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Special paper

The author dedicates this paper to the memory
of Dr Jerzy Wiszniewski (1908–1944),
the first who described the ecology and taxonomy of rotifer fauna
in lake psammolittoral

Jolanta EJSMONT-KARABIN

Centre for Ecological Research, Polish Academy of Sciences, Hydrobiological Station, Leśna 13,
11-730 Mikołajki, Poland, e-mail: jolantaek@poczta.onet.pl

ROTIFERA OF LAKE PSAMMON: COMMUNITY STRUCTURE *VERSUS* TROPHIC STATE OF LAKE WATERS*

ABSTRACT: Rotifer communities inhabiting wet sands of lake beaches are dependent in their functioning on permanent input of organic matter from neighbouring sites. The aim of the study is to test the hypothesis that trophic state of lake waters may influence densities and structure of psammon communities of Rotifera.

Studies were carried out in hydro-, hygro- and euarenal of 44 beaches in 18 lakes of different trophy in summer 1999 (since 2 till 17 July) and 38 beaches in 16 lakes in spring 2000 (since 10 till 23 May). Psammon was sampled always between 10 a.m. and 2 p.m. at similar weather conditions (no shadow, rains and strong winds).

Interstitial waters were mostly alkaline and contained less oxygen than lake ones and oxygen concentrations decreased upward water line. Very high variability of phosphate P content made differences between trophic groups of lakes not significant. Similarly, concentrations of P total were more or less similar in all studied trophic groups of lakes. Total nitrogen values were increasing from meso--eutrophic to hypertrophic lakes in spring, whereas this trend was not observed in summer. Chlorophyll *a* concentrations were similar in meso-, meso-eu- and eutrophic and markedly higher in hypertrophic lakes.

In general, some tendency to increasing values of chemical parameters with increasing trophy may be seen if their ranking list is compared.

Rotifers were present in all studied stations. In total, 110 species (i.e. *ca.* 26% of all records of rotifer species in Poland) were found with 22 species occurring exclusively in psammon. Three species new in rotifer fauna of Poland were discovered – *Cephalodella psammophila, Collotheca wiszniewski* and *Euchlanis dapidula.*

Generally all trophic groups of lakes were relatively similar as regards species structure of rotifer communities with rotifers of the genus *Lecane* playing most important role. The index of Percentage Similarity of Community calculated for randomly chosen 30 pairs of particular beaches from the same lake and for beaches of different lakes was in both cases almost identical.

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Species of high frequency constituted the overwhelming majority of individuals forming rotifer communities of all beaches. Taxons met in 1 to 5 lakes decided on faunistic originality of the communities. Some tendency was observed for higher diversity of psammon rotifer communities in mesotrophic and eutrophic lakes. The lowest values of diversity index occurred mostly in hypertrophic lakes. Psammobionts constituted only 20% and psammoxens 10% of the community abundance in all lakes and all zones of the beaches, whereas psammophilic rotifers decidedly dominated (70%).

Rotifer abundance was relatively similar in eu- and hypertrophic lakes and markedly higher in mesotrophic and lower in meso-eutrophic lakes. However, due to high fluctuations of the values noted in particular beaches the differences were not significant in any of the possible configurations of compared data. Monogononta played much more important role in rotifer densities than bdelloids.

The hypothesis on advantageous influence of high trophy of lake waters on abundance of psammon communities of Rotifera cannot be supported by results of this work. In lakes of moderate trophy (from meso- to eutrophy) the amount of nutrients and chlorophyll does not seem to influence psammon communities. In hypertrophic lakes this impact is observed, but it seems to be rather unfavourable for psammon rotifers. The communities in hypertrophic lakes are poorer in species, less diversified and less original. The group of animals developing well in this group of lakes are bdelloids.

Species composition nad community structure of psammon rotifers seem to be rather determined by many different factors, lake trophy being only one of them and probably not the main one.

