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KÜLLI LOKKO

Seasonal and spatial variability of zoopsammon communities in relation to environmental parameters

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Estonian Marine Institute and Department of Zoology, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following papers, which are referred to in the text with the respective Roman numerals:

I. Lokko, K., Virro, T. & Kotta, J. 2014. Taxonomic composition of zoopsammon in the fresh and brackish waters of Estonia, the Baltic province ecoregion of Europe. *Estonian Journal of Ecology* 63: xx–xx (accepted for publication)

II. Lokko, K., Virro, T. & 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.

III. Lokko, K. & 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.

IV. Lokko, K., Kotta, J. & 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.

The papers are reproduced by kind permission of the Estonian Academy Publishers (paper I), the Springer Science+Business Media (papers II and III) and Biological Society of Washington (paper IV).

The author contributed to the design of all the studies, was responsible for collecting all the field data, had substantial role in analysing the data, and is the leading author of all four publications.

1. INTRODUCTION

Sandy beaches are dynamic environments that may seem almost deserted, yet are deeming with life in closer observation (McLachlan & Brown, 2006). The dynamic nature of sandy beaches renders them an unstable and very fluctuating habitat and yet beach sands host a large variety of species (Pejler, 1995; Schmid-Araya, 1998). The representatives of protists, nematodes, rotifers, small crustaceans, tardigrades, gastrotrichs, turbellarians, oligochaetes and insect larvae are regularly found from this habitat (Thane-Fenchel, 1968; Whitman & Clark, 1984; Schmid-Araya, 1998, Kotwicki et al., 2005a,b).

While in the marine literature the sandy beach meiofauna is mostly referred to simply as meiofauna, *psammon* is a special term for microscopic organisms inhabiting the interstitial water of sandy beaches. Nowadays the term *zoopsammon* is primarily used for freshwater sandy beach meiofauna, although its habitat was originally defined as ‘a transitional zone between aquatic and soil habitats’ (Schmid-Araya, 1998). Psammic habitat (often referred to as *arenal* or *psammolittoral zone* in lakes) differs from benthic environment as it does not have overlying water layer: sandy sediment is regularly exposed to air for a longer or shorter period of time. In marine environments areas adjacent to the waterline in nontidal beaches and the intertidal zone in tidal beaches can be considered as psammic habitat if the sediment consists of sand and is regularly exposed (papers I and IV).

As the narrow beach zone meiofauna consists of many specialised species (Nogrady et al., 1993), this zone is certainly important from the perspective of biodiversity. In addition, the populations in beach sand can reach extremely high densities as compared to their adjacent habitats (Ejsmont-Karabin, 2003; Giere, 2009) and these communities may significantly contribute to the transfer of energy and matter between terrestrial ecosystems and water bodies.

Zoopsammon communities have received relatively little attention compared to lower littoral and sublittoral meiobenthos, and have been seldom treated as a single entity, as the majority of studies include information only on one or a few taxonomic groups (phyla or lower units). Moreover, frequently these studies have a strong taxonomic focus, but ecological questions, i.e. relations to their habitat and biotic interactions, are still often neglected.

The taxonomic composition and dynamics of psammon communities are apparently controlled by many biotic and abiotic factors and their interactions. However, to date only a limited number of environmental factors have been included in studies and the results are often inconsistent. Psammon seasonality has received quite large attention, especially in freshwater ecosystems (e.g. Haque et al., 1997; Ejsmont-Karabin, 2001; Radwan et al., 2001; Radwan & Bielańska-Grajner 2001; Bielańska-Grajner, 2005; Covazzi Harriague et al., 2013). However, seasonal trends are rather taxon specific (e.g. Thane-Fenchel, 1968) and interrelated with many environmental and biotic factors. Sediment structure and grain size are considered a key habitat characteristic for meiofauna

(Nogrady et al., 1993; Ejsmont-Karabin, 2004; Giere, 2009) and salinity has a substantial effect in marine environments (Mazei & Burkovsky, 2006; Giere, 2009). Nevertheless, even these factors/environmental variables are not necessarily related with psammic communities (Bielańska-Grajner, 2005; Ngo et al., 2013). Other factors that are likely important in structuring beach meiofaunal communities (e.g. water quality/water body trophic state, content of sediment organic matter and chlorophyll *a*, vegetation coverage) have received relatively little attention (e.g. Ejsmont-Karabin, 2003; Covazzi Harriague et al., 2013).

The spatial patterns of beach meiofauna are expected to vary as a function of distance from the waterline and the sediment surface (Giere, 2009). Since the works of Wiszniewski in the 1930s, three shore height levels have been traditionally distinguished with respective psammon assemblages: hydroarenal – slightly submerged sediment (inhabited by hydropsammon), hygroarenal – wetted beach at the waterline (hygropsammon) and euarenal – moist beach upwards from the waterline (eupsammon) (Schmid-Araya, 1998; Ejsmont-Karabin, 2004). However, while it has been shown that the uppermost few centimetres of beach sand host the majority of nematodes, harpacticoids, turbellarians (Kotwicki et al., 2005b) and ciliates (Mazei & Burkovsky, 2003), little is known about the horizontal patterns of beach meiofauna. The spatial distribution of psammon seems to be site and taxon specific as no general patterns have been found (e.g. Golemansky, 1976, 1998a,b; Gheskiere et al., 2005a; Bielańska-Grajner & Poznańska, 2010; Covazzi Harriague et al., 2013).

In freshwater psammic habitats rotifers have received relatively much attention (e.g. Pejler, 1995; Bielańska-Grajner, 2001; Segers & Chittapun, 2001) while nematodes tend to be the most thoroughly researched taxa in marine beaches (e.g. Gheskiere et al., 2004, 2005; Liu et al., 2008; Maria et al., 2012, 2013). However data on sandy beach meiofauna from the Baltic Sea is to date very limited including only some local case studies (e.g. Czapik & Fyda, 1992; Golemansky, 1983, 1998b; Sørensen, 2001; Gheskiere et al., 2005) and even less is known about the psammon in Estonia.

Objectives and hypotheses

To date, the only works on the interstitial beach fauna in Estonia are from the 1980s about psammic testate amoebae from the Gulf of Finland (Golemansky, 1983) and rotifers from Lake Võrtsjärv (Kutikova & Haberman, 1986). Thus, one of the main objectives of the present thesis was to describe the psammic communities in different Estonian water bodies. Based on the earlier studies (e.g. Neel, 1948; Kotwicki et al., 2005b; Kalinowska, 2008), nematodes, rotifers and ciliates were expected to be the most abundant taxa in zoopsammon.

Rotifers have been dealt with in greater detail as they are considered important carbon transporters in freshwater food webs (Nogrady et al., 1993) and they are one of the main groups of zoopsammon. In paper III, psammic rotifer trophic traits and quantitative parameters are investigated at the seasonal scale, as trophic properties of organisms have proved to be particularly useful functional traits in community analyses.

Another broad objective of the thesis was to study the seasonal dynamics and spatial patterns of zoopsammon communities and to assess the role of key environmental variables in these patterns. Based on the above the specific hypotheses were as follows: (1) Seasonality is the key variable structuring the psammon communities with the communities expected to have the highest density and taxonomic richness in summer. (2) Sediment properties define the spatial patterns of psammic communities. (3) Species richness is related to the trophic state and anthropogenic impact of the water body with eutrophic water bodies having less intense competition for food and thus lower variability in psammic communities. (4) The majority of psammon taxa show species-specific responses to their environment. (5) Nematodes are abundant in heavily vegetated sites, as roots and degrading plant material increase the content of organic matter in sand.

2. MATERIALS AND METHODS

2.1. Study area

The present study is based on samples collected in 2008–2014 from Lake Saadjärv (papers I, II, III), Lake Võrtsjärv (papers I, II, III), Lake Verevi (paper I), Lake Männiku (paper I) and three sandy beaches along the Estonian coast of the Gulf of Finland, Baltic Sea (papers I, IV). The location of the sampling sites is shown in Figure 1.

Figure 1. Location of the sampling stations. Blue dots represent the sampled coastal beaches and red dots beaches of the studied lakes.

The three natural lakes (L. Saadjärv, L. Võrtsjärv and L. Verevi) were chosen as they belong to the same East Estonian drainage basin and are all characterised by somewhat alkaline waters. In addition, some background information (e.g. chemical parameters of water, trophic state) is available about these lakes. The mesotrophic L. Saadjärv is characterised by high water transparency, high hardness and slightly alkaline water (Ott, 2007). It is the deepest (max depth 25 m; Mäemets, 1977) and has the lowest trophic status of the studied lakes. Lake Saadjärv was sampled at two beaches several kilometres apart from each other. In 2008 the sampled beach was relatively remote, whereas the beach sampled in 2011–2012 was located adjacent to a local motorway and was popular among swimmers. However, both beaches had similar medium to coarse sands. The eutrophic L. Võrtsjärv is a large shallow lake (second largest in Estonia – surface area 27 000 ha; max depth 6 m) with a short water residence time (Timm, 1973; Tuvikene et al., 2004). The sampling site at L. Võrtsjärv was located in a remote locality at the eastern coast of the lake, where beach sand is often mixed with pebbles. The hypertrophic L. Verevi is the smallest of the studied lakes and relatively deep (max 11 m, average 3.6 m; surface area 12.6 ha) with a low water exchange rate (Loopmann, 1984; Ott et al., 2005). It is located in a small town of Elva and is also very much exploited by swimmers. The lake was sampled at the edge of the popular beach characterised by relatively fine sand. The youngest of the studied lakes is L. Männiku, which belongs to a complex of several lakes/water bodies within a sand quarry, which was established in the early 20th century. It is a moderately deep (max depth 9 m, average 5 m; surface area 118.7 ha) eutrophic lake of anthropogenic origin (Tamre, 2006; EEA Environmental Register, http://register.keskkonnainfo.ee/envreg/main?list=VEE&mount=view, accessed 14.08.2014), with steep slopes and medium to coarse sediment grain size.

The coastal sampling sites were located along the Estonian coast of the Gulf of Finland, Baltic Sea, 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 Gulf of Finland has a relatively large catchment area and freshwater inflow, therefore the gulf has a strong horizontal salinity gradient. The surface salinity in the gulf varies from 0 in 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 the most eutrophicated basins in the Baltic Sea area (HELCOM, 2003; Pitkänen et al., 2007). An overview of the studied beaches with their main environmental characteristics and sampling times is presented in Table 1.

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; NA – not analysed.

	Võrtsjärv	Saadjärv	Verevi	Männiku	Nõva	Pirita	Narva-Jõesuu
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 range (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	0.579 (0.446–0.775) mS	0.626 (0.399–0.942) mS	0.629 (0.513–0.711) mS	NA	11.05 (9.09–12.43) mS	11.19 (7.19–12.80) mS	5.46 (0.72–9.09) mS
Porewater salinity	NA	NA	NA	NA	5.41 (4–6.2) ppt	5.46 (3–6.6) ppt	2.4 (0–4) ppt
Sand temperature range	19.9 (8,7–30.2) °C	16.6 (5.1–28.3) °C	20.1 (7.7–32) °C	15.8 °C	15.67 (6.2–23.2) °C	15.16 (6–22.6) °C	14.99 (5.2–23.6) °C
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)

2.2. Sampling and analyses

The samples were collected with sharp-edged corers 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. Up to four samples were collected from each zone.

