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ROTIFERA XVI

Review Paper

Rotifers of lake psammon: a knowledge synthesis

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Abstract Most information on rotifers living in lake sands comes from the 1930s, when the first reports on this subject by Jerzy Wiszniewski appeared. After some decline in the interest in lake psammon in the following years, research on lake psammon returned in the last decade of the twentieth century. The last comprehensive review of ecology of psammon Rotifera was included in the excellent 1998 publication by Schmid-Araya on Rotifera in interstitial sediments. More than 20 papers have been published since that time. So far, research conducted almost exclusively in the northern hemisphere have dealt with issues related to distribution of rotifers, their species structure and diversity as well as to their relation to abiotic and biotic factors. The aim of the present study was to collect all available information on psammon rotifers, assess the shortcomings in our knowledge and fill these gaps with the results of some of my recent research. The results of the study show that the species richness of this group in geographical terms is still unknown. It means we also do not know the level of endemism among the psammon rotifers. The role of psammon rotifers in benthic food webs is another issue requiring research.

Keywords Meiofauna · Lake · Arenal · Abundance · Diversity · Ecology

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Introduction

Although there are far more non-plankton forms of small invertebrates living in littoral habitats than planktonic ones, little is known about their physiology, taxonomy, biology and ecology. The sandy habitat in lake littoral (referred to as arenal, which means sand in Spanish) has been subdivided by Wiszniewski (1934b, 1937) into three categories: hydro-, hygro- and euarenal occupied by hydro-, hygro- and eupsammon. Focussing on lake psammon, the hydroarenal is a layer of submerged sands along the edge of a lake. The hygroarenal is a layer of sand which is above and adjacent to the water level and is completely saturated by cappillar and wave action. Finally, the euarenal is a part of beach partially saturated and submerged only during periods of high water. On the sand surface there is often a layer of dry sand. The biological assemblages of the three habitats are subjected to different level of physical disturbance with the hydropsammon being the least exposed to environmental stress while the hygropsammon is subjected to strong mechanical disturbances, because the waves cause constant mixing, transfer and destruction of some of organisms (Neel, 1948). A characteristic feature of the eupsammon microhabitat is its strong daily variation, i.e. humidity drop and temperature increase during the day, humidity increase and temperature drop at night, as well as susceptibility to atmospheric factors. A zone of wet sand would seem to be a very unfavourable environment for life. High fluctuations of temperature during the day and night, small living space, low concentration of oxygen and very high concentrations of organic and mineral compounds are factors that affect the life of organisms inhabiting this habitat decisively (Wiszniewski, 1937; Pennak, 1951; Schmid-Araya, 1998; Radwan & Bielańska-Grajner, 2001; Ejsmont-Karabin, 2003a, b; Bielańska-Grajner, 2005). Capillary water in the euarenal may change over a short period of time due to strong changes in temperature and heavy rains. The hygroarenal may be under the influence of wave actions and heavy rains. The least disturbed zone is the hydroarenal which may be influenced by changing temperature and the concentration of organic particles.

In the psammon nematodes and rotifers seem to be the most abundant and richest groups, although Protozoa, Platyhelminthes, Tardigrada and Harpacticoida may be sometimes even more abundant as well (Zhadin et al., 1972; Whitman et al., 1994; Nawrot & Mieczan, 2012).

Most information on rotifers living in the sand of lake beaches comes from the 1930s, when the first reports on this subject by the Polish scientist—Jerzy Wiszniewski appeared (Wiszniewski, 1932, 1933, 1934a, b). The discovery of this living in quite unusual conditions community caused a short-term increase of interest in the psammon, which resulted in the appearance of several studies devoted to this habitat in this and the next decade (e.g. Myers, 1936; Pennak, 1940; Neel, 1948; Pennak, 1951). However, for five decades, publications from this period remained the most complete source of information about the characteristic features of the psammolittoral and its organisms, as this period saw a decline in the interest in lake psammon, and the published works were of a contributing nature and most often concerned taxonomic issues.

Research on the ecology of lake psammon was revived in the last decade of the twentieth century, and the topic was often addressed by Polish researchers. The studies in this period include a description of the species structure and functioning of psammon algae (Czernaś & Krupa, 1998 and subsequent studies) and rotifers (Radwan et al., 1998, 2001; Bielańska-Grajner, 2001, 2005; Ejsmont-Karabin, 2003a, b, and many others). Nawrot and Mieczan (2014) have shown significant differences in the horizontal distribution of ciliates and rotifers in the diurnal cycle. Studies of psammon in brackish and fresh waters of Estonia have shown that rotifers play a different functional role in food webs in those environments (Lokko & Virro, 2014; Lokko et al., 2017). At the beginning of the twenty-first century, first publications concerning faunistic research on psammon rotifers in Asia appeared (Segers & Chittapun, 2001; Dang et al., 2015; Duong et al., 2020, 2021).

Although knowledge about the distribution and species structure of psammon rotifers is greater than the knowledge about the functioning of the community, even the former topic is insufficiently known. The last comprehensive review of ecology of psammon Rotifera was included in the excellent publication by Schmid-Araya (1998) on Rotifera in interstitial sediments. However, while describing the ecology of broadly understood interstitial environments, this review focussed on ecology and assemblage structure of hyporheos. More than twenty papers have been published since that time, greatly expanding our knowledge of psammon Rotifera.

The question is: What do we know now, 90 years after the discovery of the communities of rotifers inhabiting lake sands? Thus, the aim of the present study was to collect all available information from all over the world on psammon rotifers, assess the shortcomings in our knowledge and, if possible, fill these gaps with the results of some of my recent research.

The analyzes of the quantitative and qualitative structure of rotifer communities, their spatio-temporal distribution and ecological role in the lake arenal included both literature data and data from own research. Therefore, the chapter of Results has been divided into 5 sub-chapters: the first three deal with the results of the literature review and the last two deal with new data.

Methods

A literature review included publications from 1930 to 2022. Most of them came from my collection of reprints, accumulated over 50 years of my scientific work, as well as from the collection of publications of the Hydrobiological Station on Wigry stored in the library of the Nencki Institute of the Polish Academy of Sciences. I updated my review with recent publications found in scientific databases, like Google Scholar and Web of Science. Key words used during the literature review were: Rotifera, psammon, psammolittoral, arenal, interstitial water, lake, in various combinations. All publications found were cited in this work.

In the studies of density, species richness and frequency (i.e. number of lakes with recorded presence of a given species), samples collected in spring and summer from the arenal of 32 lakes of different mictic type and trophy (North-eastern Poland) were used. I used both published (Ejsmont-Karabin, 2003a, b) and unpublished data from my research conducted from 1999 to 2022. The examined stations covered up to 44 beaches in spring and 71 beaches in summer. Seasonal succession studies were carried out on the beach of Lake Mikołajskie in 2020, every week from April 11 to September 12.

For quantitative sampling I used the method of rinsing rotifers collected with a sharp-edged cylinder from sand material by briefly mixing it energetically with tap water. This method is often used (Ejsmont-Karabin, 2003a, b; Bielańska-Grajner & Poznańska, 2010; Lokko, 2014) as it allows rotifer density to be established in units of area or volume of sand. Rotifers were determined from sand samples shaken six times with 0.5 L of tap water. The supernatant was filtered through a net with 30 µm mesh-size. All rotifers were counted and identified in five subsamples each equal to 10% of the sample. The first subsample was analyzed while alive, while the remaining were fixed with 4% formalin.

Regression analyses correlating the density of rotifer species to their frequency were conducted using data from samples collected from eu-, hygro-, and hydroarenal of 32 lakes in North-eastern Poland. The same set of samples was used to estimate cumulative species richness dependence on sampling effort, i.e. number of samples taken after 10 randomization of sampling order. In order to assess the closest possible number of species that could be identified from particular arenal zones in spring and summer I used 2 estimates of total species richness: Chao 2 and Jackknife 2 (Gotelli & Colwell, 2011).

Results

Spatio-temporal distribution of psammon communities of Rotifera

The lake arenal is inhabited by numerous organisms. However, in Lokko's (2014) opinion rotifers dominate those communities only occasionally and there is no single phylum or other higher taxa that can be considered generally dominant there.