KEY WORDS: Rotifera, psammon, nutrients, chlorophyll, lakes

1. INTRODUCTION

Rotifers (Rotifera) living in sandy shores create together with other organisms in the habitat (i.e. Protozoa, Turbellaria, Nematoda, Gastrotricha, Tardigrada and Oligochaeta) a community called psammon (Sasuchin *et al.* 1927). Although in his paper on freshwater beach microfauna Pennak (1939) wrote: “in this small volume of water ... is concentrated a great population, finding all conditions necessary for a flourishing existence...” – sandy beach habitats seem to provide rather unfavourable conditions for life due to high daily fluctuations of temperature, small living space, low concentrations of oxygen and high – of chemical compounds (due to high evaporation) (Wiszniewski 1933, 1934a). Despite of that, psammon communities of Rotifera reach extremely high densities, up to several thousands (Pennak 1939, Radwan *et al.* 1998) or even several hundred thousands (Ejsmont-Karabin 1998) individuals in 1 litre of wet sand, thus often one or even three orders of magnitude higher than those in pelagic communities. Schmid-Araya (1998) explains the phenomenon writing: “these changing environments seem to be ideal for a group of organisms that reproduce quickly, occupy vacant habitats rapidly and exhibit a wide range of feeding habits”, i.e. for rotifers.

Despite of the abundance of the communities and their high metabolic activity expressed by very high rate of phosphorus excretion (Ejsmont-Karabin 2001) a role of psammon rotifers in functioning of the water/land transitory zone in a lake shore is still unknown.

Wiszniewski (1932, 1933, 1934a, b, 1935a, b, 1937, 1938, 1947), who was the first to carry out ecological studies of lake psammolittoral showed:

(1) instability of the habitat – both physical (generated by the movements of sand at wave action) and thermal (due to daily fluctuations of temperature),

(2) high fertility of the habitat (high oxygen demand of the interstitial water) due to condensation caused by the constant evaporation, decomposition of substances brought by waves and metabolic activity of psammon organisms.

Next few publications dealing with psammon rotifers described mainly taxonomic structure of the communities. Myers (1936) gave a list containing 145 rotifer species from psammolittoral of Lenape and Union Lakes (New Jersey) with 27 of them described as psammobiotic and 11 – new for science. Varga (1936) introduced 47 psammon species from beaches of Lake Balaton with two of them new for science: *Monostyla balatonica* and *Collotheca wiszniewskii.* Similarly to lake psammon also marine studies were most often of a taxonomic character, like those conducted in Black Sea (Althaus 1957) and Baltic and North Sea (Remane 1949).

However, some very interesting contributions to ecology of the microfauna of marine sands appeared as well. Thane-Fenchel (1968) studying rotifers from sands of Niva Bay described food demands of many species and found that these communities play less important role than psammon rotifers in freshwaters.

The series of papers published by Wiszniewski (1932–1938) on rotifer fauna of lake psammolittoral resulted in many subsequent studies in the same habitat in different lakes of the world. Neel (1948) presented results of his studies made at Douglas Lake (Michigan) to determine limnological relationships of the psammolittoral zone. Ecology and spatial distribution of psammon rotifers have been studied by Ruttner-Kolisko (1953, 1954, 1956) and some taxonomic remarks on psammon rotifers in Lake Boden were given in paper by Koch-Althaus (1962a) and those from Neusiedler Sea by Donner (1972).

Recently freshwater psammolittoral habitats are rarely studied. Russian rotiferologists have published a set of papers describing rare species (Kutikova and Arov 1985) and rotifer communities (Arov 1985, 1990) in Lake Baikal. In Poland Radwan and Bielańska-Grajner (1998) have undertaken studies of the communities in lakes of the Łęczyńsko-Włodawskie Lakeland (East Poland) and Bielańska-Grajner (2001) has been studying psammon communities of Pomeranian (West Poland) lakes of differing pH.

However, still more attention is paid to psammon rotifers of marine beaches (Tzschaschel 1983, Kameswara and Mohan 1984, Turner 1990, 1993,) and interstitial communities of streams and rivers (Ruttner-Kolisko 1961, Ferrarese and Sambugar 1976, Evans 1984, Schmid-Araya 1993, 1998, Schmid-Araya and Schmid 1995, Turner and Distler 1995, Turner 1996, Turner and Palmer 1996).