Corers with diameters of 2.9 cm and 4.75 cm were pushed down to a depth of 3−5 cm in the sand, depending on the sampling campaign. This sampling depth was chosen because according to previous studies the largest parts of the abundance and biomass of the majority of psammic taxa are concentrated in the upper few centimetres of the sediment (e.g. Bielańska-Grajner, 2001, 2004; Mazei & Burkovsky, 2003; Ejsmont-Karabin, 2008). Samples for studying the vertical zonation of psammon were taken from the euarenal down to 10 cm in the sand, and samples were divided into four subsamples: 0–1 cm, 1–2 cm, 2–3 cm and 3–10 cm. Altogether 362 samples were taken in 2008−2014 during the ice-free period between February and November.

To extract the animals, each sample was transferred to a plastic container and immediately rinsed three times with carbonated drinking water. Every time the supernatant was poured off into a plastic bottle and then the sample was fixed with Lugol's solution. Thereafter the samples were condensed to 100 ml by sedimentation for at least 4 days and siphoning off excess water. From each sample, five 2 ml subsamples were taken wherein all organisms were counted under microscope in a Bogorov chamber. For the identification, specimens were slide-mounted in glycerol and determined to the lowest possible taxon. Illoricate rotifers were identified by their trophy; these were dissolved out using the household disinfectant Domestos®, which contains sodium hypochlorite (NaClO <5%).

The nomenclature of higher taxonomic units is based on classifications in Halanych (2004), the Catalogue of Life (Roskov et al., 2013, 2014; papers II−IV and I, respectively) and the World Register of Marine Species (WoRMS Editorial Board, 2014; paper I) and that of rotifers on Melone et al. (1998) and Sørensen & Giribet (2006). The classification of protists is based on Mazei & Tsyganov (2006) and Cavalier-Smith (2010). The nomenclature of rotifer species follows Segers (2007) and Jersabek et al. (2012). For testaceans, Mazei & Tsyganov (2006) was used. In other cases, the Catalogue of Life (Roskov et al., 2013, 2014; papers II−IV and I respectively) was consulted.

At each sampling time various environmental parameters such as sand grain size and structure, vegetation coverage, sand organic matter and chlorophyll *a* content, pH, temperature and salinity were estimated. In addition, wave activity and the number of people at the beach segment were evaluated (paper IV). The details of measuring and estimating environmental parameters are described in papers II and IV.

2.3. Statistical analyses

The Sørensen index (Krebs, 1989) was used in papers I and III to evaluate similarity between zoopsammic communities of the sampling sites. In addition, in paper I a similarity profile (SIMPROF) test was applied (Clarke et al., 2008) to identify clusters of stations that are statistically dissimilar from each other. The SIMPROF test allows taking into account the abundances of taxa, not just the presences/absences (Clarke et al., 2008), thus it helps to identify differences in the dominance structure of psammon communities among different beaches and sampling sites.

In paper III, the Shannon diversity index (Margalef, 1957) was used to describe the diversity of communities and the Guild Ratio Index (Obertegger et al., 2011) was employed to analyse the trophic structure of the rotifer communities. To calculate the Guild Ratio Index, the 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; Obertegger et al., 2011). The Kruskal–Wallis test was used to analyse the relationship between vegetation coverage, coarseness of sand and psammic rotifers, as the data were not normally distributed and the number of samples was unequal. To detect differences in the diversity and GRI values between lakes, the Mann–Whitney U-test was applied as the simplest suitable statistical test. The STATISTICA software was used for both tests.

In paper II, the repeated measures analysis of covariance (RMA) was applied to relate the seasonal and horizontal patterns of psammic taxa in lakes Saadjärv and Võrtsjärv to wave activity, sediment grain size, vegetation cover and sand temperature to the densities of different psammon taxa. In this analysis, sampling time was considered as a repeated measure and sand temperature was included as a time-varying covariate. The analyses were performed by the statistical software SPSS Predictive Analytics SoftWare (PASW) Statistics version 18. In order to describe the response of psammon taxa at the community level canonical correspondence analysis (CCA) was carried out. This analysis allows testing the effects of environmental variables on biological communities, even in case of large variation in abundance and if not all of the factors determining species composition are known or if the environmental variables intercorrelate (Palmer, 1993; ter Braak & Verdonschot, 1995). In addition, the graphical output of CCA makes the results easily interpretable.

Boosted Regression Trees modelling (BRT) (Elith et al., 2008) was used in paper IV to assess the relationships between environmental parameters and psammon communities. BRT is a modelling tool that incorporates algorithms of machine learning and properties of traditional statistics. BRT was chosen because it 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). In addition, CCA was used in paper IV to describe the response of psammon taxa to environmental variables.

The BRT, CCA and SIMPROF analyses were performed in the R environment (R Core Team, 2014). The details of the analyses and the used packages in the R environment are described in the respective papers.

3. RESULTS AND DISCUSSION

3.1. Taxonomic composition and diversity

During the studies on which the present thesis is based a total of 159 non-overlapping taxa belonging to 12 phyla were found from psammic habitats (papers I–IV). The most common taxa that were found from all studied beaches were nematodes, rotifers, ciliates, testate amoebae and harpacticoids (Figure 2). In addition, turbellarians, annelids, tardigrades, gastrotrichs and insect larvae were often present. The majority of rotifers and testate amoebae were identified to species level. Altogether 37 rotifer species, 33 testate amoebae species and 6 nematode, 1 tardigrade, 1 oligochaete, 1 copepod taxa were new records for Estonia (Table 2).

Table 2. Zoopsammon taxa from Lake Võrtsjärv, Lake Saadjärv, Lake Verevi, Lake Männiku, Nõva, Pirita and Narva-Jõesuu beaches. Asterisked (*) taxa are new records for Estonia reported in publications included in the present thesis.

Taxon	**L. Võrtsjärv beach**	**L. Saadjärv beaches**	**L. Verevi beach**	**L. Männiku beach**	**Nõva beach**	**Pirita beach**	**Narva-Jõesuu beach**
Phylum Amoebozoa							
Class Lobosea							
Order Arcellinida							
Arcella sp.					x	x	
Arcella artocrea Leidy, 1876*			x				
Arcella catinus Penard, 1890*			x				
Arcella crenulata Deflandre, 1928*	x						
Arcella discoides Ehrenberg, 1843	x	x	x				
Arcella hemisphaerica Perty, 1852*		x			x	x	
Centropyxis aerophila Deflandre, 1929*	x	x	x		x		x
Centropyxis aculeata (Ehrenberg, 1838)	x	x	x	x			
Centropyxis cassis (Wallich, 1864)*	x	x					
Centropyxis constricta (Ehrenberg, 1841)*	x	x	x				
Centropyxis discoides Penard, 1902*					x		
Centropyxis delicatula Penard, 1902*	x	x	x				
Centropyxis ecornis (Ehrenberg, 1841)*	x		x				
Centropyxis hirsuta Deflandre, 1929*			x				
Centropyxis cf. *laevigata* Penard, 1890*			x				
Centropyxis orbicularis Deflandre, 1929*			x	x			
Centropyxis platystoma Penard, 1890*	x	x					
Cyclopyxis spp.					x	x	x
Cyclopyxis arcelloides (Penard, 1902) *	x	x					

Taxon	**L. Võrtsjärv beach**	**L. Saadjärv beaches**	**L. Verevi beach**	**L. Männiku beach**	**Nõva beach**	**Pirita beach**	**Narva-Jõesuu beach**
Cyclopyxis eurystoma Deflandre, 1929*			x				
Cyclopyxis kahli (Deflandre, 1929)*	x		x				
Difflugia amphora (Leidy, 1874) Penard, 1902*							x
Difflugia bidens Penard, 1902*		x					
Difflugia brevicolla Cash et Hopkinson, 1909*		x					
Difflugia elegans Penard, 1890*	x		x		x		
Difflugia globulosa (Dujardin, 1837) Penard, 1902*			x				
Difflugia gramen Penard, 1902	x	x					
Difflugia lacustris (Penard, 1899)*					x	x	x
Difflugia lithophila (Penard 1902) Gauthier-Lièvre et Thomas, 1958 *	x		x				
Difflugia lobostoma Leidy, 1879*	x		x				
Difflugia penardi Hopkinson, 1909*	x	x	x		x		
Difflugia cf. *pulex* Penard, 1902*			x				
Difflugia urceolata Carter, 1864*		x			x		x
Lesquereusia modesta Rhumbler, 1895*	x						
Netzelia tuberculata (Wallich, 1864)*	x		x				
Phryganella acropodia (Hertwig et Lesser, 1874) Hopkinson, 1909*			x		x		
cf. *Trigonopyxis* sp.*			x				
Zivkovicia cf. *spectabilis* (Penard, 1902)*					x		
Phylum Ciliophora							
Ciliophora indet.	x	x	x	x	x	x	x
Phylum Cercozoa							
Class Imbricatea							
Cyphoderia ampulla (Ehrenberg, 1840) Leidy, 1879	x			x	x		x
Psammonobiotus communis Golemansky, 1967					x		
Phylum Foraminifera							
Class Monothalamea							
cf. *Allogromia* sp.*					x		
Phylum Platyhelminthes							
Class Rhabditophora							
Rhabditophora indet.	x	x		x	x	x	x

Taxon	L. Võrtsjärv beach	L. Saadjärv beaches	L. Verevi beach	L. Männiku beach	Nõva beach	Pirita beach	Narva-Jõesuu beach
Phylum Gastrotricha							
Chaetonotidae gen. et spp. indet.		x			x	x	x
Chaetonotus sp.				x			
Phylum Rotifera							
Class Bdelloidea							
Bdelloidea gen. et spp. indet.	x	x	x		x	x	x
Philodina roseola Ehrenberg, 1832*			x				
Class Monogononta							
Cephalodella catellina (Müller, 1786)		x					
Cephalodella elegans Myers, 1924*	x						
Cephalodella forficula (Ehrenberg, 1838)	x	x					
Cephalodella gibba (Ehrenberg, 1830)	x	x					
Cephalodella gracilis (Ehrenberg, 1830)		x					
Cephalodella intuta Myers, 1924*	x	x					
Cephalodella labiosa Wulfert, 1940*		x					
Cephalodella limosa Wulfert, 1937*		x					
Cephalodella megalocephala (Glascott, 1893)	x	x					
Cephalodella tenuiseta (Burn, 1890)*	x	x					
Cephalodella spp.	x						x
Colurella adriatica Ehrenberg, 1831		x		x	x		
Colurella colurus (Ehrenberg, 1830)	x	x			x	x	
Colurella dicentra (Gosse, 1887)*	x				x		
Colurella geophila Donner, 1951*					x		
Colurella hindenburgi Steinecke, 1916*					x		x
Colurella marinovi Althaus, 1957*					x		x
Dicranophorus capucinus Harring et Myers, 1928*	x	x					
Dicranophorus hercules Wiszniewski, 1932	x	x					
Dicranophorus leptodon Wiszniewski, 1934*	x						
Dicranophorus semnus Harring et Myers, 1928*	x						
Dicranophorus sigmoides Wulfert, 1950*		x					
Elosa spinifera Wiszniewski, 1932				x			
Elosa worrallii Lord, 1891*				x			
Encentrum belluinum Harring et Myers, 1928*					x	x	x
Encentrum boreale Harring et Myers, 1928*					x	x	x
Encentrum limicola Otto, 1936*					x		