An important group among organisms living in interstitial waters of sandy shores are those limited in their occurrence to wet sands and assessed as psammobionts (Wiszniewski, 1937). They are strictly adapted to life among the particles of sand, although some of them may be met sporadically and in low numbers beyond the arenal (microzone of sands). As typical representatives of psammon rotifers Wiszniewski (1933, 1934a, b) lists such species as: *E. spinifera*, *W. velox, W. sabulosa, W. depressa, T. pygocera, T. taurocephala, L. psammophila, L. levistyla* (species names due to recent nomenclature). Myers (1936) studying the psammon of acid Lenape and Union lakes in New Jersey listed 27 psammobiotic species and described 11 species new for science. Radwan and Bielańska-Grajner (2001) added *D. hercules* to the list. Psammophiles are species occurring in wet sands and beyond it, however they are markedly more abundant in psammon communities. The third group creating the psammon are psammoxenes, i.e. species that get into the zone by accident. In Lake Wigry the relation of the three groups was as follows: among 83 found species 17 were psammobionts, 19-psammophiles and 47 psammoxenes (Wiszniewski, 1933).

According to Wiszniewski (1933) the farther away from the lake shore the fewer animals there are in the eupsammon, although, individual species may reach up to twenty meters from the water line. At the same time, constantly submerged underwater sands are relatively poor in psammon both quantitatively and qualitatively. As a result the zone richest in psammon organisms is often the hygroarenal. This statement was confirmed by Varga (1957) who noted a marked contrast between the species-rich hygropsammon and the species-impoverished eupsammon community in Lake Balaton. On the contrary, in Ejsmont-Karabin's (2003a, b) studies the hydropsammon was the community richest in species. The high species diversity of psammon rotifers found in Lake Kuc can be explained, among others, by the impact of intermediate environmental stress (Ejsmont-Karabin, 2003a, b). The course of changes in the species diversity of the community in the hydro-euarenal transect confirms Connell's (1978) Intermediate Disturbance Hypothesis, because the highest species diversity values were recorded in hydropsammon—a community under the influence of rather moderate interference. At the same time, the species diversity of hygro— and eupsammon communities subjected to strong mechanical, physical and chemical disturbances was almost twice lower.

Hydropsammon rotifers, during day and night hours, are concentrated in a thin 0.5 cm deep layer of the epihydroarenal (Ejsmont-Karabin, 2008). The permanent concentration of rotifers in this layer may be explained by a high abundance of permanently renewed food resources, both bacteria and algae (Czernaś, 1991; Krupa et al., 1991).

Psammon communities of Rotifera are subject to seasonal succesion. Wiszniewski (1933, 1934b), who studied seasonal changes in the occurrence of rotifers in the arenal of Lake Wigry (North-eastern Poland), described phenological periods in the seasonal occurrence of psammon rotifers:

Spring—hydropsammon rotifers appear, but in low densities. The most important role in the community is played by psammophiles *Cephalodella catellina* and *C. ventripes.*

Summer, in June maxima of densities of psammophilic species are built by *Cephalodella auriculata, C. gibba, L. patella, C. colurus, L. closterocerca* and psammobionts like *L. levistyla, L. psammophila, T. taurocephala*. In the second half of summer the density of hygropsammon rotifers decreases. However, density of rotifers in eupsammon may sometimes increase.

Autumn – eupsammon gradually disappears. Species met in spring appear again and reach high densities. Species rare in spring and summer, like *W. sabulosa, W. velox, B. tenella* also appear.

Winter—with the appearance of the first frosts rotifers disappear.

This may be confirmed by the studies of Ejsmont-Karabin (2001) and Lokko et al. (2017), which indicated some commonalities in the seasonal patterns of rotifer occurrence, such as low abundances in early spring and late autumn.

Densities of rotifers in the arenal are extremely variable, both in space (Ejsmont-Karabin, 2006) and time (Ejsmont-Karabin, 2005). They can reach very high values up to 41,755 ind. 100 cm^{-2} (i.e. equal to 208,775 ind l^{-1}) in the euarenal in Lake Kuc in spring, and up to 50,521 ind. 100 cm^{-2} (=252,605 ind l^{-1}) in the hygroarenal in Lake Wiartel in summer. The species that determined these maximum densities was, in both cases, *L. psammophila*, a typical psammobiotic species, not found in other littoral subhabitats.

Taking into account the relatively difficult conditions in the habitat occupied by psammon organisms, the species diversity of psammon rotifers can be considered surprisingly high. In studies conducted in lakes in North-eastern Poland (Ejsmont-Karabin, 2003a, b), rotifers were found at all examined beaches. In total, 110 species were found (this accounted for 26% of all rotifers species recorded in Poland), of which 22 species belonged to those found only in the psammon and three species were new for Poland (*C. psammophila*, *C. wiszniewski* and *Euchlanis dapidula* Parise, 1966). A total of 72 taxa were found in two Estonian lakes, eutrophic Lake Saadjärv and mesotrophic Lake Võrtsjärv. Of these, 11 rotifer species were new records for the fauna of Estonia (Lokko et al., 2013). Similarly, rich in species were the psammon communities of Vietnam (Duong et al., 2020) with 76 species in the hygropsammon and 49 species in the eupsammon. Psammon community of Lake Bajkal (Arov, 1990) contained fewer species, just 40. Most of them were species common in the arenal of European lakes. Two endemic species found in Lake Bajkal were *Notholca kozhovi* Vassijeva & Kutikova, 1969, and *Colurella grandiuscula* Kutikova & Arov, 1985.

The list of psammon rotifers from Lenape and Union Lakes in New Jersey (Myers, 1936) contained 145 species with 11 species new for science and only 44 previously recorded by Wiszniewski (1934a, b) in Poland. This difference may result from differences in the pH of the studied American (acid waters) and Polish (alkaline waters) lakes. Results of studies carried out in so-called lobelian lakes (Bielańska-Grajner, 2001) suggested that pH was one of the most important factors affecting the density and diversity of psammon communities. However, Bielańska-Grajner's (2001) record of 43 species cannot explain the very high diversity of rotifers from the New Jersey lakes.

Research on psammon rotifers has generally been focussed on temperate regions; extremely rare reports on psammon rotifers from the tropics concern Asia (Segers & Chittapun, 2001; Dang et al., 2015). Studies conducted during both the dry and rainy season in Bau Thiem Lake in Vietnam (Dang et al., 2015) gave a total of 89 rotifer species belonging to 21 genera and 13 families. Among them 54% were new to Vietnam, with three species *Lecane phapi*, *L. dorysimilis* and *Trichocerca bauthiemensis* new to science. Less intensive studies of rotifers inhabiting the arenal of a coastal freshwater peat swamp on Phuket Island, Thailand (Segers & Chittapun, 2001), recorded a total of 19 species, three of which were described as new to science and six taxa were new to Thailand.

Impact of abiotic and biotic factors on psammon rotifers

Sand grain size is among important factors characterizing psammon habitat (Giere, 2009). Particular species differed in their relation to different sand fractions (Ejsmont-Karabin, 2004). In general, however, the abundance of most of the dominant species was positively correlated with the "optimal" sand fraction. Several species, both large and small, seemed to avoid this fraction, preferring larger sand grains (> 2 mm). The only taxonomic group preferring the tiniest fraction of sand were bdelloids. These results confirm the significant impact of sand grain structure on the species composition of psammon communities of Rotifera. It has also been shown that uniformity of dominant species composition depends on the homogenous granulometric sand composition (Zhadin et al., 1972). Research on Lake Baikal's psammon (Arov, 1990) has shown that grain-size structure influences morphological structure, diet and movement of species adapted to life among sand grains. Thus, the relation of rotifers to the size of sand grains that dominate the environment may be an element of an ecological niche, at least for some species. A statistically significant relationship between the occurrence of such species as *E. marinum, E. worallii, Trichocerca intermedia* and others and the sand fraction was found in the studies by Bielańska-Grajner (2005).