Psammon organisms are dependent in their existence on microscopic particles of organic detritus as a basic food source and as well as on algae and bacteria (Pennak 1951). Thus nutrient abundance in lake waters should significantly influence densities and structure of psammon communities of Rotifera as some portion of organic matter reaches the habitat with waves spilling and sprinkling beach sands. Neel (1948) attributes the special role to moderate and light onshore waves in disposing organic debris in manner that permits it to remain in the psammolittoral region for varying periods of time. The author concludes that much of the organic material in the sand originates in lakes. It can be then assumed that in lakes of higher trophy i.e. more abundant in organic matter in a form of small algae or detritus with bacteria, rotifer abundance in psammolittoral should be higher. However, results of preliminary studies carried out in two lakes of different trophy, i.e. mesotrophic Lake Kuc and eutrophic Mikołajskie Lake (Masurian Lakeland, Poland), seem to contradict the above hypothesis. Rotifer numbers were about one magnitude higher in the lake of lower trophy (Ejsmont-Karabin 2001). However, the analyses done for only two lakes and from single stations could have been insufficient to evaluate an influence of trophic state of lakes on densities of their psammon. Apart of abundance of psammon communities also their diversity may be influenced by trophy of lake waters. Radwan and Bielańska-Grajner (2001) suggest that the highest species diversity of eupsammon in mesotrophic lake was connected with high content of organic matter in the arenal zone.

On the other hand, in their studies on activity of algal communities in shore zone of a mesotrophic lake (Lake Piaseczno) Czernaś and his colleagues (Czernaś and Krupa 1998, Czernaś *et al.* 1991a, b) suggested that the main source of nutrients for algal production in psammolittoral is nutrient influx from land into the lake.

The purpose of the paper is the examination of the hypothesis on advantageous influence of high trophy of lake waters on abundance of psammon communities of Rotifera by investigations conducted in a large number of lake beaches in four trophic groups of lakes (meso-, meso-eu-, eu- and hypertrophic ones).

It has been assumed that the influence of trophic state of lakes on their psammon fauna should be reflected by relationships described below:

– concentrations of nutrients and chlorophyll *a* in interstitial water should depend on lake trophy

– rotifer communities of beaches of the same lake should be more similar in their species structure nad abundance than communities inhabiting beaches of different lakes.

– abundance and species structure of psammon communities should be different in lakes of different trophy

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2. STUDY SITES AND METHODS

Studies were carried out in 18 lakes in Masurian Lake District (North-eastern Poland) of different mictic type and trophy (Table 1). The lakes are situated from 53°43' to 54°11' latitude and from 21°18' to 21°52' longitude. Measured in summer 1996 and 1999 Secchi's discc visibility has been used for the calculation of the trophic state index (TSI) (Carlson 1977). It was assumed that lakes with a TSI under 45 were mesotrophic, between 45 and 55 – meso-eutrophic, those with a TSI from 55 to 65 – eutrophic and all lakes with a TSI above 65 – hypertrophic.

Samples were collected on two occasions: in summer 1999 (from 2 to 17 July) and spring 2000 (from 10 to 23 May). From 1 to 3 beaches were examined in each lake. Forty-four lake beaches (10 lakes with 3 beaches, 6 lakes with 2 beaches and 2 single ones) were sampled in summer. Spring investigations covered lower number of stations, as some of the examined beaches were not accessible. As a result, spring expedition visited 38 beaches in 16 lakes. Beaches were usually small, i.e. 5 to 50 m long and 1 to 10 m wide and surrounded with trees, grass or scrubs. Only beaches with well-developed hygro- and euarenal were selected for investigations.

Samples of wet sand were taken from three zones of arenal, i.e. sand layer inhabited by psammon organisms (Wiszniewski 1934b): in hydroarenal (from lake bottom 1 m from the water line, hygroarenal – at the edge of the zone wetted by lake waves and euarenal – from the beach, 0.5 to 1m from the water line (Fig. 1).