Taxon	L. Võrtsjärv beach	L. Saadjärv beaches	L. Verevi beach	L. Männiku beach	Nõva beach	Pirita beach	Narva-Jõesuu beach
Encentrum marinum (Dujardin, 1841)					x	x	x
Encentrum matthesi Remane, 1949*					x		x
Encentrum rousseleti (Lie-Pettersen, 1905)*	x						
Encentrum uncinatum (Milne, 1886)	x						
Euchlanis dilatata Ehrenberg, 1832		x					
Gastropus stylifer Imhof, 1891		x		x			
Keratella cochlearis (Gosse, 1851)		x	x	x		x	x
Keratella cruciformis (Thompson, 1892)					x		
Keratella hiemalis Carlin, 1943	x	x					
Keratella quadrata (Müller, 1786)					x	x	
Lecane bulla (Gosse, 1851)		x					
Lecane closterocerca (Schmarda, 1859)	x	x	x	x			
Lecane doryssa Harring, 1914*			x				
Lecane flexilis (Gosse, 1886)	x	x	x				
Lecane galeata (Bryce, 1892)*	x	x					
Lecane hamata (Stokes, 1896)		x	x				
Lecane luna (Müller, 1776)		x	x		x		
Lecane nana (Murray, 1913)*							x
Lecane perpusilla (Hauer, 1929)*		x					
Lecane psammophila (Wiszniewski, 1932)	x	x					x
Lecane punctata (Murray, 1913)	x	x					
Lecane pusilla Harring, 1914*			x		x		
Lecane scutata (Harring et Myers, 1926)*	x	x		x			
Lecane stenroosi (Meissner, 1908)			x				
Lecane subulata (Harring et Myers, 1926)*		x		x			
Lepadella ovalis (Müller, 1786)	x	x					
Lepadella patella (Müller, 1773)	x	x	x	x			
Lindia torulosa Dujardin, 1841			x		x		x
Monommata sp.*			x				
Mytilina mucronata (Müller, 1773)		x					
Notholca squamula (Müller, 1786)	x	x			x		
Notommata cyrtopus Gosse, 1886		x					
Notommata cf. *doneta* Harring et Myers, 1924*						x	
Notommata stitista Myers, 1937*	x						
Pleurata vernalis (Wulfert, 1935)*				x			
Polyarthra dolichoptera Idelson, 1925	x						
Polyarthra luminosa Kutikova, 1962				x			
Polyarthra remata Skorikov, 1896				x			

Taxon	**L. Võrtsjärv beach**	**L. Saadjärv beaches**	**L. Verevi beach**	**L. Männiku beach**	**Nõva beach**	**Pirita beach**	**Narva-Jõesuu beach**
Proales globulifera (Hauer, 1921)*					x	x	x
Proales halophila Remane, 1929*					x	x	x
Proales reinhardti (Ehrenberg, 1834)					x	x	x
Proales theodora (Gosse, 1887)					x	x	x
Proales spp.	x					x	
Proalinopsis caudatus (Collins, 1872) *						x	x
Synchaeta cecilia Rousselet, 1902*					x		x
Synchaeta tremula (Müller, 1786)							x
Trichocerca dixonnuttalli (Jennings, 1903)	x	x			x	x	x
Trichocerca intermedia (Stenroos, 1898)	x	x					
Trichocerca obtusidens (Olofsson, 1918)		x					
Trichocerca rousseleti (Voigt, 1902)		x					
Trichocerca similis (Wierzejski, 1893)		x			x		x
Trichocerca tenuidens (Hauer, 1931)*		x					
Trichocerca tenuior (Gosse, 1886)	x	x			x		x
Trichotria pocillum (Müller, 1776)		x					
Trichotria truncata (Whitelegge, 1889)							x
Wierzejskiella sabulosa (Wiszniewski, 1932)	x						x
Wierzejskiella velox (Wiszniewski, 1932)	x	x					
Wigrella depressa Wiszniewski, 1932*	x	x					
Phylum Annelida							
Class Polychaeta							
Hediste diversicolor (Müller, 1776)					x		
Polychaeta juv.					x		x
Class Clitellata							
Clitellata indet.	x			x			
Chaetogaster diastrophus (Gruithuisen, 1828)		x					
Chaetogaster setosus (Svetlov, 1925)*		x					
Chaetogaster sp.		x					
Lumbricillus lineatus (Müller, 1774)					x		
Marionina sp.					x	x	x
Nais elinguis Müller, 1774					x		x
Paranais litoralis (Müller, 1780)						x	
Tubificidae juv.		x					

Taxon	**L. Võrtsjärv beach**	**L. Saadjärv beaches**	**L. Verevi beach**	**L. Männiku beach**	**Nõva beach**	**Pirita beach**	**Narva-Jõesuu beach**
Phylum Mollusca							
Class Bivalvia							
Bivalvia juv.		x					
Phylum Nematoda							
Nematoda indet.	x	x	x	x	x	x	x
Class Adenophorea							
Leptolaimidae indet.	x						
Prochromadora sp.*					x		
Microlaimus sp.					x		
Enoplida indet.		x					
Enoplolaimus sp.*						x	
Amphimonhystera sp.*						x	
Linhystera sp.*					x	x	x
Retrotheristus sp.*					x		
Valvaelaimus sp.*					x		
Phylum Tardigrada							
Class Eutardigrada							
Milnesium sp.	x	x	x	x			
Class Heterotardigrada							
Oreella 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
Harpacticus uniremis Krøyer, 1842 *		x			x		
Parastenocaris brevipes Kessler, 1913		x		x	x		
Mesocyclops leukarti (Claus, 1857)		x					
Cyclopidae juv.	x	x					
Nauplii indet.			x	x	x	x	x

Taxon	**L. Võrtsjärv beach**	**L. Saadjärv beaches**	**L. Verevi beach**	**L. Männiku beach**	**Nõva beach**	**Pirita beach**	**Narva-Jõesuu beach**
Class Branchiopoda							
Alona sp.			x				
Chydorus sphaericus (Müller, 1776)	x	x					
Peracantha truncata (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: 159	**65**	**81**	**42**	**25**	**61**	**32**	**42**

Freshwater beaches host more taxa and have higher taxonomic richness both at small and large scale (sample and areal taxonomic richness) than coastal beaches, as shown in paper I. A total of 69 taxa were found in the psammic zone of the Gulf of Finland and 126 taxa from lake beaches, whereas 93 taxa were found only from lakes and 39 from coastal beaches. The taxonomic richness appeared to be related with trophic state of and anthropogenic impact on the sampling site; the presence of Rotifera was especially sensitive to these factors. The most taxon-rich water body proved to be the mesotrophic L. Saadjärv with 81 taxa from 10 phyla. The largest number of taxa from the coastal beaches was found from the remote Nõva Beach. Lake and coastal beaches with a higher trophic state and greater anthropogenic impact had lower taxonomic richness. Interestingly, the number of testate amoebae species had a reversed pattern in lakes: the hypertrophic L. Verevi beach hosted 23 testate amoebae taxa and L. Saadjärv only 14.

The relationship between psammon communities and lake trophic state has been studied for psammic rotifers and ciliates. It has been shown that the taxonomic richness of psammon rotifers is generally lower in lakes with a higher trophic state (Radwan et al., 2001; Bielańska-Grajner, 2005), especially in hypertrophic lakes (Ejsmont-Karabin, 2003). A similar relationship was also found between nematode species richness in littoral meiofauna and trophic state (Ristau & Traunspurger, 2011). However, it is not known if these samples can be considered samples of psammon because the water depth or distance from the waterline were not specified. Unlike the taxonomic richness of rotifers and nematodes, that of psammic ciliates has no relation with trophic state; instead, other type of human activity seems to be a significant factor (among others) determining ciliate communities in beach habitats (Kalinowska, 2013).

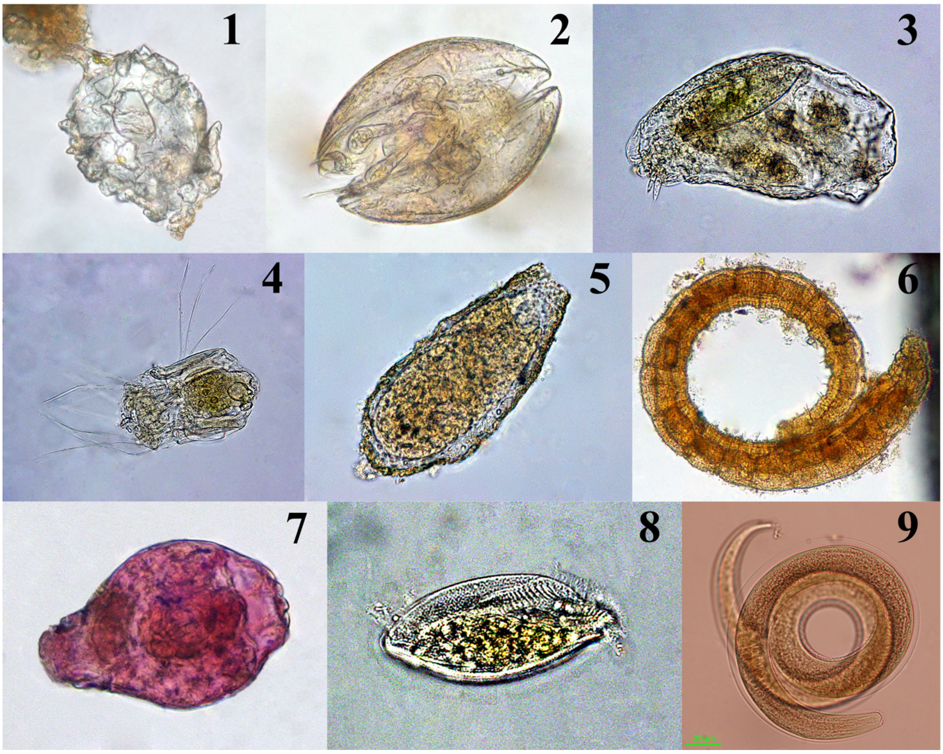

Figure 2. Some representatives of the taxa: 1 – *Difflugia elegans,* 2 – ostracod, 3 – *Encentrum* sp., 4 – *Polyarthra* sp., 5 – *Allogromia* sp., 6 – oligochaeta, 7 – *Philodina roseola*, 8 – ciliate, 9 – nematode.