The structure of the inhabited substrate is particularly important for the psammon organisms that inhabit it (Pennak, 1951). The capacity of the inhabited space depends on the size of sand grains and amounts to approx. 37% to 43% by volume of sand (Ruttner-Kolisko, 1961; Giere, 1993). Arov (1990), in studies carried out on the beach of Lake Baikal, showed that the taxonomic structure of rotifer communities was strongly differentiated within the same beach and highly dependent on the granulometric structure of sand. Similarly, in studies of 38 beaches of the lakes of the Masurian Lake District (Ejsmont-Karabin, 2004), a highly significant positive correlation was found between the number of rotifers and the proportion of 0.25–1.00 mm size fraction of sand grains (i.e. fraction considered as optimal for existence of rotifers). A negative and weak relationship was noted between the share of gravel (grain size > 1 mm) and dusty (< 0.25 mm) sand and the total number of rotifers. Of the three ecological groups of the psammon, only psammobionts were dependent on the structure of the sand and preferred sand grains with a size of 0.5 to 1 mm, while this fraction was avoided by psammophiles and psammoxenes (Ejsmont-Karabin, 2004).

Results of studies carried out during two seasons on 44 beaches of 18 lakes with different trophic state from the Masurian Lake District in Poland (Ejsmont-Karabin, 2003b) showed that with the increase in lake trophy, which was determined on the basis of the state of pelagic waters, there was also a tendency of increasing concentration of nutrients (phosphorus and nitrogen) and chlorophyll in interstitial waters. Although nutrient and chlorophyll concentrations did not have any impact on psammon rotifers, the trophic state of the lakes seems to cause a decrease in the species richness of the psammon communities of rotifers. In mesotrophic lakes, both the value of the fauna originality index and the number of species were higher than in lakes of higher trophy, whereas in hypertrophic lakes the value of these indicators, as well as the species diversity of the communities were by far the lowest. This suggests the important role of oxygen concentration, which is much lower in habitats with high content of detritus produced in adjacent waters (Pennak, 1951). According to Pennak (1951), rotifers are more sensitive to oxygen deficits than other groups of psammon invertebrates.

The taxonomic structure of the phytopsammon could have an impact on the species structure of psammic rotifers. Bielańska-Grajner and Molenda

(2008) found a significant correlation between the abundance of taxonomic groups of algae and densities of different rotifer species. *C. gibba*, *C. gracilis*, *Colurella adriatica* Ehrenberg, 1831, *L. lunaris*, and *L. psammophila* densities were correlated with abundance of chlorophytes. The density of *C. gibba* was also significantly correlated with Euglenophyta, and *C. adriatica* and *L. lunaris*, with Bacillariophyceae.

Statistical models performed by Lokko (2014) indicated that relationships between chemical factors and psammon organisms are highly complex and usually non-linear. Due to bacterial activity, oxygen content in the interstitial waters of lake psammolittoral is usually markedly lower and carbon dioxide much higher than in adjacent waters (Pennak, 1939, 1951). Among factors affecting the abundance and diversity of psammon communities is pH (Bielańska-Grajner, 2001). Its high impact was suggested by Wiszniewski (1936). Both authors observed species poor rotifer communities in interstitial waters with pH < 7.0. Some impact of pH on the density of psammon communities of rotifers was found in studies in a shallow, eutrophic lake by Nawrot and Mieczan (2014). However this impact was weak and different in the eu- and hydroarenal.

Role of psammon rotifers in lake littoral functioning

Our knowledge of the role of psammon rotifers in freshwater food webs is very poor. Although it may be assumed that there are some trophic interactions between freshwater meiofauna and macrofauna. Some undetailed studies have shown that the dominant macrofaunal predators in Mirror Lake, tanypod midges, feed on, among others, rotifers (Strayer, 1986).

According to Czernaś (2003) phytopsammon plays a significant role in drawing and capturing nutrient loads from the catchment area into the lake. Some support for this conclusion may be found in the extremely high turnover time for algal phosphorus in the hydroarenal of Lake Mikołajskie (Ejsmont-Karabin et al., 2012). However, taking into account the much lower turnover time for phosphorus involved in the biomass of bacteria we can suppose that bacteria play a much more important role than phytopsammon in the food web in lake arenal.

The research conducted in the mesotrophic Lake Kuc and the eutrophic Lake Mikołajskie (Ejsmont-Karabin, 2001) confirms the insignificant impact of psammon rotifers on phosphorus cycling in the littoral zone. Mineral phosphorus forms supplied as a result of P excretion by psammon rotifers constituted only 5% and 0.12% of phosphorus load from all external sources, respectively. However, the role of all groups of psammon organisms may be markedly more significant (Ejsmont-Karabin et al., 2012). Calculated for all ciliates, rotifers and crustaceans P remineralization was ca. 10 times higher than the maximum rate noted in lake pelagial. Nevertheless, rotifers' share in P regeneration in the arenal was negligible when compared to that of ciliates and small cladocerans (Ejsmont-Karabin et al., 2012).

When comparing the rates of P release from littoral sediments in Eau Galle Reservoir, i.e. 3.6 mg m^{-2} h^{-1} (James & Barko, 1991) and P regeneration by the hydropsammon of Lake Mikołajskie—6.4 mg m^{-2} h^{-1} (Ejsmont-Karabin et al., 2012) with the rate of P assimilation by hydropsammon in Lake Piaseczno, i.e. 24.5 mg m^{-2} h^{-1} (Czernaś, 2003), it tourns out that phytopsammon and psammic bacteria demands probably cannot be satisfied merely from internal sources, i.e. through remineralization by microinvertebrates.

Seasonal succession and abundance of psammon Rotifera in Lake Mikołajskie

Year-round observations of psammon in Lake Mikołajskie (Fig. 1) showed strong dynamics of changes in the abundance and species structure of psammon rotifers in all three zones of the arenal. The rapid increase in the numbers of rotifers in the hydroarenal in spring included mostly cold-water pelagic species of the genera *Synchaeta* and *Notholca* which may have been due to their high abundance in the littoral plankton. In summer, maxima in all three zones of the arenal were occupied mostly by psammophilic *L. closterocerca*, but in the euarenal this species was often changed to psammobiotic *L. psammophila*. In autumn, higher abundance of psammobiotic *W. velox* and *W. sabulosa* was noted (Fig. 1).

The role of the psammon ecological groups changed during the season, and in a different way in particular zones of the arenal (Fig. 2). In spring, psammoxenic (mostly pelagic) species dominated in all zones. In summer, psammobionts dominated in the eupsammon, psammobionts and psammophiles in the hygropsammon, and psammophiles in the

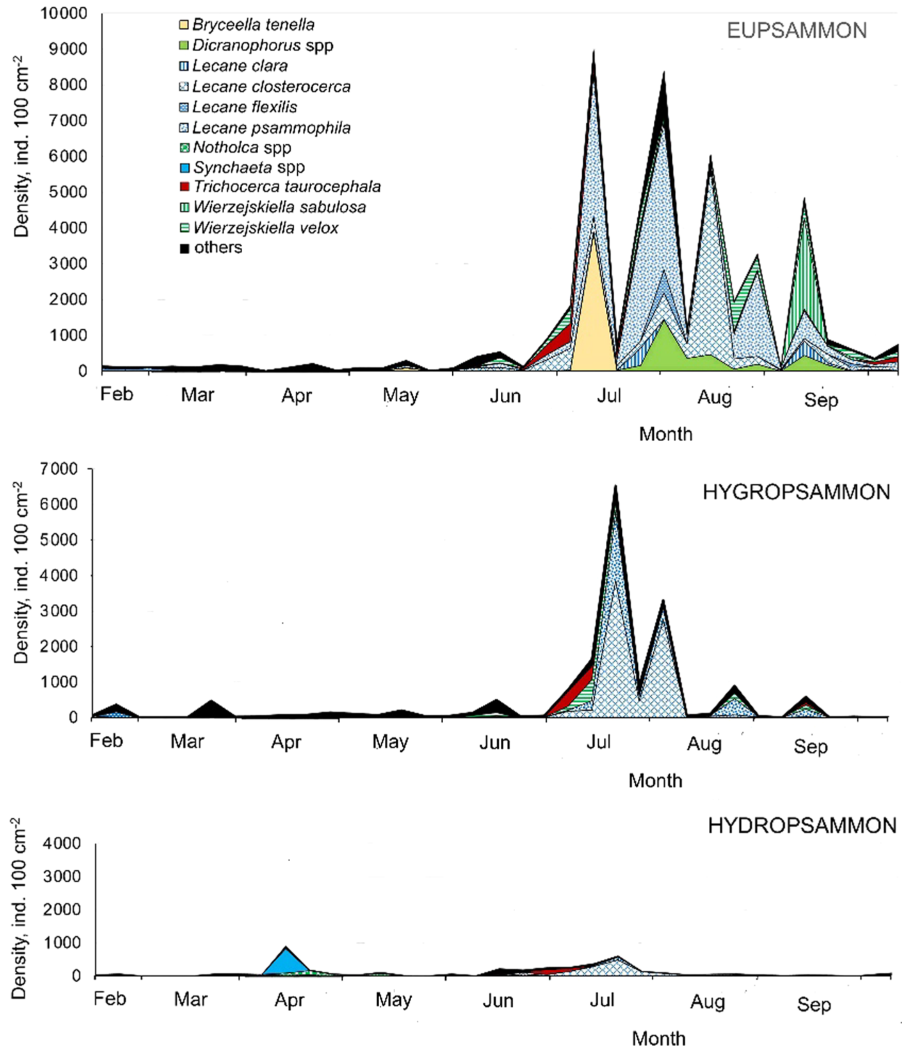

Fig. 1 Seasonal changes in the density (ind. 100 cm^{-2}) of psammon rotifers in three horizontal layers of the arenal of Mikołajskie Lake in the year 2020