Neel (1948) and Sasuchin *et al.* (1927) have shown that organisms of psammon and particularly rotifers are restricted to the uppermost 1–1.5 cm because they are un-

Table 1. Description of the study lakes in Masurian Lakeland (Poland) (Brodzińska *et al.* 1999): TSI – Trophic State Index according to Carlson 1977

Lake	Area (ha)	Maximum Depth (m)	Mean Depth (m)	Visibility of Secchi's disc value in m and (TSI)	Trophic state
Majcz Wielki	163.5	16.4	6.0	5.40 (36)	Mesotrophy
Kuc	98.8	28.0	8.0	4.10 (40)	Mesotrophy
Mamry Pln.	2504.0	43.8	11.9	3.60 (41)	Mesotrophy
Dobskie	1776.0	22.5	7.8	3.10 (44)	Mesotrophy
Dargin	3030.0	37.6	10.6	2.50 (47)	Meso-eutrophy
Nidzkie	1818.0	23.7	6.2	2.50 (47)	Meso-eutrophy
Śniardwy	11340.4	23.4	5.8	1.70 (52)	Meso-eutrophy
Głębokie	47.3	34.3	11.8	1.65 (53)	Meso-eutrophy
Bełdany	940.6	46.0	10.0	1.45 (54)	Meso-eutrophy
Inulec	178.3	10.1	4.6	1.35 (56)	Eutrophy
Mikołajskie	497.9	25.9	11.2	1.20 (57)	Eutrophy
Czos	279.1	42.6	11.1	1.10 (59)	Eutrophy
Tałty	1160.4	44.7	15.6	1.05 (59)	Eutrophy
Jagodne	942.7	37.4	8.7	0.90 (62)	Eutrophy
Tuchlin	219.3	4.9	2.8	0.70 (65)	Hypertrophy
Tyrkło	236.1	29.2	9.7	0.70 (65)	Hypertrophy
Juno	380.7	33.0	11.9	0.60 (67)	Hypertrophy
Kocioł	291.6	26.4	9.5	0.50 (70)	Hypertrophy

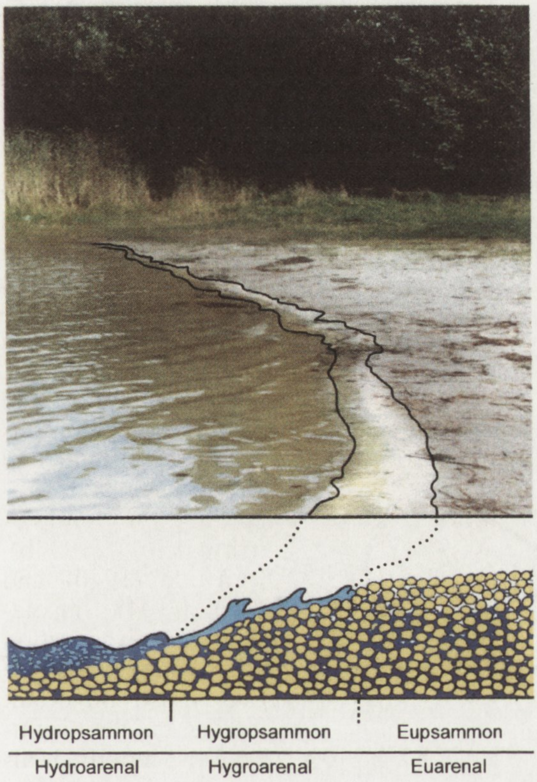

Fig. 1. A beach typical for Masurian lakes with marked zones of arenal and a schematic profile of psammolittoral according to Wiszniewski (1934b)