Despite the high overall species richness, L. Saadjärv had a relatively low average number of taxa per sample compared to the other studied beaches. Moreover, although the total number of taxa found in lake and coastal beaches decreased with increasing trophic state and anthropogenic impact, the taxonomic richness per sample followed this pattern only in coastal areas. This suggests that beach habitat is more homogeneous in space and time in coastal areas than in lakes and the high areal richness in lakes with a lower trophic state is provided by the high patchiness and complex seasonal dynamics.

In addition, the coastal sampling sites clustered together in SIMPROF analysis, showing that their communities are more similar to each other than in lake beaches (paper I). The dendrogram of SIMPROF analysis also supported the idea of higher patchiness in lakes: the samples from lake beaches, especially from L. Saadjärv, varied more than the samples from the coastal areas, as the latter were less scattered in the dendrogram (paper I, figure 4). The higher similarity of psammon in coastal areas was also shown by the Sørensen similarity coefficient values: the zoopsammon communities of coastal sampling sites proved to be much more similar with each other than the zoopsammon in different lakes. When calculated separately for different taxa, the values of the

Sørensen similarity coefficient revealed that rotifer communities differed much more from beach to beach than testate amoebae communities.

Lake Männiku was represented by only one sample, yet this sample contained 25 taxa and had thus the highest sample taxonomic richness as well as the highest recorded abundance in one sample in Estonia (279 ind cm^{-3}; paper I). At the time of sampling (May), the psammon community in L. Männiku was dominated by rotifers: *Keratella cochlearis* accounted for over 83% of the total psammon abundance.

The dominating taxa varied depending of the season both in lake and coastal beaches (papers II and IV). However, nematodes, protists or rotifers were mostly dominating in lake psammon, and ciliates or rotifers in coastal beaches. Occasionally, testate amoebae were the dominant taxon in L. Verevi, oligochaetes in L. Saadjärv and nematodes in Narva-Jõesuu beach. These results are generally in accordance with the expectations described in the objectives and hypotheses section; however, the regular dominance of ciliates or rotifers instead of nematodes was rather surprising.

It is difficult to compare the dominating structure of psammon communities in Estonian waters with psammon communities elsewhere. The reason is that the majority of studies do not include information on all taxa in detail, even not at higher taxonomic level. However, contrary to the results of the present thesis, it has been shown in several studies that nematodes generally dominate in the beach meiofauna of marine and brackish water habitats (e.g. Gheskiere et al., 2005b; Kotwicki et al., 2005b; Rubal et al., 2012; Covazzi Harriague et al., 2013). The difference may be partly related to the biased sampling of meiofauna, as ciliates and other protists are often neglected in meiobenthological studies (Giere, 2009) in spite of having been reported at very high densities on sandy sediments (e.g. Wickham et al., 2000). While copepods are also found to be an important (Thane-Fenchel, 1968; Rubal et al., 2012) or sometimes even dominating (Papageorgiou et al., 2007) part of beach meiofaunal communities, in the Gulf of Finland copepods were present in very low numbers or were even lacking in some seasons (paper IV). The domination of rotifers observed in the current thesis is plausibly related to the low salinity of the Gulf of Finland allowing freshwater species to persist. Though, many rotifer species are euryhaline (e.g. Thane-Fenchel, 1968) and they have been also found at high densities from beaches of the fully marine Adriatic Sea (Covazzi Harriague et al., 2013). Gastrotrichs, turbellarians, and testaceans constituted also a substantial part of the psammon in coastal beaches, but they never dominated in the psammon communities. This is in accordance with several earlier studies carried out in beaches of the Mediterranean, North and Baltic seas: gastrotrichs and turbellarians have been reported as relatively numerous but never as dominating taxa (Thane-Fenchel, 1968; Gheskiere et al., 2005b; Kotwicki et al., 2005b; Papageorgiou et al., 2007; Rubal et al., 2012).

In freshwater habitats, the dominating taxa varied depending on the season and lake (paper II). While psammon communities in L. Võrtsjärv were generally dominated by nematodes, ciliates were usually the dominating group in L. Saadjärv. In L. Verevi, nematodes and testatceans seemed to be the dominating taxa during most of the year (Lokko, unpublished data). Rotifers dominated psammon communities only occasionally, although they contributed substantially to the overall density in all sampled freshwater beaches. Based on earlier studies, it seems that there is no single phylum or other higher taxon that is generally dominant in freshwater psammon. Moreover, the dominating group may vary even between beaches of a single lake (Neel, 1948). Still, nematodes, rotifers, ciliates, oligochaetes and testaceans are often the most numerous in freshwater psammon (e.g. Neel, 1948; Nawrot & Mieczan, 2012).

The taxonomic composition of psammon rotifer communities in Estonian waters is similar to other areas in Europe (papers I–IV). This could be expected, as most rotifers tend to have cosmopolitan distribution. A total of 35 rotifer species were found from coastal beaches, with as many as 26 rotifer taxa recorded from Nõva Beach. This is close to the numbers recorded from interstitial habitats with analogous salinity in Askö Harbor, Scandinavia, and a number of species overlap (Thane-Fenchel, 1968). From lakes, altogether 64 taxa of psammic rotifers were found. Again, the number of rotifer species found in the studied lakes is rather comparable with the numbers recorded from Polish lakes with the similar trophic state and a considerable number of species overlap in the two countries (Radwan & Bielańska-Grajner, 2001; Ejsmont-Karabin, 2005). Moreover, one of the most abundant genera in psammic rotifer communities in the current study was the genus *Lecane,* which has been found to be often among the dominating taxa in psammic rotifer communities (e.g. Bielańska-Grajner, 2001; Ejsmont-Karabin, 2004; Nawrot & Mieczan, 2012). Other relatively abundant rotifer taxa in psammon were Bdelloidea in L. Võrtsjärv and representatives of the genera *Lepadella, Cephalodella* and *Trichocerca* in L. Saadjärv (papers II and III).

Although testate amoebae have received much less attention than rotifers, some studies about psammic testate amoebae from the Baltic Sea are available (e.g. Golemansky 1973, 1983, 1998b). Interestingly, unlike the rotifer communities, the taxonomic composition of the psammic testate amoebae described in the present thesis is considerably different from the previous studies. According to the present work, the majority of testate amoebae found from coastal beaches belong to Arcellinida (Phylum Amoebozoa) and only a few to the phylum Cercozoa (papers I and IV). This is contrary to previous studies carried out in the Baltic Sea, where testate amoebae belonging to Cercozoa dominated (Golemansky 1973, 1983, 1998b). Moreover, only one taxon (*Cyclopyxis* sp.) overlap in Pirita Beach, which was sampled during this work, overlaps with records by Golemansky in the early 1980s (Golemansky, 1983). This may be caused by different sampling and analysing techniques, as well as a wider habitat range compared to the present work. The dominating testate amoebae genera in freshwater psammon proved to be *Arcella*, *Centropyxis* and *Difflugia* (papers I and II). These genera are found dominating also in testate amoebae communities in interstitial habitats of shallow freshwater ponds (Burdíková et al., 2012) and in other freshwater habitats (Alves et al., 2010; Wu et al., 2011).

3.2. Seasonal and spatial patterns

The total zoopsammon abundance was generally much higher in lake beaches than in coastal beaches (papers I–II and IV). The maximum abundance reached 279 ind cm^{-3} in L. Männiku and 203 ind cm^{-3} in L. Võrtsjärv. The maximum abundances in L. Saadjärv and L. Verevi remained somewhat lower, yet were considerably higher than in the coastal areas. The maximum abundance from coastal beaches recorded in a single sample was only 46.6 ind cm^{-3} in Nõva Beach. Although psammon densities are known to fluctuate greatly even within days (e.g. Ejsmont-Karabin, 2005) and only a few works on the overall abundance of psammon are available, the abundances recorded in freshwater psammon during the present study are comparable with those recorded by Neel (1948) at the same distances from the waterline of Lake Douglas (USA). The psammon densities in coastal areas (paper IV) proved to be somewhat higher than reported elsewhere from beaches of the Baltic Sea (Gheskiere et al., 2005b; Kotwicki et al., 2005a), but are comparable with beaches in the North and Mediterranean seas (Gheskiere et al., 2005b; Kotwicki et al., 2005a,b; Rubal et al., 2012). However, due to the suboptimal extraction method for ciliates, the number of ciliates was likely largely underestimated in the present work and therefore the actual psammon densities in the Gulf of Finland may be even higher.

The overall population densities of zoopsammon varied substantially throughout the year in all sampled beaches (papers II and IV). There was no clear seasonal pattern for the overall abundance of zoopsammon during the vegetation period, as the seasonal pattern varied from beach to beach. Though, in autumn the abundances were low in all coastal beaches while lake beaches tended to have lower abundances in early spring. Nevertheless, the seasonal pattern of diversity was quite similar in all sampled beaches as the most taxon-rich season was summer. The diversity peaked later in lakes (in August) than in coastal beaches (June or July; paper I).

Seasonal density fluctuations are probably caused by changes in water temperature, life cycles and/or feeding conditions. To date, only a few studies have focused on the psammon seasonality of marine or brackish waters. However, psammon densities are generally the lowest in winter and highly variable in the rest of the year depending on the sampling area and taxa (e.g. Thane-Fenchel, 1968; Covazzi Harriague et al., 2013). All the sampled coastal beaches in the present study showed different seasonal patterns (paper IV). The psammon density peaked in June in Nõva Beach, whereas in Pirita Beach the psammon densities had two peaks: May and August, and a clear depression in between. In Narva-Jõesuu Beach the abundance was the highest in April. The psammon density was very low in all coastal sampling sites only in autumn which may be caused by life cycles of the taxa and poor feeding conditions.

The information about general seasonal patterns is sparse also for freshwater habitats, as most studies include only a few psammic phyla. However, the abundances of psammon communities in freshwater habitats are at least as fluctuating as in marine and brackish waters (e.g. Ejsmont-Karabin, 2001, 2005; Kalinowska, 2008). Despite the high variability, this study (paper II) as well as some previously published papers show some commonalities such as a slow density increase in tardigrades, rotifers, copepods and ciliates in spring (e.g. Pennak, 1940; Kalinowska, 2008) and peak densities in the late summer (Pennak, 1940; Ejsmont-Karabin, 2001; Bielańska-Grajner, 2004; Kalinowska, 2008).

The abundance of rotifers peaked in summer (June or July) both in lake and coastal beaches (papers II–IV). This is in contrast to several previous studies, where it has been shown that psammic rotifers have the highest abundance in spring or autumn (e.g. Ejsmont-Karabin, 2001; Radwan et al., 2001; Radwan & Bielańska-Grajner 2001; Bielańska-Grajner, 2005). However, similarly to findings by Ejsmont-Karabin (2005), rotifer densities were very fluctuating also in the current work.

According to the Guild Ratio Index, microphagous rotifers dominated in L. Võrtsjärv during the whole growing season, whereas raptors dominated in L. Saadjärv in summer and autumn (paper III). Also the Shannon diversity index significantly varied seasonally with highest diversities observed in July in both L. Võrtsjärv and L. Saadjärv. The lowest diversities occurred in June in both lakes.