hydropsammon. A marked increase in the importance of psammoxenes was observed in early autumn only in the hygroarenal, which was probably the effect of strong winds and therefore waves at that time. Thus, it seems that psammobiotic species develop best in mechanically stable conditions, subject to strong fluctuations in nutrient and oxygen concentration as well as temperature.

The maximum densities in the arenal are achieved by species most often observed in this habitat, as there was a clear positive relationship between species frequency in the arenal of different lakes and densities of Rotifera (Fig. 3). In spring, species with the same or similar frequency were most abundant in the eupsammon, whereas the lowest abundance was noted for the hydropsammon. In summer, a similarly low density was observed in the hydropsammon, however the most frequent species from the euarenal and hygroarenal were of similar densities (Fig. 3). The relationship was markedly stronger in spring ($R^2=0.43$ to 0.64; $P<0.0001$ in all cases). In summer, the weakest relationship was found for hydropsammon ($R^2=0.06$; $P=0.048$), and the highest one for the eupsammon ($R^2=0.52$; $P<0.0001$).

Species richness of psammon rotifers in lakes

The results of my many-years' research of more than 42 beaches in spring and 71 beaches in summer revealed significant differences among ecological zones as regards the number of species inhabiting them (Fig. 4). The highest number of species

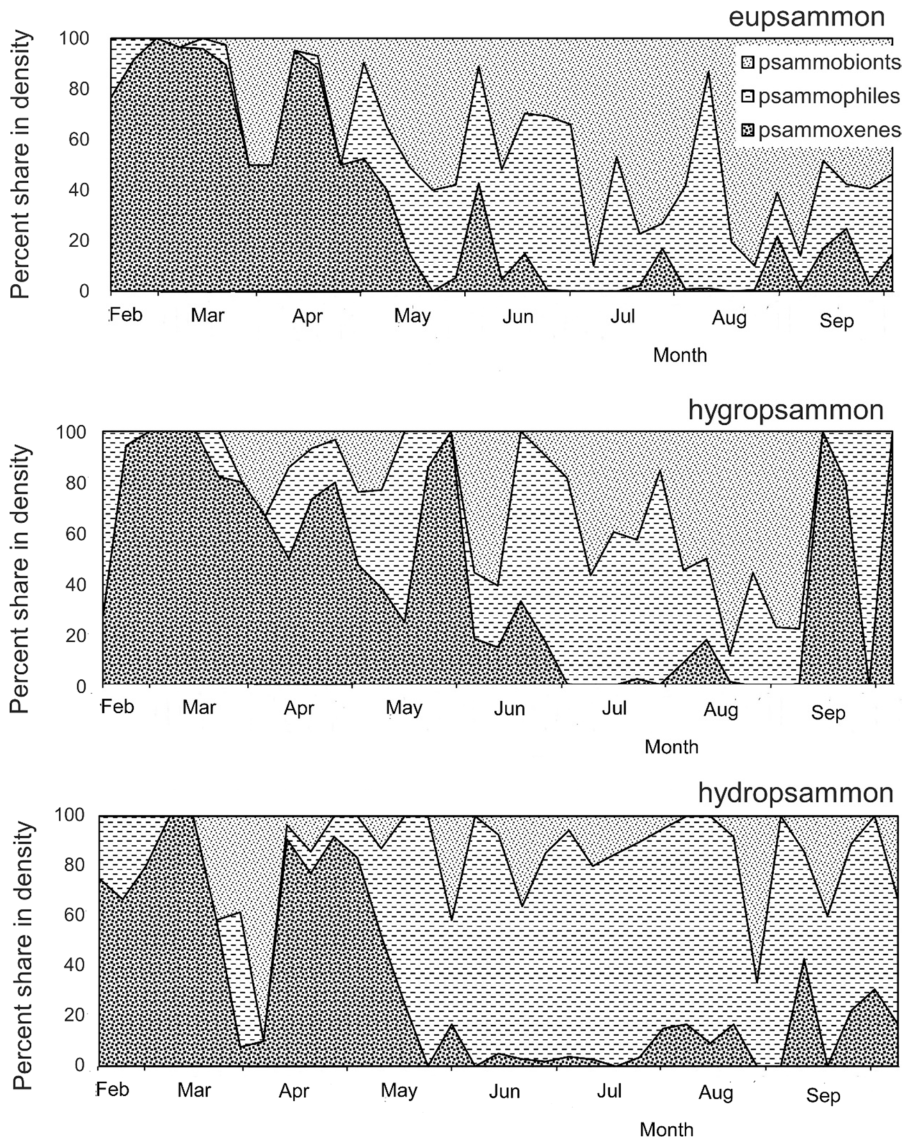

Fig. 2 Seasonal changes in the percentage of the ecological groups of psammon rotifers in their densities in three horizontal layers of the arenal of Mikołajskie Lake in the year 2020

was recorded in the hygroarenal, both in spring and summer. The analysis also shows that the psammon community is primarily composed of thermophilic species. Clearly, the number of species registered in all three zones in spring is much lower than in summer (Fig. 4). The difference between the values for summer and spring is about 1.3–1.4 fold with 40 measurements and it is even higher when we take into account more measurements.

However, there were still many species not found, which is well seen when we use estimators of the total number of species, like Chao 2 and Jackknife 2 (Table 1). Especially the latter estimator strongly increases the potential number of species. This increase is higher for samples taken in summer than for samples collected in spring. Markedly more species can be also found in the arenal when we study beaches of various lakes in summer, than in samples taken from one lake during the season.

A comparison of the lists of psammobiotic species from three continents shows that they are different. This applies to both habitats in different climate zones (Europe vs Asia) and similar ones (Europe vs North America) (Table 2; Fig. 5). It is worth noting that among the species of rotifers from the arenal habitats in Vietnam (Duong et al., 2020), those