able to exist in sulfide layers. This was a reason why sand samples were 2 cm thick. They were cut out in three points of each zone by means of a sharp-edged cylinder with an area of 28 cm^2. Then, in a laboratory, the samples were transferred to glass containers and rinsed 6 times with tap water. After sedimentation of sand grains (lasting up to 10 seconds) the upper layer of water was filtered through a 30 μm mesh-size plankton net. All rotifers were identified and counted (by means of a microscope Nikon Alphaphot-2-PH) in three subsamples, each equal to 5% of the sample. The first subsample was analysed alive, next after fixing them with 4% formalin. Species stated as rare or new for fauna of Poland were described and photographed. Interstitial water for chemical analyses was sampled concurrently with psammon. For these purposes, a pipette with a large rubber bulb was used to suck in and transfer 1 litre of interstitial water to glass bottles, separately for the three studied psammolittoral zones. Temperature, pH and oxygen concentrations were measured in a field using pH-meter and an oxymeter type OXY 197 (WTW, Germany). The remaining chemical compounds were analysed in a laboratory. Total (after wet digestion with 60% perchloric acid) and mineral phosphorus were analysed by spectrophotometric determination (molibdenian-blue method) according to Standard Methods (1960). The sum of total Kjeldal nitrogen (analysed in unfiltered water by standard Kjeldal combustion) and nitrate-nitrogen (with phenyldisulphonic acid and evaporation of the sample to dryness) was taken as total nitrogen. Chlorophyll *a* was determined by the spectrophotometric analysis of acetone extracts on Whatman GF/C filters (Golterman 1969) and the content of suspended material dried up at 105°C and weighted on Whatman GF/C filters.

The index of percentage similarity of community (*PSC*) (Whittaker and Fairbanks 1958) was used:

$$PSC = 100 - 0.5\sum(a-b) = \sum min(a-b)$$

where *a* and *b* are percentages of individuals of each species in total numbers of the communities of lakes A and B, compared in pairs. The index takes into account the quantitative relations between different pairs of species.

An index of floral originality (*IFO*) (Puchalski 1987) was used to evaluate differences in species structure of rotifer fauna between lakes:

$$IFO = (\sum 1/M)/S$$

where: M = number of samples in which a species occurs; S = number of species in a sample. The theoretical maximal value of the index is 1.0, if species found in a lake were not noticed in another lake.

The Shannon-Weaver, species-diversity index, *H'* (Margalef 1958) was used:

$$H' = -\sum n_i/N \log_2 n_i/N$$

where: N = total numbers of rotifers; n_i = numbers of a species *i*.

Statistical analyses were run with STATISTICA (Statsoft. Inc.) software. Probability levels of ≤ 0.05 were considered significant.

3. RESULTS

3.1. SITE CONDITIONS

3.1.1. TEMPERATURE, pH AND OXYGEN CONCENTRATIONS

In freshwater beaches the surface temperatures of the sand were described (Pennak 1951) to be relatively homogenous due to influence of the capillary water and its evaporation. Thus even on a hot summer day the surface temperature seldom exceeds 32ºC.