Population densities varied also along shore heights both in lake beaches and in coastal beaches (papers II–IV). In general, the psammon abundance in coastal beaches was higher in the euarenal and the lowest in the hydroarenal (paper IV). The abundance was the highest in euarenal even in the flat Narva-Jõesuu Beach. The spatial pattern in lake beaches was different and depended on the season. The density maxima in L. Võrtsjärv were in the hydroarenal in the spring and the first half of summer, but moved upward the waterline later in the late summer and autumn (paper II). Such seasonal pattern of horizontal distribution may be related to the higher stability of the environment adjacent to the waterline in spring. In addition, seasonal changes in psammon abundance seemed to follow plant densities on the beach. It was not possible to distinguish a reliable horizontal pattern in L. Saadjärv: due to unfavourable sampling conditions the sandy beach was too narrow for full 50 cm transect during most of the year 2008. However, in this lake the population density was generally the lowest in the hydroarenal zone.

Only a few taxa showed a distinct horizontal distribution pattern both in lake and coastal beaches. Small crustaceans, insect larvae and oribatid mites had higher densities closer to the waterline in lakes, whereas rotifers, gastrotrichs and turbellarians had the highest abundance in the euarenal (papers II and IV).

Although it is expected that environmental conditions vary considerably at different shore heights, the majority of earlier studies conducted in marine and brackish waters have not reported a clear spatial pattern of psammon along beach slope (e.g. Golemansky, 1976, 1998a,b; Gheskiere et al., 2005a; Covazzi Harriague et al., 2013). However, there is some evidence that the proportion of nematodes decreases and the proportion of rotifers increases towards upper beach (Covazzi Harriague et al., 2013), which was also found in the present study (paper IV). Also, in freshwater habitats it is not clear which arenal zone hosts the highest abundance, as the zone with the highest abundance varies from lake to lake and also seasonally (e.g. Bielańska-Grajner, 2004; Mieczan & Nawrot, 2012). In some studies the highest rotifer abundance was recorded from the euarenal (Radwan et al., 2001; Bielańska-Grajner, 2004), while in others the abundance maximum was observed in the hygroarenal (Bielańska-Grajner, 2001) or is highly variable with the lowest values in the hydroarenal (Bielańska-Grajner & Molenda, 2008).

Poor predictability and high variability of psammon communities along beach slope may result from active migration of psammic organisms: the psammic organisms may actively search for more favourable microhabitats. It has been found that intertidal beach meiofauna shows a distinct vertical and horizontal migration (Fernando & Natarajan, 1987). In addition, considerable diurnal changes in the community structure along the gradient of shore height have been shown also for rotifers and ciliates (Nawrot & Mieczan, 2014).

Psammic communities are also expected to vary vertically, depending on the depth stratum. The meiofauna is generally concentrated to the uppermost few centimetres of the sediment both in lake and marine beach habitats (e.g. Mazei & Burkovsky, 2003; Bielańska-Grajner, 2004; Kotwicki et al., 2005b), whereas vertical distribution is believed to be related with wave activity (Schmid-Araya, 1998). The topmost layer has generally good oxygen and feeding conditions due to wave agitation, thus creating favourable conditions for many taxa. Also the results in paper IV showed that the density of psammon was often the highest closer to the sediment surface. However, the vertical distribution proved to be taxon-specific and dependent on the sediment type (paper IV). In general, rotifers avoided the surface layer as they were primarily found in the subsurface layer. Oligochaetes, polychaetes and nematodes were at highest numbers in the topmost layers whereas testaceans were primarily found in the lowest layer. Ciliates had high densities both in the topmost and lowest layers. This is in contrast to Mazei & Burkovsky (2003), who reported the highest abundances of ciliates in the surface layer. However, the sediments sampled in paper IV were well oxygenated in contrast to the study area of Mazei & Burkovsky (2003).

3.3. Relationships between environmental parameters and psammic patterns

The psammon communities are shaped by both abiotic environmental parameters and biotic interactions as shown in papers I–IV (Figure 3). The evaluation of some environmental parameters in papers II and III gave some initial insight into psammon relations with its habitat. However, the additional sampling and measurements together with BRT modelling allowed more detailed analysis of the relationship between the environment and psammon communities (paper IV). The BRT models described reasonably well the variability of psammon density, considering large natural variability of the sandy beach habitat both in space and time. Moreover, the models enabled identifying environmental variables that were behind the psammon seasonality (temperature, content of sand organic matter and chlorophyll *a*, human trampling) and spatial patterns (sediment characteristics, porewater pH and salinity). The performance of BRT models was related to the taxonomic aggregation with generally better predictive performance at higher taxonomic resolution (e.g. genera and species levels). According to BRT models, the majority of psammon taxa had species-specific responses to their environment. Also the CCA analysis showed that different psammic taxa responded very differently to changes in environmental conditions.

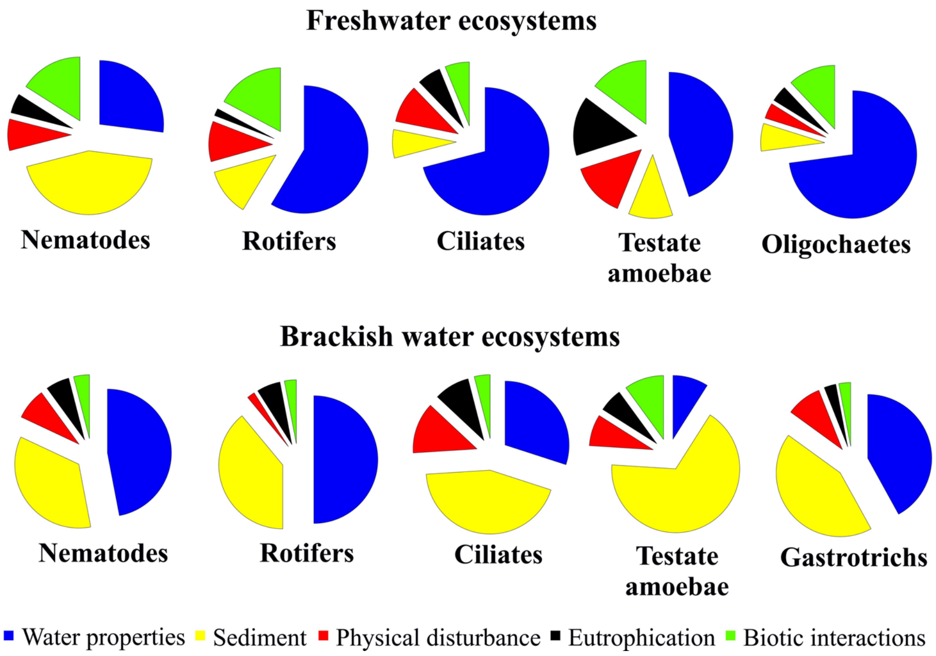

Figure 3. Schematic diagram illustrating the relative contribution of different environmental variables on most abundant psammon taxa in brackish and freshwater ecosystems.

The BRT models also indicated that the relationships between the environment and biota were often nonlinear and highly complex. Therefore they are difficult to describe effectively using traditional statistical methods.

While the most important environmental factors describing population densities varied among phyla, the sand structure, pH, salinity, temperature, sand organic matter and chlorophyll *a* content were often the key variables in the BRT models for coastal psammon communities. The vertical layer was a key environmental predictor for oligochaetes and rotifers belonging to Bdelloidea and *Trichocerca*, however some taxa showed no clear preferences along the vertical gradient. The arenal zone and wave stress were never among the key factors in the BRT analyses (paper IV). In lake beaches, the sediment grain size and vegetation cover at the transect were significantly related with psammon densities (paper II) and rotifer community structure (paper III).

3.3.1. Sediment structure and grain size

In general, the highest abundances of psammon tend to occur at medium sand grain size (papers II and IV). Population densities were related also to sand structure, i.e. sediment sorting, with higher densities observed in moderately or well sorted sand. However, sand structure was among the key factors only for oligochaetes and some testaceans (genus *Centropyxis*). Sand grain size is probably one of the most important parameters that characterise psammic habitat, as it directly determines spatial and structural conditions and indirectly determines the physical and chemical environment of the sediment (Giere, 2009). Nevertheless, there are studies where no relationship between sediment type and psammon densities has been found (e.g. Pennak, 1940; Bielańska-Grajner, 2005). Coarse sand can be unfavourable for psammic organisms as waves may wash out nutrients and resuspend psammic organisms into the water column (Pennak, 1940; Boeckner et al., 2009). On the other hand, very fine muddy or clay-rich sand tends to be unsuitable for many taxa as interstices can be easily clogged with silt (Nogrady et al., 1993; Giere, 2009). Thus, medium sand grain size may be the most suitable for many taxa. Also the highest diversities of psammic rotifer communities were measured at intermediate sediment grain size (paper III).

However, large differences were found within and between taxa with different species being favoured by different sediment fractions in both coastal and lake beaches (papers II and IV). In addition, the relation between sand grain size and abundance of some taxa differed between lake and coastal beaches. For example, in the coastal beaches, the abundances of rotifers and testatceans increased with the growing proportion of medium-size sand grain, while ciliates abundance had the reverse relation with grain size. On the other hand, the sand grain size had no effect on ciliate abundance in lakes. Nematode population density was positively correlated with coarse sand proportion in coastal beaches, which is in contrast to previous studies where it has been shown that nematodes have often a strong affinity to sediments of fine grain size (Heip et al., 1985; Boeckner et al., 2009). However, nematodes as well as testaceans, small crustaceans and tardigrades were most abundant in fine sand in lake beaches.

Rotifer taxa with higher abundances were included individually into the analysis in paper II. This revealed that the preferences of sand grain size vary also at lower taxonomic levels. Namely, the bdelloid rotifers were the most abundant at medium sediment grain size, whereas the genus *Lecane* was the most abundant in fine sand and the genus *Lepadella* in coarse sand. Thus, the present work together with previous studies (Nucci et al., 2001; Ejsmont-Karabin, 2004; Kalinowska, 2008) indicates that habitat preferences of psammic organisms are taxa specific and generalities are difficult to detect.

The sediment structure and grain size modulated also the vertical distribution of psammon. The abundance was the highest in the deepest layers of coarse sediment, whereas in fine sand habitat, psammon had the highest density in the topmost sediment. For example, in Nõva Beach, which is characterised by relatively coarse sand and a steep slope, psammon had the highest density in the deepest layer (3−10 cm) of sediment, possibly in order to avoid being flushed out. In general, rotifers avoided the surface layer as they were primarily found in the subsurface layer. Rotifers may thus avoid the stress generated by wave action (Schmid-Araya, 1998), which has probably a stronger effect in coarse sand.

3.3.2. Salinity and pH

The relationship between psammon abundance and porewater pH and salinity was studied in coastal beaches (paper IV). In general, higher porewater pH and salinity were associated with higher population densities. However, ciliates tended to be more abundant in sand with a lower porewater pH, but salinity was not among the key variables for them. In brackish water, species richness minimum may occur among meiofauna, but it is not very distinct (Giere, 2009). On the contrary to species richness, psammic abundance does not necessarily correlate with salinity (Ngo et al., 2013).