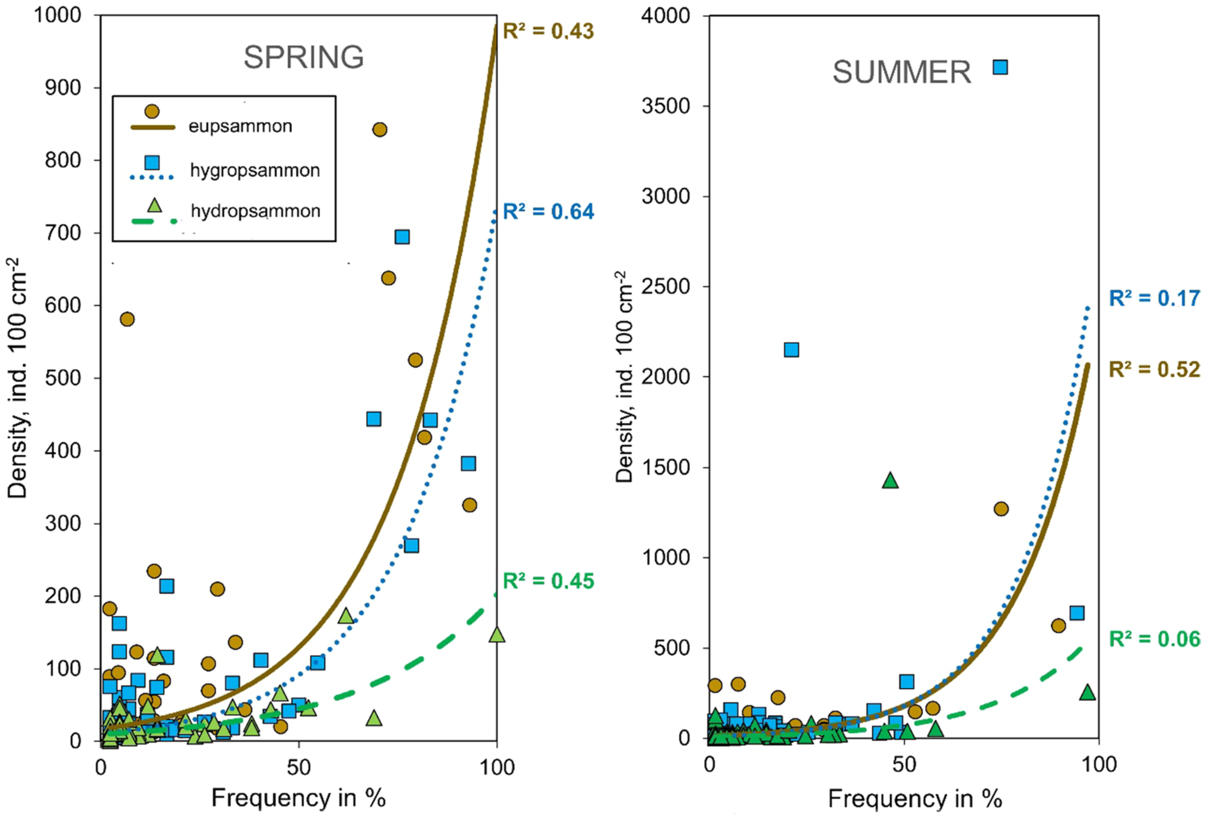

Fig. 3 The relationship between frequency and densities of psammon rotifers in two phenological periods in different lakes in North-eastern Poland

defined as psammobiotic have not been recorded so far in Europe and North America, while at least some of the psammophilic species (e.g. *Lecane lunaris, Cephalodella gibba*) and the psammoxenic species, e.g. *L. bifurca* and *L. bulla* (Gosse, 1851), are much more widely spread. From among all psammobiotic and psammophilic species recorded in this habitat 71%, and 77% (respectively) are those exclusive for particular continents.

Discussion

Rotifer abundance and species structure in the psammolittoral undergo the seasonal succession with low rotifer densities observed in spring and autumn, and maximum abundance in summer. The role of the psammon ecological groups changes as well, however in a different way in particular zones of the lake arenal. In spring, psammoxenic species dominate in all zones. In summer, the eupsammon is dominated by psammobionts, whereas psammobionts and psammophiles dominate in the hygropsammon, and psammophiles in the hydropsammon.

Low abundance of psammon rotifers in early spring and late autumn observed in Lake Mikołajskie was earlier noted in the studies of Ejsmont-Karabin (2001) and Lokko et al. (2017). However, there were some discrepancies, like occurrence of *Bryceella tenella,* which in my studies achieved its maximum density in early summer, whereas according to Wiszniewski (1933, 1934b) the species was characteristic for autumn. Seasonal changes in the occurrence of individual species may be of a local nature. In Lakes Saadjärv and Võrtsjärv, studied by Lokko and Virro (2014), *B. tenella* and *L. closterocerca* did not appear at all, while the dates of the occurrence of *L. psammophila*, *W. sabulosa* and *W. velox* coincided with those observed in Lake Mikołajskie.

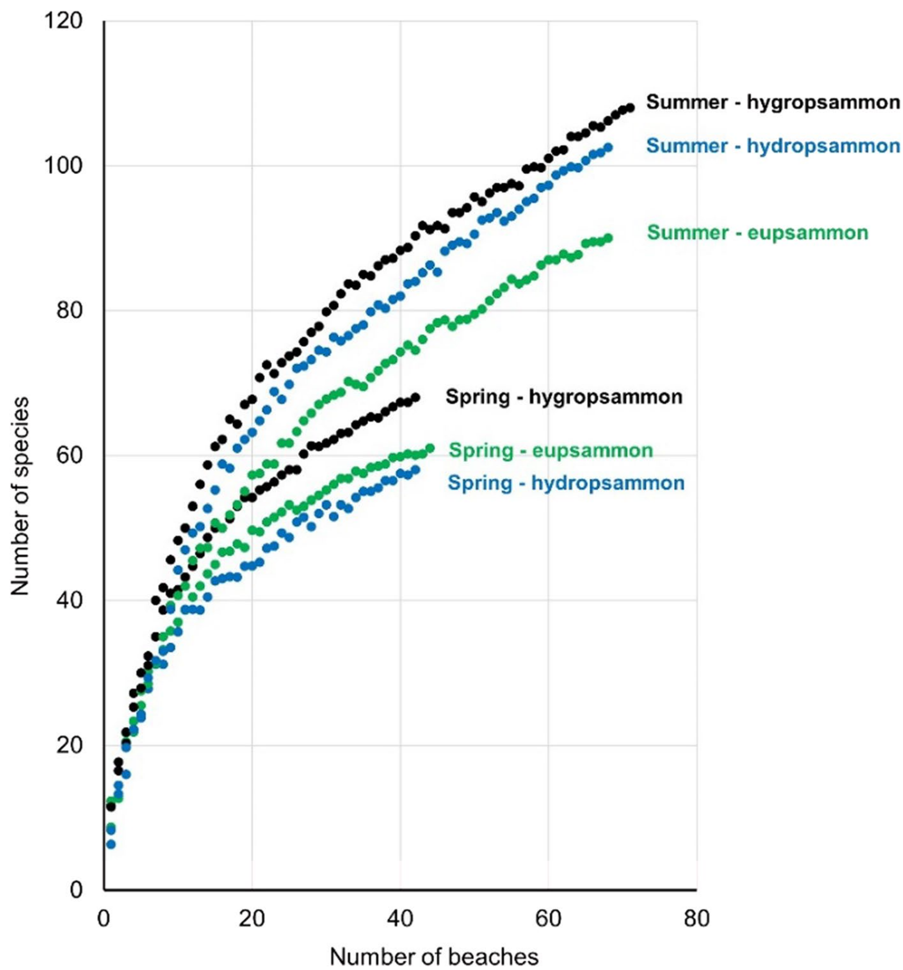

Fig. 4 The cumulative sum over the sampling effort (i.e. number of beaches sampled) of the number of species calculated with 10 randomizations of sampling order

In my studies, rotifer densities in the arenal reached very high values, up to several hundred thousand individuals per liter of wet sand. They seem to be markedly higher than those found in the very limited literature on the subject. Densities of rotifers in the lake beaches studied by Bielańska-Grajner (2005) were lower, up to 20,030 ind l^{-1} in spring (euarenal, Lake Czarnówek) and up to 4871 ind l^{-1} in summer (hygroarenal, Lake Wilczkowo). However, densities of rotifers in the arenal are extremely variable, both in space and time (Ejsmont-Karabin 2005, 2006). This means that the assessment of the abundance of rotifers in this habitat is largely dependent on the period and frequency of sampling, so its result is largely accidental. Moreover, so far, researchers have mainly focussed on the qualitative characteristics of psammon.

Rotifer species the most often observed in the lake arenal achieve the highest densities. They usually build maxima of rotifer abundance. According to Schmid-Araya (1998), these species are eurytopic and they are *r*-strategists. This may be indicated by the fact that they achieve exceptionally high values of density in a very short time (Ejsmont-Karabin, 2005). One of those species is *L. closterocerca*, which occurs in all littoral habitats, where it often dominates (Bielańska-Grajner, 2005; Ejsmont-Karabin & Karpowicz, 2021). However, *L. psammophila* most often dominates and reaches the highest numbers in the arenal, but it does not occur outside this habitat. While *L. psammophila*, as well as *W. sabulosa*, *W. velox* and other psammobionts can be considered r-strategic, they are most likely stenotopic, unable to live outside the waters of the arenal.