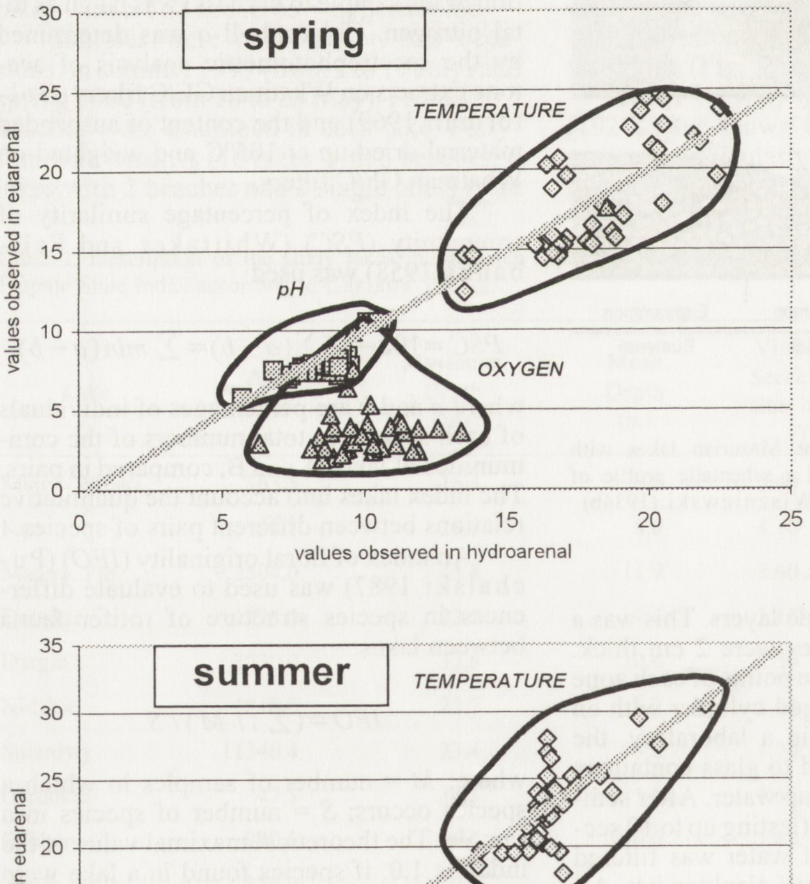

Fig. 2. Comparison of values of temperature (ºC), pH and oxygen concentration (mg l^{-1}) in psammolittoral of 18 lakes in summer 1999 and spring 2000

In Masurian lakes temperatures of interstitial waters in hydroarenal were relatively high both in spring and summer (Fig. 2). They ranged from 13.5 to 22.5ºC with mean value of 18.1 ± 2.3ºC in spring and 19.6 to 30.8 (mean = 23.5 ± 2.0ºC) in summer. Temperatures noted in euarenal were almost the same like those in hydroarenal. They ranged from 14.5 to 24.5 (mean = 18.0 ± 3.4ºC) in spring and from 18.0 to 30.5 (mean = 23.1 ± 2.9ºC) in summer. The lack of differences between the zones resulted probably from a manner of sampling (always between 10 a.m. and 2 p.m.) and weather conditions (no shadow, rains and strong winds). According to Wiszniewski (1934b), Pennak (1940) and Neel (1948) insolation and evaporation of interstitial water are two most important factors, but their influence is modified always by meteorological conditions.

Values of pH have been found to be one of the most important factors influencing the number and diversity of psammon rotifers (Bielańska-Grajner 2001), i.e. in lakes with low pH the density of rotifers was markedly lower than in lakes with higher pH. According to Wiszniewski (1937) pH determines also distribution of particular species of psammon rotifers. So thus the author divided the species into three groups corresponding to different levels of pH values.

Values of pH in interstitial waters of the studied stations were (with one exception) above 7.0. Hydroarenal waters were always more alkaline than euarenal ones, both in spring (mean = 8.6 ± 1.0 and 7.9 ± 0.9, respectively) and summer (mean = 9.1 ± 0.6 and 7.9 ± 0.8) (Fig. 2). These differences were statistically very significant ($P<0.001$). It supports results achevied by Neel (1948) for interstitial waters of Douglas Lake (Michigan, USA).

Oxygen concentrations in hydroarenal waters were nearly 3 times higher than those found at a surface (0–2 cm depth) of euarenal (Fig. 2). Mean spring values were 10.2 mg O_2 l^{-1} ± 1.9 in hydroarenal and 4.0 ± 2.7 in euarenal, whereas in summer the values were 9.0 ± 1.1 and 3.3 ± 2.1, respectively. All differences between the zones were very significant statistically ($P<0.001$). At the same time spring and summer values for the same zone were not different. The differences between them were not significant ($P = 0.43$ and 0.75). Also Wiszniewski (1934b), Pennak (1940) and Neel (1948) showed that interstitial waters always contained less oxygen than lake ones and that oxygen concentrations decreased upward water line.

3.1.2. MINERAL AND TOTAL PHOSPHORUS

Concentrations of mineral phosphorus were generally high and, as a rule, the lowest in hydro- and highest in euarenal (Table 2). However, despite of the fact that the observed differences between mean values in the three studied zones were very high, except two cases, they were no significant statistically (at $P<0.05$). The only exceptions were sand beaches of mesotrophic lakes in summer. The lowest phosphate concentrations were there noted in hygroarenal.

In general, phosphate P concentrations in interstitial water were higher in spring (143 ± 351 µg l^{-1}, n = 114) than in summer (92 ± 148 µg l^{-1}, n = 132). The difference, however, was significant at $P = 0.13$. Also differences between trophic groups of lakes in phosphate P content were not significant, probably because of very high variability of particular values. In spring the lowest values were observed in mesotrophic lakes (mean = 58 ± 71 µg l^{-1}, n = 30), whereas the highest – in meso-eutrophic ones (215 ± 395 µg l^{-1}, n = 36). In summer the lowest value was noted in meso-eutrophic lakes (65 ± 66 µg l^{-1}, n = 39), and the highest – in hypertrophic ones (126 ± 228 µg l^{-1}, n = 21).