In the present work, rotifers as well as turbellarians were more abundant at higher salinity levels. Rotifers are known to tolerate and reproduce in a wide range of salinity (e.g. Thane-Fenchel, 1968), whereas turbellarian species are specialised either for limnetic, brackish or marine conditions with some overlapping (Noreña et al., 2007). Thus the abundance of turbellarians might remain unchanged along the salinity gradient, but the taxonomic composition changes. The higher abundances at higher salinities (up to 6.6 ppt) in beaches of the brackish-water Gulf of Finland may be caused by the co-occurrence of brackish and limnetic or marine turbellarian species.

Thane-Fenchel (1968) reported number of rotifer species and their total abundance in psammon to decrease with increasing salinity values. In the present work, however, rotifer abundance was several times higher than reported under similar salinity conditions (Thane-Fenchel, 1968). Moreover, rotifer abundance increased with increasing salinity in the present work. Thus, it is likely that within a brackish-water ecosystem other factors such as sand structure contribute more to the density of rotifers as compared to salinity.

The porewater pH value contributed most in the BRT model of ciliates with higher abundances in sand with lower pH. A reduction of the pH in a psammic habitat may be an indicator of increasing pollution. It is supported by the fact that the porewater pH was considerably lower at Pirita, whereas the pH of the overlying water did not differ among sites. High ciliate population densities have been reported from polluted areas (e.g. Czapik & Fyda, 1992) and from areas of high human impact (trampling by swimmers) (Kalinowska, 2013).

3.3.3. Temperature

It is likely that the effect of temperature is partly uncoupled of that of seasonality. While no significant relation appeared in lake beaches, temperature was among the key variables for nematodes, oligochaetes and some rotifer taxa in coastal beaches (papers II and IV). Again, the relation between temperature and abundance was taxon specific with increasing temperatures favouring nematodes and certain species of rotifers but disfavouring oligochaetes. However, the BRT models suggest that temperature is probably not the most important environmental factor for most psammic taxa. Instead, food availability and life cycles may contribute more to the variability of abundance.

3.3.4. Plant densities, sand organic matter and chlorophyll *a* content

In addition to the physical environment, the feeding conditions play most likely an important role in structuring psammon communities. Microphytobenthos, higher plants and degrading plant material together with bacteria living on this substance are probably important food sources in beach habitats. For example, abundant bacteria associated with plant debris (i.e. organic matter) can sustain the elevated population growth of protists (Kalinowska, 2008). However, too abundant degrading plant material in the interstitial space may result in silty sediments and such sands are avoided by many ciliates (Giere, 2009).

The BRT models did not reveal very clear relationships between the sediment organic matter content and the densities of different psammic taxa (paper IV). Yet there were some indications that an elevated content of organic matter decreased the density of oligochaetes, turbellarians and gastrotrichs, whereas ciliates abundance increased with the increasing organic matter content. The high total content of organic matter does not necessarily indicate good feeding conditions, instead the ratio of sediment proteins to chlorophyll *a* determines the food value of sediment organics (Covazzi Harriague et al., 2013). The positive relationship between chlorophyll *a* and total psammon density has been noted earlier as well (Ngo et al., 2013). Nevertheless, the sediment chlorophyll *a* was among the key variables in the BRT models for only a few taxa, possibly due to the lack of bottom-up interactions. On the other hand, the high abundance of copepod nauplii at elevated chlorophyll *a* levels suggests the food limitation for copepods in the study area.

The content of organic matter and chlorophyll *a* were not determined in lake beaches, but plant densities at the transect were evaluated (papers II and III). High plant densities were generally associated with the reduced diversity and densities of zoopsammon and the highest abundances were observed at moderately vegetated habitats. Although some taxon-specific differences occurred, nematodes were the only taxa that had the highest population densities with the highest plant densities. Plants, degrading plant material and associated bacteria provide probably good feeding conditions for many psammic nematodes. The highest proportion of raptorial rotifers (highest Guild Ratio Index values) occurred at low plant densities (paper III).

3.3.5. Feeding conditions in relation to seasonality

As shown above, the seasonal trends of psammon are rather taxon specific (e.g. Pennak, 1940; Thane-Fenchel, 1968) and interrelated with many abiotic and biotic environmental parameters. Nevertheless, the feeding conditions are likely to play an important role in the observed seasonal patterns of abundances. Differences in the food quality and availability between seasons may shape the life cycle patterns (e.g. Conde-Porcuna, 2000). Summer seems to be the most favourable time for the majority of psammic taxa, yet competition, food limitation, predation and human activities (e.g. trampling, mechanical cleaning of the sand) may inhibit the population growth. In autumn sand often contains large amounts of decaying plant debris in lake beaches and thus the competition for food is low. This can lead to a rapid population growth of opportunistic taxa, for example among nematodes and oligochaetes.

In 2008 nematodes had very high densities in L. Võrtsjärv in September, concurrent with a high vegetation coverage at the sampling transect (paper II). The same year in L. Saadjärv the density of oligochaetes peaked in October when the decaying plant material (leaves, macroalgae) significantly enriched the psammon food supply. Other taxa showed relatively low abundances in both lakes in autumn 2008 (paper II). This suggests that food availability is one of the main factors that determine the abundance of nematodes and oligochaetes.

Low abundances in autumn in coastal beaches may also be related to impoverished feeding conditions, as the content of chlorophyll *a* and organic matter of sand were low at that time of the year. Also, earlier studies have shown that occasional peaks of rotifer and nematode densities may be associated with short-term food pulses (Ejsmont-Karabin, 2001; Michiels & Traunspurger, 2005).

3.3.6. Anthropogenic impacts

In addition to feeding conditions, seasonal fluctuations may be related to anthropogenic impacts. It is possible that the seasonal pattern observed in Pirita Beach may be related with beach season, as it is a very popular beach within Tallinn City and its sand is regularly mechanically cleaned during the beach season (paper IV). Trampling together with mechanical beach cleaning physically disturbs the sand and reduces sediment porosity, permeability and the content of organic matter (Gheskiere et al., 2005b). The seasonal changes observed in Narva-Jõesuu might be also partly related to anthropogenic impact in the form of trampling by swimmers. Narva-Jõesuu is also a popular beach, but less crowded and the sand is not mechanically cleaned. The psammon population density in Narva-Jõesuu beach was the highest in spring (April) before the beginning of the beach season, and then decreased rapidly. However, unlike Pirita Beach, Narva-Jõesuu Beach showed some increase in July to which ciliates contributed the most. Ciliates seem to be one of the few taxa that benefit from such human activity with higher densities observed in popular beaches and/or during the beach season. The abundance of psammic ciliates in the two sampled beaches of L. Saadjärv also differed largely with higher numbers recorded from the more popular beach adjacent to a local motorway (Lokko, unpublished data). Interestingly, according to Kalinowska (2013), the popularity of a lake among swimmers seems to have a larger effect on ciliates abundance than the trophic state of the lake, possibly due to differences in the chlorophyll *a* content.

4. CONCLUSIONS

Synthesis

Although seemingly lifeless, the present thesis showed that the beach sands host a considerably variegated biota. The psammic communities varied both in time and space. However, no general seasonal patterns of abundances were detected; therefore the first hypothesis was partly rejected. The seasonal patterns of psammon seem to be not only taxon specific but also modulated by human activities and feeding conditions of psammon which are not necessarily related to seasonal changes. Thus, the community dynamics of psammon are often driven by short-term stochastic disturbances and therefore it is very difficult to draw any long-term and large-scale generalities (e.g. Ejsmont-Karabin, 2005). Nevertheless, both taxon richness and the Shannon diversity index of rotifers were the highest in summer as assumed.

It was also expected that the sediment properties were among the key variables structuring the psammon communities. Indeed the sediment grain size and occasionally sand sorting were among the key variables determining psammon abundances in coastal and lake beaches. In addition, the vertical distribution patterns of psammic taxa seemed to be related to sediment properties, although several taxon-specific differences were detected.

The zoopsammon communities in lake beaches had higher taxonomic richness than in coastal beaches both at small and large scales. Also the abundances were higher in the lake beaches than in coastal areas. The taxonomic richness was related with the trophic state of and anthropogenic impact on the sampling site, as expected. In general, the beach habitat in coastal areas was more homogeneous in space and time than at lakes. Zoopsammon of the mesotrophic L. Saadjärv seemed to have the highest variability in space and time of the studied beaches as it had a relatively low average number of taxa per sample compared to the other studied beaches; nevertheless L. Saadjärv had the highest overall species richness. Thus the third hypothesis of the current thesis was confirmed.

The fourth hypothesis was that the majority of psammon taxa had species-specific responses to their environment. The results of the thesis clearly support this hypothesis. Although this idea may be considered trivial, the results of the BRT models and also the CCA ordination in paper IV show the importance of taking into account the differences in relation to environmental parameters at higher taxonomic resolution (i.e. at species and genera levels) when exploring the relationships between environment and biota.

The fifth hypothesis stated that nematodes were more abundant in heavily vegetated sample sites. This was confirmed for lake beaches, whereas nematode abundances were low in coastal beaches where other environmental parameters (e.g. temperature) were more important than vegetation or sediment organic content. However, the plant density at a transect was significantly related to the abundances of many taxa in lake beaches and sediment chlorophyll *a* and organic contents were among the key variables in the BRT models in coastal beaches.

The main findings of the thesis:

- Freshwater beaches host more taxa and have higher taxonomic richness both in small and large scale than brackish-water beaches.
- The total zoopsammon abundance is much higher in lake beaches than in coastal beaches.
- Summer is the most taxon-rich season in sandy beach habitats.
- The horizontal pattern of psammon communities is highly variable and poorly predictable, although generally the highest abundances are observed in the eupsammon in coastal beaches.
- Sand structure, pH, salinity, temperature, sand organic matter content and chlorophyll *a* content were often the key variables in the BRT models for coastal psammon communities.
- In lake beaches, the sediment grain size and vegetation cover at the transect were significantly related with psammon densities (paper II) and rotifer community structure (paper III).
- Habitat preferences of psammon organisms are species specific implying that ecological models based only on total density cannot effectively recapture distribution patterns and dynamics of psammon.
- Seasonal patterns of psammon abundance and taxonomic composition are related to feeding conditions and anthropogenic impact in the form of human trampling and mechanical beach cleaning (papers II and IV).

SUMMARY IN ESTONIAN

Väliskeskkonna mõju zoopsammoni koosluste ruumilisele ja ajalisele varieeruvusele

Psammon on veekogu kaldaäärses niiskes liivas setteosakeste vahelises ruumis elavate mikroskoopiliste organismide kooslus. Ehkki psammonit ja põhjaelustikku käsitletakse tihti koos, on psammon ainulaadne, kuna on regulaarselt eksponeeritud kuivamisele. Seetõttu on arvestatav osa zoopsammoni hulka kuuluvatest loomaliikidest just sellele elupaigale spetsialiseerunud, kuigi mitmeid zoopsammoni hulka kuuluvaid organisme võib leida ka mujal: veekogude põhjas, veetaimedel, veesambas, aga ka maismaa ökosüsteemides. Psammon pole ainult elurikkuse allikaks, neil loomakestel on oluline roll ka veekogude aine- ja energiaringes. Nimelt võib psammoni arvukus tihti ületada veekogude põhjamudas olevate pisiloomade oma.