Table 1 Observed numbers of species and Chao 2 and Jackknife 2 estimates of total species richness from spring and summer samples collected from the arenal of 32 lakes and from the seasonal studies in Lake Mikołajskie (North-eastern Poland)

	Number of samples	Observed	Chao 2	Jackknife 2
Spring				
Eupsammon	44	61	68	79
Hygropsammon	42	68	78	91
Hydropsammon	42	58	70	81
Summer				
Eupsammon	68	90	115	133
Hygropsammon	71	108	164	178
Hydropsammon	69	104	173	182
February—October				
Eupsammon	35	62	75	87
Lake Mikołajskie				
Hygropsammon	35	58	66	78
Hydropsammon	35	50	86	93

Comparison of species richness in spring and summer shows that in all layers there are markedly more species in summer. Chao 2 and Jackknife 2 estimators indicate a very strong increase in the maximum number of species in summer in the hygro- and hydroarenal zones. The high values of both estimators in this period and in these zones result from the high share of singletons in the rotifer communities. Most of the singletons are psammoxenic species derived from the epiphyton associated with macrophytes, which reach the highest biomass in this period. The singletons appear in the arenal, carried with waves. It should also be noted that the number of species both observed and estimated for many different lakes is much higher than that observed over the entire season in one lake. This phenomenon is probably determined by the presence of different singletons in various lakes, because dominant and subdominant species are usually psammophiles and psammobionts, which are the same in most lakes (Ejsmont-Karabin 2003a, b; Bielańska-Grajner, 2005). These are the species that reach the highest numbers, as illustrated by the existence of a clear relationship between the frequency and density of rotifers in all zones of the arenal.

The above observations may explain also the highest number of species recorded in the hygroarenal and the hydroarenal, both in spring and summer. Rotifers carried away from the macrophytes by the waves can reach only these zones, while the euarenal is inhabited primarily by psammobiotic and psammophilic species. The highest number of rotifer species in the hygroarenal is consistent with the findings of Bielańska-Grajner (2005), while Ejsmont-Karabin (2003a, b) the highest species richness noted in the hydroarenal.

The important role of macrophytes in shaping the species richness of psammon also explains why species diversity is the lowest in hypertrophic lakes (Ejsmont-Karabin, 2003a, b). In these lakes, due to the high turbidity of the water, macrophytes do not form species-rich communities, and they are easily decomposed. In such conditions, oxygen deficits at the bottom may limit the occurrence of rotifers. Results of studies carried out in two Estonian lakes of different trophy (Lokko et al., 2013) show that vegetation cover may affect taxonomic structure of zoopsammon through differentiated impact on particular taxons.

The high proportion of singletons in psammon communities means that, although the arenal forms a habitat strongly separated from other lake habitats in terms of most of the physical and chemical conditions, its boundaries do not completely prevent the penetration of this habitat by pelagic communities. However, these are boundaries that are generally not crossed by most psammobionts. Species such as *L. psammophila*, *L. levistyla, W. velox*. are not observed outside the arenal zone.

While on a local and regional scale the groups of psammobionts and the psammophiles are composed of the same species, on a wider geographical scale these groups are very different. The lists of psammobiotic species from Europe, North America and Asia are different, e.g. psammobiotic rotifers from the arenal habitats in Vietnam have not been recorded so far in Europe and North America. However some of the psammophilic species are much more widely spread. From among all the psammobiotic and psammophilic species recorded in the arenal, 71% and 77% (respectively) are those exclusive for particular continents.

Table 2 A list of psammon species recorded in the arenal of freshwaters on different continents (based on A—the author's observations and literature: 1. Wiszniewski 1933; 2. Wiszniewski 1934a; 3. Myers, 1936; 4. Neel, 1948; 5. Pejler, 1995; 6. Segers and Chittapun, 2001; 7. Bielańska-Grajner, 2004; 8. Bielańska-Grajner, 2005; 9. Bielańska-Grajner & Poznańska, 2010; 10. Trinh Dang et al., 2015; 11.Duong et al. 2020)

Species	Psammobiotic			Psammophilic		
	Europe	North America	Asia	Europe	North America	Asia
Aspelta egregia Myers, 1936		3				
Bryceella tenella (Bryce, 1897)	A	4		2,8	3	
Cephalodella apocolea Myers, 1924					3	
Cephalodella auriculata (Müller, 1773)				2,7,8	3	
Cephalodella catellina (Müller, 1786)				7,8,9		
Cephalodella compacta Wiszniewski, 1934	A,2	3				
Cephalodella elongata Myers, 1924					3	
Cephalodella exigua (Gosse, 1886)					3	
Cephalodella gibba (Ehrenberg, 1830)				A,2,7,8,9	3	10,11
Cephalodella gracilis (Ehrenberg, 1830)				2,7,8,9		
Cephalodella hoodi (Gosse, 1886)				8		
Cephalodella megalocephala (Glascott, 1893)				2		
Cephalodella megalotrocha Wiszniewski, 1934	2,8					
Cephalodella psammophila Koch-Althaus, 1962	A		6			
Cephalodella remanei Wiszniewski, 1934					3	
Cephalodella tachyphora Myers, 1934				2,8		
Cephalodella ventripes (Dixon-Nuttall, 1901)				7		
Collotheca wiszniewskii Varga, 1938	A,8	4				
Colurella colurus (Ehrenberg, 1830)				A,2,7		
Colurella obtuse (Gosse, 1880)					3	10
Dicranophorus artamus Harring & Myers, 1928					3	
Dicranophorus capucinus Harring & Myers, 1928					3	
Dicranophorus hercules Wiszniewski, 1932	A,1,2,8,9	3,4				
Dicranophorus leptodon Wiszniewski, 1934	A,1,8					
Dicranophorus luetkeni (Bergendal, 1892)				2,8	3	10
Dicranophorus rostratus (Dixon-Nuttall % Freeman, 1902)					3	
Elosa spinifera Wiszniewski, 1932	A,1,2,8		6			
Elosa worrallii Lord, 1891					3	
Encentrum arvicola Wulfert, 1936				7,8		
Encentrum diglandula (Zavadovsky, 1926)	A,1,2,8		10			
Encentrum insolitum Myers, 1936		3				
Encentrum pornsilpi Segers & Chittapun, 2001			6			
Euchlanis arenosa Myers, 1936		3,4				
Gastropus minor (Rousselet, 1892)					3	
Lecane abanica Segers, 1994						10,11
Lecane bifurca (Bryce, 1892)						11
Lecane clara (Bryce, 1892)				A,2,8	3	
Lecane closterocerca (Schmarda, 1859)				A,2,7,8,9		
Lecane dorysimilis (Trinh Dang et al., 2015)						10,11
Lecane flexilis (Gosse, 1886)				8	3	
Lecane inermis (Bryce, 1892)						10
Lecane inquieta Myers, 1936		3				

Table 2 (continued)

Species	Psammobiotic			Psammophilic		
	Europe	North America	Asia	Europe	North America	Asia
Lecane junki Koste, 1975			10			
Lecane levistyla (Olofsson, 1917)	A,1,2			8		
Lecane lunaris (Ehrenberg, 1932)				7,8	3	10,11
Lecane minuta Segers, 1994			10,11			
Lecane mitella (Myers, 1936)		3				
Lecane mucronata Harring & Myers,1926		3,4				
Lecane phapi Trinh Dang et al. 2015			10,11			
Lecane psammophila (Wiszniewski, 1932)	A,1,2,7,8,9	3,4				
Lecane scutate Harring & Myers, 1926						
Lecane spiniventris Segers, 1994			10,11	A,7		
Lecane tenuiseta Harring, 1914						10
Lecane tenuua Myers, 1936		3				
Lepadella desmeti Segers & Chittapun, 2001			6			
Lepadella ovalis (Müller, 1786)					3	10
Lepadella patella (Müller, 1773)				A,2,7,8,9	3	
Lindia janickii Wiszniewski, 1934	A,2,8					
Lindia pallida Harring & Myers, 1922				7		
Monommata astia Myers, 1930				8	3	
Myersinella tetraglena (Wiszniewski, 1934)	A	3				
Notholca labis Gosse, 1887				8		
Notholca striata (Müller, 1786)				2		
Notommata cerberus (Gosse, 1886)						10
Notommata diasema Myers, 1936		3				
Notommata doneta Harring & Myers, 1924	A,8					
Notommata tripus Ehrenberg, 1838					3	
Proales minima (Montet, 1915)				8,9		
Taphrocampa annulosa Gosse, 1851	A,8				3	
Trichocerca bauthiemensis Trinh Dang et al., 2015			10			
Trichocerca insolens (Myers, 1936)		3,4				
Trichocerca intermedia (Stenroos, 1898)				A,2,7,8		10
Trichocerca myersi (Hauer,1931)	A,8					
Trichocerca pygocera (Wiszniewski, 1932)	A,1,2,5,8					
Trichocerca taurocephala (Hauer, 1931)	A,2,7,8,9	4				
Trichocerca tenuior (Gosse, 1886)				A,2,7,8		
Trichocerca tigris (Müller, 1786)				8	3	
Trichocerca tortuosa (Myers, 1936)					3	
Trichocerca uncinata (Voigt,1902)				7,8		
Wierzejskiella elongata (Glascott, 1893)	8					
Wierzejskiella sabulosa (Wiszniewski, 1932)	A,1,2,8					
Wierzejskiella velox (Wiszniewski, 1932	A,1,2,8	3,4				
Wigrella depressa Wiszniewski, 1932	A,1,2,8					

