presented in Table 3. Lake Männiku was not included in comparisons as it was represented by only one sample. According to the Sørensen similarity coefficient, the zoopsammon communities of coastal sampling sites were much more similar with one another than zoopsammon at different lakes, and rotifer communities differed much more from beach to beach than testate amoebae communities. SIMPROF analysis showed that all sampling sites had significantly different psammic communities. Nevertheless, the coastal sampling sites clustered together, showing that their communities were more similar to each other than those of lakes (Figs 3 and 4).

Table 3. Sørensen similarity coefficient between the studied areas

	All taxa	Only rotifer taxa	Only testate amoebae taxa
Võrtsjärv vs Saadjärv	0.566	0.590	0.606
Võrtsjärv vs Verevi	0.374	0.170	0.619
Saadjärv vs Verevi	0.279	0.246	0.324
Võrtsjärv vs Nõva	0.238	0.200	0.194
Võrtsjärv vs Pirita	0.186	0.163	0.000
Võrtsjärv vs Narva-Jõesuu	0.243	0.207	0.083
Saadjärv vs Nõva	0.298	0.229	0.308
Saadjärv vs Pirita	0.214	0.136	0.111
Saadjärv vs Narva-Jõesuu	0.230	0.176	0.211
Verevi vs Nõva	0.233	0.205	0.229
Verevi vs Pirita	0.189	0.143	0.000
Verevi vs Narva-Jõesuu	0.190	0.162	0.071
Nõva vs Pirita	0.516	0.537	0.500
Nõva vs Narva-Jõesuu	0.641	0.640	0.471
Pirita vs Narva-Jõesuu	0.595	0.564	0.444

**Fig. 3.** A dendrogram of the Similarity Profile Analysis based on the total average number of species showing statistical differences among sites in terms of psammonic communities. Different colours denote statistically different clusters. NJ – Narva-Jõesuu.

Although this study compiled different data sets with different spatial and temporal extent, we were able to discover some generic psammonic patterns in the Estonian fresh- and brackish-water bodies. In general, the abundance and richness of psammonic taxa were higher in lake than in coastal beaches. Besides, variability between samples of psammon communities was higher in lake than in coastal beaches. Psammon taxonomic richness was higher in beaches with a lower trophic state and/or anthropogenic impact. However, such relationship appeared only at a wide spatial scale pooling a large number of samples. The sample taxonomic richness followed regional taxonomic richness only in coastal areas. This also suggests that the communities of psammon vary more in space and time in lake beaches than in coastal beaches.

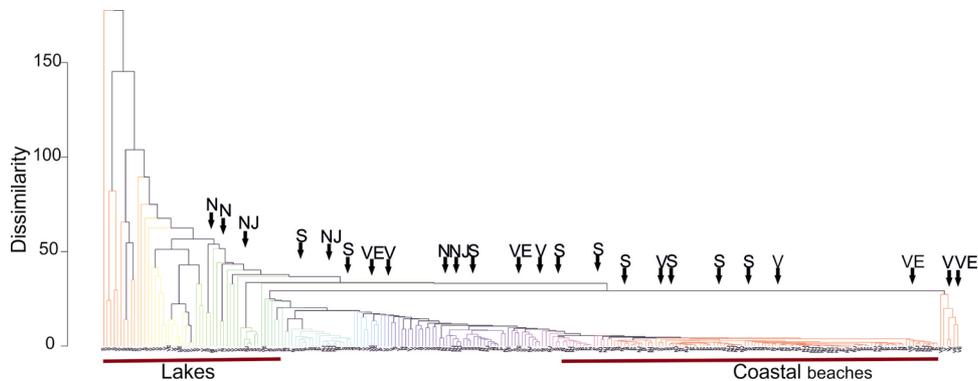


Fig. 4. A dendrogram of the Similarity Profile Analysis showing statistical differences among samples in terms of psammic communities. Different colours denote statistically different clusters. Areas marked with a red line and the text ‘Lakes’ or ‘Coastal beaches’ denote areas in the dendrogram dominated by samples from lake beaches or from coastal beaches, respectively. Coastal beaches: N – Nõva Beach, NJ – Narva-Jõesuu Beach, P – Piritä Beach; lake beaches: V – Võrtsjärv, VE – Verevi, S – Saadjärv.