Võrreldes planktoni või bentosega, on psammonikooslusi väga vähe uuritud. Enamik varasemaid uuringuid käsitlevad vaid mõnd üksikut loomarühma ning psammonikoosluse kui terviku kohta teaduspublikatsioonid sisuliselt puuduvad. Seetõttu on senised teadmised zoopsammoni ajalis-ruumilise varieeruvuse ja seda mõjutavate tegurite osas väga napid.

Käesoleva doktoritöö eesmärkideks oli kirjeldada zoopsammoni koosluste taksonoomilist koosseisu ning domineerimissuhteid ruumis ja ajas. Saadud tulemusi seostati veekogu tüübi ja omadustega, et selgitada, millistel keskkonnateguritel on suurem tähtsus zoopsammoni koosluste kujunemisel. Kuna zoopsammoni üheks olulisemaks komponendiks võib lugeda keriloomi (*Ph. Rotifera*) (Bielańska-Grajner 2004) ning selle rühma kohta on ilmunud rohkem võrreldavat materjali, siis on doktoritöös seda loomarühma teistest loomarühmadest ka põhjalikumalt käsitletud.

Zoopsammoni koosluste uurimiseks kogusin proove nelja järve (Saadjärv, Võrtsjärv, Verevi ja Männiku järv) rannaliivast ja kolmest Soome lahe liivasest rannast (Nõva, Pirita ja Narva-Jõesuu rannad). Keriloomad, tsiliaadid, ümarussid, kodaamööbid ja rullikulised olid tüüpilisimad zoopsammoni esindajad, keda leidus kõigis uuritud randades. Lisaks esinesid psammoni koosseisus sageli ripsussid, rõngussid, loimurid ja ripskõhtsed. Kokku leiti töö käigus 159 taksonit, millest 80 taksonit on Eesti faunale uued leiud.

Järvedes olid psammonikooslused taksonirikkamad kui rannikumeres, seda nii väikeses kui suures ruumimastaabis. Samuti oli zoopsammoni arvukus järvedes palju kõrgem. Zoopsammoni taksonirikkust mõjutasid uuritava ala troofiline tase ja inimtegevus. Üldjuhul oli psammoni liike enam seal, kus inimmõju oli väiksem ja troofiline tase madalam. Siiski oli madalatoitelises Saadjärves väikesemastaapne taksonirikkus suhteliselt madal, võrreldes teiste järvedega. Selline erisus viitab psammonikoosluste suurele ajalis-ruumilisele varieeruvusele. Üldiselt varieerusidki psammonikooslused järvedes palju enam kui rannikumeres.

Zoopsammoni koosluste horisontaalne varieeruvus oli väga suur ning ajas muutuv. Siiski oli rannikumeres veepiirist ülalpool (maa pool) zoopsammoni arvukus enamasti kõrgem kui veepiiril ja allpool. Vertikaalne varieeruvus oli suuresti seotud liiva struktuuri ja konkreetse taksoniga.

Kuigi zoopsammoni arvukuse osas ei ilmnenud ühtset sesoonset mustrit, oli suvel taksonirikkus suurim. Sesoonsusest enam mõjutas psammoni kooslusi liiva struktuur, toidubaas (orgaanika ja klorofüll *a* sisaldus liivas, kõrgem taimestik rannas) ja inimtegevus (sh suvitajate hulk rannas). Seosed keskkonnaparameetrite ja arvukuse vahel sõltusid enamasti konkreetsest taksonist ning erinevusi esines isegi ühe perekonna eri liikide vahel. Üldiselt oli psammoni arvukus suurim keskmise terasuurusega liivas ning madalaim rohke taimestikuga rannaliivas. Vaid ümarusside arvukus oli suurim just rohtunud rannas. Rannikumere psammonis oli mitmete taksonite arvukus seotud ka liiva kapillaarvee soolsuse ja pH-ga. Üldjuhul oli psammoni arvukus kõrgem suurema soolsuse ja pH juures, samas tsiliaadid olid arvukaimad just madalama pH tingimustes. Väheste psammoniorganismidena lõikasid tsiliaadid kasu intensiivistunud inimtegevusest.

Käesolev doktoritöö näitas, et veekogu näiliselt elutus kaldaliivas elab väga mitmekesine kooslus, mis võib olla vägagi kõrge arvukusega, hoolimata keskkonnatingimuste suurest varieerumisest. Kuna inimtegevusel on oluline mõju zoopsammoni kooslustele, siis on psammoni uurimisel oluline perspektiiv looduskaitse valdkonnas. Samas on oluline mõista zoopsammoni rolli vee ökosüsteemis.

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REFERENCES

Alves, G. M., Velho, L. F. M., Simões, N. R. & Lansac-Tôha, F. A. 2010. Biodiversity of testate amoebae (Arcellinida and Euglyphida) in different habitats of a lake in the Upper Paraná River floodplain. *European Journal of Protistology* 46, 310–318.

Bielańska-Grajner, I. 2001. The psammic rotifer structure in three Lobelian Polish lakes differing in pH. *Hydrobiologia* 446/447, 149–153.

Bielańska-Grajner, I. 2004. Preliminary investigations of psammon rotifers in two reservoirs in upper Silesia. *Oceanological and Hydrobiological Studies* 33, 37–45.

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. & Molenda, T. 2008. Dependence between occurrence of selected species of psammic rotifers and phytopsammon abundance. *Annales Universitatis Mariae Curie-Skłodowska. Sectio C, Biologia* 63, 7–11.

Bielańska-Grajner, I. & Poznańska, M. 2010. The biodiversity of psammon rotifers in Włocławek Reservoir. *Oceanological and Hydrobiological Studies* 39, 111–117.

Boeckner, M. J., Sharma, J. & Proctor, H. C. 2009. Revisiting the meiofauna paradox: dispersal and colonization of nematodes and other meiofaunal organisms in low- and high-energy environments. *Hydrobiologia* 624: 91–106.

Burdíková, Z., Čapek, M., Švindrych, Z., Gryndler, M., Kubínová, L. & Holcová, K. 2012. Ecology of testate amoebae in the Komořany Ponds in the Vltava Basin. *Microbial Ecology* 64, 117–130.

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. & 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.

Conde-Porcuna, J. M. 2000. Relative importance of competition with *Daphnia* (Cladocera) and nutrient limitation on *Anuraeopsis* (Rotifera) population dynamics in a laboratory study. *Freshwater Biology* 44, 423–430.

Covazzi Harriague, A., Misic, C., Valentini, I., Polidori, E., Albertelli, G. & Pusceddu, A. 2013. Meio- and macrofauna communities in three sandy beaches of the northern Adriatic Sea protected by artificial reefs. *Chemistry and Ecology* 29, 181–195.

Czapik, A. & Fyda, I. 1992. Contribution to the knowledge of psammophilic ciliates from the Baltic Sea. *Acta Protozoologica* 31, 109–114 (in French with English summary).

Ejsmont-Karabin, J. 2001. Psammon rotifers in two lakes of different trophy – their abundance, species structure and role in phosphorus cycling. *Verhandlungen des Internationalen Verein Limnologie* 27, 3856–3859.

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. 2004. Are community composition and abundance of psammon rotifera related to grain-size structure of beach sand in lakes? *Polish Journal of Ecology* 52, 363–368.

Ejsmont-Karabin, J. 2005. Short time-response of psammic communities of Rotifera to abiotic changes in their habitat. *Hydrobiologia* 546, 423–430.

Ejsmont-Karabin, J. 2008. Vertical microzonation of psammon rotifers (Rotifera) in the psammolittoral habitat of an eutrophic lake. *Polish Journal of Ecology* 56, 351–357.

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC., Peterson, A. T., Phillips, S. J., Richardson, K. S., Scachetti-Pereira, R., Schapire, R. E., Soberón, J., Williams, S., Wisz, M. S. & Zimmermann, N. E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.

Elith, J., Leathwick, J. R. & Hastie, T., 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77, 802–813.

Fernando, O. J. & Natarajan, R., 1987. Diurnal migration of estuarine intertidal meiofauna. *Mahasagar – Bulletin of the National Institute of Oceanography* 20, 255–262.

Gheskiere, T., Hoste, E., Vanaverbeke, J., Vincx, M. & 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. & Degraer, S. 2005a. Nematodes from wave-dominated sandy beaches: diversity, zonation patterns and testing of the isocommunities concept. *Estuarine, Coastal and Shelf Science* 62, 365–375.

Gheskiere, T., Vincx, M., Weslawski, J. M., Scapini, F. & Degraer, S. 2005b. Meiofauna as descriptor of tourism-induced changes at sandy beaches. *Marine Environmental Research* 60, 245–265.

Giere, O. 2009. *Meiobenthology. The Microscopic Motile Fauna of Aquatic Sediments.* 2nd ed. Springer-Verlag, Berlin–Heidelberg. 527 pp.

Golemansky, V. 1976. Contribution a l'etude des Rhizopodes et des Heliozoaires du psammal supralittoral de la Mediterranee. *Acta Protozoologica* 15, 35–45 (in French with English summary).

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., 1998a. Interstitial testate amoebae (Rhizopoda: Testacea) from the Italian Coast of the Mediterranean Sea. *Acta Protozoologica* 37, 139–143.

Golemansky, V. 1998b. 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.

Haque, A. H., Szymelfenig, M. & Węsławski, J. M., 1997. Small-scale vertical distribution of zoobenthos in the sandy littoral of the Gulf of Gdańsk. *Oceanologia* 39, 433–446.

HELCOM 2003. The Baltic marine environment 1999–2002. *Baltic Sea Environment Proceedings* 87. 46 pp.

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.

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., Szymelfenig, M., De Troch, M., Urban-Malinga, B. & Węsławski, J. M. 2005a. Latitudinal biodiversity patterns of meiofauna from sandy littoral beaches. *Biodiversity and Conservation* 14, 461–474.

Kotwicki, L., De Troch, M., Urban-Malinga, B., Gheskiere, T. & Węsławski, J. M. 2005b. Horizontal and vertical distribution of meiofauna on sandy beaches of the North Sea (The Netherlands, Belgium, France). *Helgoland Marine Research* 59, 255–264.

Krebs, J. C. 1989. *Ecological Methodology*. Harper & Row Publishers, New York. 620 pp.

Kutikova, L. A. 1970. *Rotifers (Rotatoria) of the Fauna of the USSR. Eurotatoria (Ploimida, Monimotrochida, Paedotrochida).* Nauka, Leningrad. 744 pp. (in Russian).

Kutikova, L. & Haberman, J. 1986. Rotifers (Rotatoria) of Lake Võrtsjärv. *Proceedings of the Academy of Sciences of the Estonian SSR. Biology* 35, 113–121.

Liu, H., Zhang, Z., Fan, S., Hua, E. & 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.