Species from Lake Baikal, a hotspot of endemic rotifer species, too different from other lakes, are not included in the table. Psammoxenes are also excluded from the table

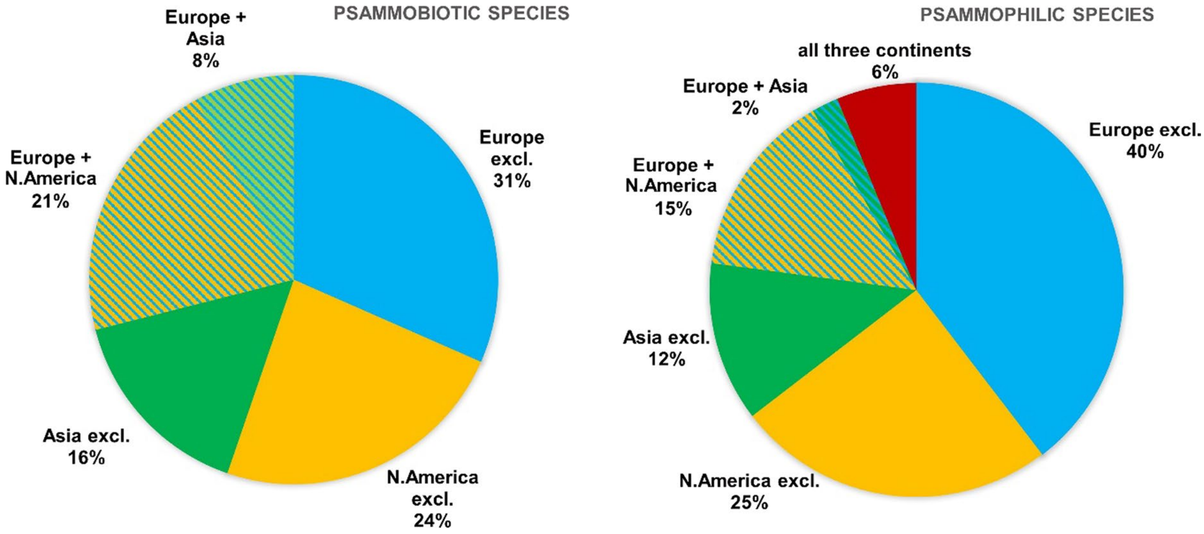

Fig. 5 The percentage of psammobiotic and psammophilic species recorded on three continents (based on data in Table 2; *excl.* exclusive)

Those observations confirm the need for further faunal research in the arenal habitat in a wide geographical range, especially in Africa and South America. Extending such studies to the freshwater ecosystems of the larger islands would allow a reliable assessment of the endemic rate of psammon rotifers. Taking into account the differences in the lists of psammobiotic species (Table 2; Fig. 5), as well as the fact endemic *N. kozhovi* and *C. grandiuscula* occurrence in Lake Bajkal (Arov, 1991) we can assume that this rate may be very high.

Conclusions

My recent studies have shown that densities of rotifers in the arenal are extremely variable, both in space and time, which means that the assessment of the abundance of rotifers in this habitat is largely dependent on the period and frequency of sampling. The highest densities are achieved by rotifer species of the highest frequency in lake arenal. Taking into account all the available results of research we have to come to the conclusion that although we have enriched our knowledge about the ecology of psammon communities of Rotifera significantly since Wiszniewski's discovery, the species richness of this group in geographical terms is still unknown. Due to the small number of studies in this area, we also do not know the level of endemism among psammon rotifers. The influence of atmospheric conditions on all zones of the arenal is still undocumented experimentally. The role of psammon rotifers in benthic food webs is another issue requiring research.

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Data availability The datasets generated during and/or analyzed during the current study are available from the author on reasonable request.

Declarations

Conflict of interest The author have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval The manuscript has not been submitted to more than one journal for simultaneous consideration, or published elsewhere in any form or language (partially or in full). The submitted work is original and presents all results of a single study clearly, honestly, and without fabrication, falsification or inappropriate data manipulation. The author adhered to discipline-specific rules for acquiring and processing data. No data, text, or theories by others are presented as if they were the authors' own. No material is verbatim copied.

References

Arov, I. V., 1990. Zhiznennye formy kolovratok v psammali ozera Bajkal. In Skarlato, O. A. (ed), Kolovratki, Reports of the Third Soviet Rotiferological Symposium, Zoologitscheskij Inst AN SSSR, Leningrad: 107–112.

Bielańska-Grajner, I., 2001. The psammic rotifer structure in three Lobelian Polish lakes differing in pH. Hydrobiologia 446(447): 149–153. https://doi.org/10.1007/978-94-010-0756-6_21.

Bielańska-Grajner, I., 2004. Preliminary investigations on psammon rotifers in two reservoirs in Upper Silesia. Oceanological and Hydrobiological Studies 33: 37–45.

Bielańska-Grajner, I., 2005. Wrotki (Rotifera) psammonowe zbiorników wodnych wybranych obszarów Polski [Psammon rotifers (Rotifera) inhabiting water reservoirs in selected areas of Poland]. Prace naukowe Uniwersytetu Śląskiego w Katowicach, nr 2342. Wydawnictwo Uniwersytetu Śląskiego, Katowice 2005, 114 pp.

Bielańska-Grajner, I. & T. Molenda, 2008. Dependence between occurrence of selected species of psammic rotifers and phytopsammon abundance. Annales Universitatis Mariae Curie-Skłodowska, Lublin—Polonia. 63, sec. C: 7–11. https://doi.org/10.2478/v10067-008-0013-2

Bielańska-Grajner, I. & M. Poznańska, 2010. The biodiversity of psammon rotifers in Włocławek Reservoir. Oceanological and Hydrobiological Studies 39: 111–117. https://doi.org/10.2478/v10009-010-0008-6.

Connell, J. H., 1978. Diversity in tropical rainforests and coral reefs. Science 109: 1304–1310. https://doi.org/10.1126/science.199.4335.1302.

Czernaś, K., 1991. Wstępne badania nad pionowym zróżnicowaniem produktywności pierwotnej eupsammonu i hydropsammonu. Studia Ośrodka Dokumentacji Fizjograficznej PAN 19: 393–399, Kraków.

Czernaś, K., 2003. Function of phytopsammon in capturing biogenes at the land/water ecotone in mesotrophic Lake Piaseczno. Acta Agrophysica 1: 47–53.

Czernaś, K. & D. Krupa, 1998. Struktura i aktywność fotosyntetyczna fitopsammonu i fitoplanktonu w litoralu jeziora Piaseczno. In: Radwan S. (ed.) Ekotony słodkowodne – struktura, rodzaje i funkcjonowanie, Radwan (ed.), Wydawnictwa Uniwersytetu Marii Curie-Skłodowskiej, Lublin: 139–145.

Dang, M. T., H. Segers & L.-O. Sanoamuang, 2015. Psammon rotifers in Central Vietnam, with the descriptions of three new species (Rotifera: Monogononta). Zootaxa 4018(2): 249–265. https://doi.org/10.11646/zootaxa.4018.2.5.