ACKNOWLEDGEMENTS

Funding for this research was provided by Institutional research funding IUT02-20 of the Estonian Research Council. The study has been also supported by the projects ‘The status of marine biodiversity and its potential futures in the Estonian coastal sea’ No. 3.2.0801.11-0029 of the Environmental Protection and Technology Programme of the European Regional Fund. We also thank Dr Tarmo Timm at the Centre for Limnology, the Estonian University of Life Sciences, for identifying the annelid taxa. We are also grateful for Dr Ilmar Kotta for estimating the organic content of sand in samples.

REFERENCES

- Alekperov, I., Buskey, E., and Snegovaya, N. 2007. The free-living ciliates of the Mexican Gulf coast near Port Aransas city and its suburbs (South Texas, USA). *Protistology*, **5**, 101–130.
- 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.
- Bielańska-Grajner, I. and Poznańska, M. 2010. The biodiversity of psammic rotifers in Włocławek Reservoir. *Oceanological and Hydrobiological Studies*, **39**, 111–117.
- Cavalier-Smith, T. 2010. Kingdoms Protozoa and Chromista and the eozoan root of the eukaryotic tree. *Biology Letters*, **6**, 342–345.
- Clarke, K. R., Somerfield, P. J., and Gorley, R. N. 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota–environment linkage. *Journal of Experimental Marine Biology and Ecology*, **366**, 56–69.
- Czapik, A. and Fyda, I. 1992. Contribution to the knowledge of psammophilic ciliates from the Baltic Sea. *Acta Protozoologica*, **31**, 109–114 (in French with English summary).

- De Smet, W. H. and Chernyshev, A. V. 2006. Two new species of Dicranophoridae (Rotifera: Monogononta) from Peter the Great Bay, Sea of Japan. *Journal of the Marine Biological Association of the United Kingdom*, **86**, 657–663.
- Eichwald, E. v. 1849. Zweiter Nachtrag zur Infusorienkunde Russlands. In *Bulletin de la Société imp. des naturalistes de Moscou*. T. XXII (Ref. Levander, 1894).
- Eichwald, E. v. 1852. Dritter Nachtrag zur Infusorienkunde Russlands. In *Bulletin de la Société imp. des naturalistes de Moscou*. T. XXV (Ref. Levander, 1894).
- Ejsmont-Karabin, J. 2001. Psammon rotifers in two lakes of different trophic state – their abundance, species structure and role in phosphorus cycling. *Verhandlungen des Internationalen Verein Limnologie*, **27**, 3848–3851.
- Ejsmont-Karabin, J. 2003. Rotifera of lake psammon: community structure versus trophic state of lake waters. *Polish Journal of Ecology*, **51**, 5–35.
- Ejsmont-Karabin, J. 2005. Short time-response of psammonic communities of Rotifera to abiotic changes in their habitat. *Hydrobiologia*, **546**, 423–430.
- Gheskiere, T., Hoste, E., Vanaverbeke, J., Vincx, M., and Degraer, S. 2004. Horizontal zonation patterns and feeding structure of marine nematode assemblages on a macrotidal, ultra-dissipative sandy beach (De Panne, Belgium). *Journal of Sea Research*, **52**, 211–226.
- Gheskiere, T., Vincx, M., Urban-Malinga, B., Rossano, C., Scapini, F., and Degraer, S. 2005. Nematodes from wave-dominated sandy beaches: diversity, zonation patterns and testing of the isocommunities concept. *Estuarine, Coastal and Shelf Science*, **62**, 365–375.
- Golemansky, V. 1983. Interstitial Thecamoebae (Rhizopoda: Arcellinida and Gromida) of the Soviet Finn Bay Coast. *Acta Zoologica Bulgarica*, **23**, 3–8 (in Bulgarian).
- Golemansky, V. 1998. Interstitial testate Amoebae (Rhizopoda: Arcellinida and Gromida) from the Finnish coast of the Baltic Sea and summary check list of the interstitial testate Amoebae in the Baltic Sea. *Acta Protozoologica*, **37**, 133–137.
- Halanych, K. M. 2004. The new view of animal phylogeny. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 229–256.
- HELCOM. 2003. The Baltic marine environment 1999–2002. *Baltic Sea Environment Proceedings*, **87**.
- Jersabek, C. D. and Leitner, M. F. 2013. The Rotifer World Catalog. World Wide Web electronic publication. <http://www.rotifera.hausdernatur.at/> (accessed 07.07.2014).
- Jersabek, C. D., De Smet, W. H., Fischer, C., Fontaneto, D., Michaloudi, E., Wallace, R. L., and Segers, H. 2012. List of available names in zoology, candidate part Phylum Rotifera, species-group names established before 1 January 2000. 1) Completely defined names (A-list), 217 pp. and 2) incompletely defined names, with no types known (B-list). http://iczn.org/sites/iczn.org/files/LAN_CandidatePart-Rotifera-2012-03-22.pdf (accessed 07.07.2014).
- Kalinowska, K. 2008. Psammon ciliates: diversity and abundance in hygroarenal of eutrophic lake. *Polish Journal of Ecology*, **56**, 259–271.
- Kalinowska, K. 2013. Community structure of psammon ciliates in sandy beaches of lakes. *Oceanological and Hydrobiological Studies*, **42**, 14–21.
- Kotwicki, L., De Troch, M., Urban-Malinga, B., Gheskiere, T., and Wesawski, J. M. 2005a. Horizontal and vertical distribution of meiofauna on sandy beaches of the North Sea (The Netherlands, Belgium, France). *Helgoland Marine Research*, **59**, 255–264.
- Kotwicki, L., Szymelfenig, M., De Troch, M., Urban-Malinga, B., and Weślowski, J. M. 2005b. Latitudinal biodiversity patterns of meiofauna from sandy littoral beaches. *Biodiversity and Conservation*, **14**, 461–474.
- Krebs, J. C. 1989. *Ecological Methodology*. New York.
- Kutikova, L. and Haberman, J. 1986. Rotifers (Rotatoria) of Lake Võrtsjärv. *Proceedings of the Academy of Sciences of the Estonian SSR. Biology*, **35**, 113–121.