Loopmann, A. 1984. *Suuremate Eesti järvede morfomeetrilised andmed ja veevahetus.* Tallinn. 150 pp [Morphometrical data and water exchange of larger Estonian lakes.] (in Estonian).

Mäemets, A. 1977. *Eesti NSV järved ja nende kaitse*. Valgus, Tallinn. 264 pp. [Lakes of the Estonian S.S.R. and their protection.] (in Estonian).

Margalef, R. 1957. Information theory in ecology. *General Systems* 3, 36–71.

Maria, T. F., Vanaverbeke, J., Esteves, A. M., De Troch, M. & 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. & 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.

Martens, P. M & Schockaert, E. R. 1986. The importance of turbellarians in the marine meiobenthos: a review. *Hydrobiologia* 132, 295–303.

Mazei, Y. A. & Burkovsky, I. V. 2003. Vertical structure of the interstitial ciliate community in the Chernaya River estuary (the White Sea). *Protistology* 3, 107–120.

Mazei, Y. A. & Burkovsky, I. V. 2006. Patterns of psammophilous ciliate community structure along the salinity gradient in the Chernaya River estuary (the Kandalaksha Gulf, the White Sea). *Protistology* 4, 251–268.

Mazei, Y. A. & Tsyganov, A. N. 2006. *Freshwater Testate Amoebae*. KMK, Moscow (in Russian). 304 pp.

McLachlan A. & Brown A. 2006. *The ecology of sandy shores*. Academic press – Elsevier. 373 pp.

Melone, G., Ricci, C., Segers, H. & Wallace, R. L. 1998. Phylogenetic relationships of phylum Rotifera with emphasis on the families of Bdelloidea. *Hydrobiologia* 387/388, 101–107.

Michiels, I. C. & Traunspurger, W. 2005. Benthic community patterns and the composition of feeding types and reproductive modes in freshwater nematodes. *Nematology* 7, 21–36.

Mieczan, T. & Nawrot, D. 2012. Vertical micro-distribution of psammonic ciliates and their relationship to physical and chemical parameters in two lakes of different trophic status. *Oceanological and Hydrobiological Studies* 41, 48–56.

Nawrot, D. & Mieczan, T. 2012. Co-occurrence of psammonic ciliates and rotifers in eutrophic lake (Łęczna-Włodawa Lakeland) Teka Komisji Ochrony i Kształtowania Środowiska Przyrodniczego – Oddzial w Lublinie Polska Akademia Nauk, 2012, 9, 125–133.

Nawrot, D. & Mieczan, T. 2014. Diel horizontal distribution of psammonic ciliates and rotifers in shallow eutrophic lake. *Polish Journal of Environmental Studies* 23, 419–425.

Neel, J. K. 1948. A Limnological Investigation of the Psammon in Douglas Lake, Michigan, with EspecialReference to Shoal and Shoreline Dynamics. *Transactions of the American Microscopical Society* 67, 1–53.

Ngo, X. Q., Smol, N. & Vanreusel, A. 2013. The meiofauna distribution in correlation with environmental characteristics in 5 Mekong estuaries, Vietnam. *Cahiers de Biologie Marine* 54, 71–83.

Nogrady, T., Wallace, R. L. & Snell, T. W. 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. 142 pp.

Noreña, C., Damborenea, C., Faubel, A. & Brusa, F. 2007. Composition of meiobenthonic Platyhelminthes from brackish environments of the Galician and Cantabrian coasts of Spain with the description of a new species of Djeziraia (Polycystididae, Kalyptorhynchia). *Journal of Natural History* 41, 29–32.

Obertegger, U., Smith, H. A., Flaim, G. & Wallace, R. L. 2011. Using the guild ratio to characterize pelagic rotifer communities. *Hydrobiologia* 662, 157–162.

Ott, I. (Ed.) 2007. *Saadjärve limnoloogilised uurimused II.* Eesti Maaülikooli Põllumajandus- ja Keskkonnainstituudi Limnoloogiakeskus, Tartu (in Estonian).

Ott, I., Kõiv, T., Nõges, P., Kisand, A., Järvalt, A. & 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.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74, 2215–2230.

Papageorgiou, N., Moreno, M., Marin, V., Baiardo, S., Arvanitidis, C., Fabiano, M. & Eleftheriou, A. 2007. Interrelationships of bacteria, meiofauna and macrofauna in a Mediterranean sedimentary beach (Maremma Park, NW Italy). *Helgoland Marine Research* 61, 31–42.

Pejler, B. 1995. Relation to habitat in rotifers. *Hydrobiologia* 313/314, 267–278.

Pennak, R. W. 1940. Ecology of the microscopic metazoa inhabiting the sandy beaches of some Wisconsin lakes. *Ecological Monographs* 10, 537–615.

Pitkänen, H., Kiirikki, M., Savchuk, O., Räike, A., Korpinen, P. & 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. & Peltonen, H., 2008. The Gulf of Finland. In: Schiewer, U. (ed.) *Ecology of Baltic Coastal Waters.* Springer, Berlin. pp. 285–308.

R Core Team 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radwan, S. & Bielańska-Grajner, I. 2001. Ecological structure of psammic rotifers in the ecotonal zone of Lake Piaseczno (eastern Poland). *Hydrobiologia* 446/447, 221–228.

Radwan, S., Ozimek, T., Bielańska-Grajner, I. & Sender, J. 2001. Structure of the water/land ecotones in trophically different Polish lakes. *Verhandlungen des Internationalen Verein Limnologie* 27, 3848–3851.

Ristau, K. & Traunspurger, W. 2011. Relation between nematode communities and trophic state in southern Swedish lakes. *Hydrobiologia* 663, 121–133.

Roskov, Y., Kunze, T., Paglinawan, L., Abucay, L., Orrell, T., Nicolson, D., Culham, A., Bailly, N., Kirk, P., Bourgoin, T., Baillargeon, G., Hernandez, F., De Wever, A. & Didžiulis, V. (Eds.) 2013. Species 2000 & ITIS Catalogue of Life, 15th August 2013. Digital resource at www.catalogueoflife.org/col. Species 2000: Reading, UK.

Roskov Y., Kunze T., Orrell T., Abucay L., Paglinawan L., Culham A., Bailly N., Kirk P., Bourgoin T., Baillargeon G., Decock W., De Wever A. & 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.

Rubal, M., Besteiro, C. & Veiga, P. 2012. Intertidal meiofauna communities along an estuarine gradient in a protected area (Ria de Foz, north-west Spain). *Journal of the Marine Biological Association of the United Kingdom* 92, 63–72.

Schmid-Araya, J. M. 1998. Rotifers in interstitial sediments. *Hydrobiologia* 387/388, 231–240.

Segers, H. & Chittapun, S. 2001. The interstitial Rotifera of a tropical freshwater peat swamp on Phuket Island, Thailand. *Belgian Journal of Zoology* 131, 65–71.

Segers, H. 2007. Annotated checklist of the rotifers (Phylum Rotifera), with notes on nomenclature, taxonomy and distribution. *Zootaxa* 1564, 1–104.

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. & 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 tehisjärved*. Tallinn, Keskkonnaministeeriumi Info- ja Tehnokeskus, 168 p.

ter Braak, C. J. F & Verdonschot, P. F. M 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57, 255–289.

Thane-Fenchel, A. 1968. Distribution and ecology of nonplanktonic brackish-water rotifers from Scandinavian waters. *Ophelia* 5, 273–297.

Timm, T. (ed.) 1973. *Võrtsjärv*. Valgus, Tallinn, 284 pp (in Estonian).

Tuvike, L., Kisand, A., Tõnno, I. & Nõges, P. 2004. Chemistry of lake water and bottom sediments. In: J. Haberman, J., Pihu, E., Raukas A. (ed.) *Lake Võrtsjärv*. Estonian Encyclopaedia Publishers, Tallinn, pp. 89–102.

Whitman, R. L. & Clark, W. J. 1984. Ecological studies of the sand-dwelling community of an east Texas stream. *Freshwater Invertebrate Biology* 3, 59–79.

Wickham, S., Gieseke, A. & Berninger, U. G., 2000. Benthic ciliate identification and enumeration: an improved methodology and its application. *Aquatic Microbial Ecology* 22, 79–91.

WoRMS Editorial Board 2014. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ (accessed 2014-06-29).

Wu, L., Feng, W., Yu, Y. & Shen, Y. 2011. Temporal and spatial variations in the species composition, distribution, and abundance of Protozoa in East Dongting Lake, China. *Journal of Freshwater Ecology* 22, 655–665.

PUBLICATIONS

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Lokko, K. & 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., Kotta, J. & 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.

Conference presentations:

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Lokko, K. & Virro, T. (2012). The structure of psammic rotifer communities in the two boreal lakes of different trophy: Lake Võrtsjärv and Lake Saadjärv (Estonia). (poster presentation) 13th International Rotifer Symposium. North-Eastern Hill University, Shillong, Meghalaya, India; November 18–24, 2012.

Lokko, K. & Virro, T. (2013). Mitmekesisus vee ja maa piiril: keriloomad ning kodaamööbid. (oral presentation) Zooloogia konverents. Tartu Ülikool, Tartu, 5. April 2013.

Lokko, K., Virro, T. & Kotta, J. (2013). Seasonal variability, horizontal and vertical distribution of zoopsammon in the Eastern Baltic Sea. (oral presentation) 15th International Meiofauna Conference. Seoul, Korea, 22–26 July 2013.

Lokko, K., Virro, T. & Kotta, J. (2014). Seasonal variability in the diversity of psammic testate amoebae in the Estonian fresh and brackish waters. (poster presentation) 7th International Symposium on Testate Amoebae. Poznań, Poland, 8–12 September 2014.

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Lokko, K. & 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., Kotta, J. & 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.

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Lokko, K., Virro, T. & Kotta, J. (2011). The structure of zoopsammon communities of Lake Võrtsjärv and Lake Saadjärv (Estonia): a pilot study. (stendettekanne) Food webs and climate change: Nordic Benthological Meeting VIII; Aalborg, Taani, 9–12. mai 2011.

Lokko, K. & Virro, T. (2012). The structure of psammic rotifer communities in the two boreal lakes of different trophy: Lake Võrtsjärv and Lake Saadjärv (Estonia). (stendettekanne) 13th International Rotifer Symposium. North-Eastern Hill University, Shillong, Meghalaya, India, 18–24. november 2012.

Lokko, K. & Virro, T. (2013). Mitmekesisus vee ja maa piiril: keriloomad ning kodaamööbid. (suuline ettekanne) Zooloogia konverents. Tartu Ülikool, Tartu, 5. aprill 2013.

Lokko, K., Virro, T. & Kotta, J. (2013). Seasonal variability, horizontal and vertical distribution of zoopsammon in the Eastern Baltic Sea. (suuline ettekanne) 15th International Meiofauna Conference. Seoul, Korea, 22–26. juuli 2013.

Lokko, K., Virro, T. & Kotta, J. (2014). Seasonal variability in the diversity of psammic testate amoebae in the Estonian fresh and brackish waters. (stendettekanne) 7th International Symposium on Testate Amoebae. Poznań, Poola 8–12. september 2014.

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