Duong Q. H., M. V. Vo, N. T. Phan, Q. A. Tran-Nguyen & M. Trinh-Dang, 2020. Diversity of rotifers in different habitats in the sandy coast of Quang Nam Province. In: HUFLIT International Conference On Ensuring A High-Quality Human Resource In The Modern Age- Oct 16, 2020. https://doi.org/10.15625/vap.2020.00019.

Duong, Q. H., N. T. Phan, Q. A. Tran-Nguyen; M. V. Vo & M. Trinh-Dang, 2021. Lecane (Rotifera: Lecanidae) community in psammon habitat in Central Coast Vietnam: Diversity and relation to environmental condition. International Journal of Aquatic Biology 9: 217–225. https://doi.org/10.22034/ijab.v9i4.1213

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., 2003a. Is sandy beach of the lake an ecotone? Psammon Rotifera in a mesotrophic Lake Kuc (Masurian Lakeland, Northern Poland). Polish Journal of Ecology 51: 219–224.

Ejsmont-Karabin, J., 2003b. 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. https://doi.org/10.1007/s10750-005-4285-0.

Ejsmont-Karabin, J., 2006. Small-scale horizontal patchiness in rotifer (Rotifera) communities of lake psammon. Verhandlungen Des Internationalen Verein Limnologie 29: 1901–1905.

Ejsmont-Karabin, J., 2008. Daily changes of the vertical microdistribution of Rotifera in lake psammolittoral. Polish Journal of Ecology 56: 717–722.

Ejsmont-Karabin, J. & M. Karpowicz, 2021. Rotifera in lake subhabitats. Aquatic Ecology 55: 1285–1296. https://doi.org/10.1007/s10452-020-09818-1.

Ejsmont-Karabin, J., Z. Gorelysheva, K. Kalinowska & J. I. Rybak, 2012. Role of psammon microinvertebrates in phosphorus cycling in hydroarenal of an eutrophic lake. Polish Journal of Ecology 60: 455–462.

Giere, O., 1993. Meiobenthology. The Microscopis Fauna in Aquatic sediments, Springer, Berlin:

Giere, O., 2009. Meiobenthology. The Microscopic Motile Fauna of Aquatic Sediments, Springer, Berlin:, 526.

Gotelli, N. J. & R. K. Colwell, 2011. Estimating species richness. In Maguirran, A. E. & B. J. McGill (eds), Biological Diversity—Frontiers in Measurement and Assessment Oxford University Press, New York: 39–54.

James, W. F. & J. W. Barko, 1991. Littoral-pelagic phosphorus dynamics during nighttime convective circulation. Limnology & Oceanography 36: 949–960. https://doi.org/10.4319/lo.1991.36.5.0949.

Krupa, D., K. Czernaś, I. Wojciechowski & J. Galek, 1991. Zróżnicowanie czasowe i przestrzenne koncentracji chlorofilu a w zbiorowiskach glonów w przybrzeżnej strefy mezotroficznego jeziora Piaseczno w latach

1983–1985. Studia Ośrodka Dokumentacji Fizjograficznej PAN 19: 381–392.

Lokko, K., 2014. Seasonal and spatial variability of zoopsammon communities in relation to environmental parameters. Dissertationes Biologicae Universitatis Tartuensis, University of Tatru Press, Tartu 263: 7–44.

Lokko, K. & T. Virro, 2014. The structure of psammic rotifer communities in two boreal lakes with different trophic conditions: lake Võrtsjärv and Lake Saadjärv (Estonia). Oceanological and Hydrobiological Studies 43: 49–55. https://doi.org/10.2478/s13545-014-0116-0.

Lokko, K., T. Virro & J. Kotta, 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 2013(700): 1–8. https://doi.org/10.1007/s10750-012-1210-1.

Lokko, K., T. Virro & J. Kotta, 2017. Seasonal variability in the structure and functional diversity of psammic rotifer communities: role of environmental parameters. Hydrobiologia 796: 287–307. https://doi.org/10.1007/s10750-016-2923-3.

Myers, F. J., 1936. Psammolittoral rotifers of Lenape and Union Lakes. New Jersey. American Museum Novitates 830: 1–22.

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

Nawrot, D. & T. Mieczan, 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 especial reference to shoal and shoreline dynamics. Transactions of the American Microscopical Society 67: 1–53. https://doi.org/10.2307/3223081.

Pejler, B., 1995. Relation to habitat in rotifers. Hydrobiologia 313(314): 267–278. https://doi.org/10.1007/978-94-009-1583-1_35.

Pennak, R. W., 1939. The miscroscopic fauna of the sandy beaches. Problem of Lake Biology A.A.A.S. Publ. 10: 94–106.

Pennak, R. W., 1940. Ecology of the microscopic metazoan inhabiting the sandy beaches of some Wisconsin lakes. Ecological Monographs 10: 537–615. https://doi.org/10.2307/1943554.

Pennak, R. W., 1951. Comparative ecology of the interstitial fauna of fresh-water and marine beaches. L'année Biologique 27: 449–480.

Radwan, S. & I. Bielańska-Grajner, 2001. Ecological structure of psammic rotifers in the ecotonal zone of Lake Piaseczno (eastern Poland). Hydrobiologia 446(447): 221–228. https://doi.org/10.1023/A:1017519910875.

Radwan, S., I. Bielańska-Grajner & B. Popiołek, 1998. Zgrupowania wrotków (Rotatoria) w różnych typach siedlisk litoralowych i pelagialu jezior Polesia Lubelskiego In Radwan, S. (ed.) Ekotony słodkowodne – struktura, rodzaje i funkcjonowanie, Wydawnictwa Uniwersytetu Marii Curie-Skłodowskiej, Lublin: 43–49.

Radwan, S., T. Ozimek, I. Bielańska-Grajner & J. Sender, 2001. Structure of the water/land ecotones in trophically different Polish lakes. Verhandlungen Des Internationalen Verein Limnologie 27: 3848–3851. https://doi.org/10.1080/03680770.1998.11901705.

Ruttner-Kolisko, A., 1961. Biotop und Biozönose des Sandufers einiger österreichischer Flüsse. Verhandlungen Des Internationalen Verein Limnologie 14: 362–368. https://doi.org/10.1080/03680770.1959.11899294.

Schmid-Araya, J. M., 1998. Rotifers in interstitial sediments. Hydrobiologia 387(388): 231–240. https://doi.org/10.1007/978-94-011-4782-8_30.

Segers, H. & S. Chittapun, 2001. The interstitial Rotifera of a tropical freshwater peat swamp on Phuket Island. Thailand. Belgian Journal of Zoology 131(Supplement 2): 65–71.

Strayer, D., 1986. The size structure of a lacustrine zoobenthic community. Oecologia (berlin) 69: 513–516. https://doi.org/10.1007/BF00410356.

Varga, L., 1957. Neurere daten Ober die Mikrofauna des Balaton-psammons. Annales Instituti Biologici Tihany 24: 271–282.

Whitman, R. L., M. C. Andrzejewski, K. J. Kennedy & T. A. Sobat, 1994. Composition, spatial-temporal distribution and environmental factors influencing the interstitial beach meiofauna of southern Lake Michigan. Verhandlungen Des Internationalen Verein Limnologie 25: 1389–1397.

Wiszniewski, J., 1932. Wrotki piaszczystych brzegów jeziora Wigry. Doniesienie Tymczasowe. Archiwum Hydrobiologii i Rybactwa 6: 86–100.

Wiszniewski, J., 1933. O Życiu w Wilgotnych Piaskach. Wszechświat 1: 1–7.

Wiszniewski, J., 1934a. Recherches écologiques sur le psammon et spécialement sur les rotifères psammiques. Archiwum Hydrobiologii i Rybactwa 8: 149–166.

Wiszniewski, J., 1934b. Wrotki psammonowe. Annales Musei Zoologici Polonici 10: 339–399.

Wiszniewski, J., 1936. Notes sur le psammon. III. Deux tourbieresaux environs de Varsovie. Archiwum Hydrobiologii i Rybactwa (suwałki) 10: 173–187.

Wiszniewski, J., 1937. Differentiation ecologique des rotifers dans le psammon d'eaux douces. Annales Musei Zoologici Polonici 13: 1–13.

Zhadin, V. N., N. A. Akatova, L. A. Kutikova & N. G. Ozereckovskaya, 1972. Presnovodnyj psammon poberezhja Kurshskoj Kosy. Gidrobiologicheskij Zhurnal 8: 74–86.