Spring and summer concentrations of total phosphorus were lowest in hydroarenal (Table 3). Differences between mean values noted for phosphorus in hydro-, higro- and euarenal were statistically significant both in spring ($P<0.00003$ and 0.0006) and summer ($P<0.04$ and 0.00002). Statistically significant were also nearly two-fold differences between P total concentration in hydro- and euarenal zones in spring and summer, with higher values noted in both zones in summer. Concentration of P total in hygroarenal was identical in both periods, but its range of variability between particular beaches was markedly higher.

Concentrations of P total were more or less similar in all studied trophic groups of lakes, and relatively weak differences be-

Table 2. Mean concentrations of P-PO_4 (µg l^{-1}) in different zones of psammolittoral of four trophic groups of lakes. Arrows indicate statistically significant (t-test, $P<0.05$) differences between neighbouring zones.

Lake trophy	Zones of psammolittoral				
	Hydroarenal		Hygroarenal		Euarenal
			SPRING DATA		
Mesotrophy	30 ± 27		56 ± 67		88 ± 95
Meso-eutrophy	163 ± 337		194 ± 436		287 ± 429
Eutrophy	56 ± 22		63 ± 51		363 ± 873
Hypertrophy	41 ± 40		98 ± 58		202 ± 250
			SUMMER DATA		
Mesotrophy	90 ± 111	↔	36 ± 42	↔	180 ± 153
Meso-eutrophy	46 ± 30		65 ± 64		84 ± 91
Eutrophy	49 ± 39		54 ± 36		175 ± 279
Hypertrophy	52 ± 59		141 ± 274		185 ± 289

Table 3. Mean concentrations of total P (μg l^{-1}) in different zones of psammolittoral of four trophic groups of lakes. Arrows indicate statistically significant (t-test, $P<0.05$) differences between neighbouring zones.

Lake trophy	Zones of psammolittoral				
	Hydroarenal		Hygroarenal		Euarenal
			SPRING DATA		
Mesotrophy	115 ± 59		276 ± 261		254 ± 274
Meso-eutrophy	140 ± 53	↔	392 ± 186	↔	264 ± 144
Eutrophy	155 ± 126		279 ± 172		334 ± 339
Hypertrophy	109 ± 46		207 ± 102		329 ± 337
			SUMMER DATA		
Mesotrophy	177 ± 92		262 ± 185	↔	530 ± 313
Meso-eutrophy	241 ± 140		326 ± 372		494 ± 595
Eutrophy	229 ± 202		279 ± 147		680 ± 687
Hypertrophy	139 ± 100	↔	378 ± 258	↔	674 ± 351

Table 4. Mean concentrations of total N (mg l^{-1}) in different zones of psammolittoral of four trophic groups of lakes. Arrows indicate statistically significant (t-test, $P<0.05$) differences between neighbouring zones.

Lake trophy	Zones of psammolittoral				
	Hydroarenal		Hygroarenal		Euarenal
			SPRING DATA		
Mesotrophy	0.99 ± 0.63	↔	1.69 ± 0.89		1.56 ± 1.41
Meso-eutrophy	0.92 ± 0.40	↔	1.51 ± 0.64		1.53 ± 0.67
Eutrophy	1.16 ± 0.78	↔	2.25 ± 1.26	↔	1.15 ± 0.69
Hypertrophy	1.57 ± 1.10		2.37 ± 0.83		2.11 ± 0.92
			SUMMER DATA		
Mesotrophy	1.62 ± 0.67		1.50 ± 0.76		2.24 ± 1.60
Meso-eutrophy	1.21 ± 0.36	↔	2.13 ± 0.90		2.57 ± 1.49
Eutrophy	1.40 ± 0.71	↔	2.23 ± 1.10		2.35 ± 1.50
Hypertrophy	1.07 ± 0.36	↔	2.06 ± 1.15		2.85 ± 2.23

tween them were always not significant statistically at $P = 0.05$.