- Levander, K. M. 1894. Materialien zur Kenntniss der Wasserfauna in der Umgebung von Helsingfors, mit besonderer Berücksichtigung der Meeresfauna. II. Rotatoria. *Acta Societatis pro Fauna et Flora Fennica*, **XII**.
- Liu, H., Zhang, Z., Fan, S., Hua, E., and Deng, K. 2008. Seasonal variability in free-living marine nematode community structure in a sandy beach of the Taiping Bay of Qingdao, China. *Acta Oceanologica Sinica*, **27**, 102–115.
- Lokko, K. and Virro, T. 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., Virro, T., and Kotta, J. 2013. Testing effects of shore height level, sediment characteristics and vegetation cover on the seasonality of zoopsammon communities in the two boreal lakes differing in their trophic state. *Hydrobiologia*, **700**, 1–8.
- Lokko, K., Kotta, J., and Virro, T. 2014. 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 morfoomeetrilised andmed ja veevahetus* [Morphometrical data and water exchange of larger Estonian lakes]. Tallinn (in Estonian).
- Mäemets, A. 1977. *Eesti NSV järved ja nende kaitse* [Lakes of the Estonian S.S.R. and their protection]. Valgus, Tallinn (in Estonian).
- Maria, T. F., Vanaverbeke, J., Esteves, A. M., De Troch, M., and Vanreusel, A. 2012. The importance of biological interactions for the vertical distribution of nematodes in a temperate ultra-dissipative sandy beach. *Estuarine, Coastal and Shelf Science*, **97**, 114–126.
- Maria, T. F., Vanaverbeke, J., Gingold, R., Esteves, A. M., and Vanreusel, A. 2013. Tidal exposure or microhabitats: what determines sandy-beach nematode zonation? A case study of a macrotidal ridge-and-runnel sandy beach in Belgium. *Marine Ecology*, **34**, 207–217.
- Mazei, Y. A. and Tsyganov, A. N. 2006. *Freshwater Testate Amoebae*. KMK, Moscow (in Russian).
- Melone, G., Ricci, C., Segers, H., and Wallace, R. L. 1998. Phylogenetic relationships of phylum Rotifera with emphasis on the families of Bdelloidea. *Hydrobiologia*, **387/388**, 101–107.
- Nesteruk, T. 2007. Diversity and abundance of Gastrotricha in the psammon of mesotrophic lake. *Polish Journal of Ecology*, **55**, 833–839.
- Nogrady, T., Pourriot, R., and Segers, H. 1995. *Rotifera. Vol. 3: The Notommatidae and the Scaridiidae. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World 8*. SPB Academic Publishing bv., Amsterdam.
- Ott, I. (ed.). 2007. *Saadjärve limnoloogilised uurimused II* [Limnological studies of Lake Saadjärv]. Eesti Maaülikooli Põllumajandus- ja Keskkonnainstituudi Limnoloogiakeskus (in Estonian).
- Ott, I., Kõiv, T., Nõges, P., Kisand, A., Järvalt, A., and Kirt, E. 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.
- Pejler, B. 1995. Relation to habitat in rotifers. *Hydrobiologia*, **313/314**, 267–278.
- Pitkänen, H., Kiirikki, M., Savchuk, O., Räike, A., Korpinen, P., and Wulff, F. 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., Lehtoranta, J., and Peltonen, H. 2008. The Gulf of Finland. In *Ecology of Baltic Coastal Waters* (Schiewer, U., ed.), pp. 285–308. Springer, Berlin.
- R Core Team. 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Radwan, S. and Bielańska-Grajner, I. 2001. Ecological structure of psammic rotifers in the ecotonal zone of Lake Piaseczno (eastern Poland). *Hydrobiologia*, **446/447**, 221–228.
- Roskov, Y., Kunze, T., Orrell, T., Abucay, L., Paglinawan, L., Culham, A., Bailly, N., Kirk, P., Bourgoïn, T., Baillargeon, G., Decock, W., De Wever, A., and Didžiulis, V. (eds). 2014.

- Species 2000 & ITIS Catalogue of Life, 2014. Annual Checklist. Digital resource at www.catalogueoflife.org/annual-checklist/2014. Species 2000: Naturalis, Leiden, the Netherlands (accessed 29.06.2014).
- 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.
- Segers, H. and Chittapun, S. 2001. The interstitial Rotifera of a tropical freshwater peat swamp on Phuket Island, Thailand. *Belgian Journal of Zoology*, **131**, 65–71.
- Schmid-Araya, J. M. 1998. Rotifers in interstitial sediments. *Hydrobiologia*, **387/388**, 231–240.
- Sørensen, M. V. 2001. Two new species of the family Dicranophoridae (Rotifera, Ploima) from the littoral psammon, with notes on other brackish water rotifers in Denmark. *Hydrobiologia*, **452**, 121–128.
- Sørensen, M. V. and Giribet, G. 2006. A modern approach to rotiferan phylogeny: combining morphological and molecular data. *Molecular Phylogenetics and Evolution*, **40**, 585–608.
- Tamre, R. 2006. *Eesti järvede nimestik. Looduslikud ja tehiskärved* [A list of Estonian Lakes. Natural and Man-made Lakes]. Keskkonnaministeeriumi Info- ja Tehnokeskus, Tallinn (in Estonian).
- Thane-Fenchel, A. 1968. Distribution and ecology of non-planktonic brackish-water rotifers from Scandinavian waters. *Ophelia*, **5**, 273–297.
- Timm, T. (ed.). 1973. *Võrtsjärv* [Lake Võrtsjärv]. Valgus, Tallinn (in Estonian).
- Tuvikene, L., Kisand, A., Tõnno, I., and Nõges, P. 2004. Chemistry of lake water and bottom sediments. In *Lake Võrtsjärv* (Haberman, J., Pihu, E., and Raukas, A., eds), pp. 89–102. Estonian Encyclopaedia Publishers, Tallinn.
- Tzschaschel, G. 1983. Seasonal abundance of psammon rotifers. *Hydrobiologia*, **104**, 275–278.
- Whitaker, D. and Christman, M. 2014. clustsig: Significant Cluster Analysis. R package version 1.1.
- Whitman, R. L. and Clark, W. J. 1984. Ecological studies of the sand-dwelling community of an east Texas stream. *Freshwater Invertebrate Biology*, **3**, 59–79.
- WoRMS Editorial Board. 2014. World Register of Marine Species. <http://www.marinespecies.org> at VLIZ (accessed 29.06.2014).