3.1.3. NITROGEN

Total nitrogen concentrations were lowest in interstitial water of hydroarenal both in spring (mean values 1.10 ± 0.80) and summer (1.36 ± 0.57 mg N l^{-1}). The highest values were observed in spring in hygroarenal (1.89 ± 0.96 mg N l^{-1}) and in summer – in euarenal (2.44 ± 1.47). Nitrogen concentrations noted at particular beaches were less differentiated than other chemical factors thus all differences between mean values of total N of neighbouring zones were statistically significant at $P = 0.5$ (Table 4).

Except summer values in mesotrophic lakes, in all trophic types of lakes and both in spring and summer higroarenal values of total nitrogen concentration were twice of those observed in hydroarenal. In spring the values were increasing from meso-eutrophic to hypertrophic lakes. This trend was not observed in summer (Table 4), although the concentration was always markedly lower in hygro- and euarenal of mesotrophic lakes if compared with eutrophic and hypertrophic ones.

3.1.4. Chlorophyll *a*

Although light penetrates only the uppermost (i.e. 0.5–2 cm) layers of the sand (Sasuchin *et al.* 1927, Neel 1948) wet sandy shores are characterised by very high abundance of psammon communities of algae, so that primary production and chlorophyll content of the communities are several times higher than those of phytoplankton (Krupa *et al.* 1991, Czernaś *et al.* 1991a, b). Also total amounts of assimilated carbon, nitrogen and phosphorus were found to be higher in hydropsammic than pelagic alga communities (Wojciechowski *et al.* 1991) In studies by Czernaś *et al.* (1991a) the proportion of primary production values between eupsammon, hydropsammon and plankton amounted 7:5:1.

Phytopsammon is often more numerous in species than phytoplankton. Czernaś and Krupa (1998) have found hydrophytopsammon of lake Piaseczno to be composed of 95 species, euphytopsammon – 84 species, whereas phytoplankton involved only 68 ones. Phytopsammon of the lake was dominated by filamentous Cyanophyceae, mainly from the genus *Oscillatoria,* green algae *Chlorococcales* dominated by *Scenedemsus acuminatus* (Lagerh.) and Conjugatophyceae dominated by *Closterium venus* Kutz. and *Cylindrocystis brebissonii* Menegh. In Neel's (1948) studies 173 taxons of psammon algae have been found with diatoms greatly outnumbering all other groups of organisms.

It is hypothesised that psammic algae play the main role in detaining and incorporating nutrients inflowing from lake watershed into lake waters (Czernaś 1991). However, the role of this process in nutrient budget of the lakes is not clear, as elements assimilated by algal communities are not permanently bonded into algal biomass (Wojciechowski *et al.* 1991).

Observed in a course of this study concentrations of chlorophyll *a* were extremely differentiated and ranged between 0.00 to 124.00 μg l^{-1} in spring and 0.00 to 311.30 μg l^{-1} in summer. In both the periods the highest chlorophyll concentrations were noted in hygroarenal, i.e. transitory zone between lake water and beach. The lowest concentrations occurred in the zone permanently covered with lake water – hydroarenal. Generally, in all three zones chlorophyll *a* concentrations were markedly higher in summer (Table 5). However, because of high variability of the chlorophyll values between particular beaches statistically significant differences were only those between mean values for hydroarenal in spring and euarenal in summer (at $P<0.002$) and euarenal in spring and summer ($P<0.029$).

Table 5. Mean concentrations of chlorophyll *a* (μg l^{-1}) in different zones of psammolittoral of four trophic groups of lakes.

Lake trophy	Zones of psammolittoral		
	Hydroarenal	Hygroarenal	Euarenal
		SPRING DATA	
Mesotrophy	4.96 ± 5.46	18.68 ± 28.76	6.71 ± 5.30
Meso-eutrophy	9.81 ± 7.85	18.02 ± 15.29	12.41 ± 10.81
Eutrophy	6.89 ± 7.75	10.78 ± 11.97	10.78 ± 8.49
Hypertrophy	22.88 ± 34.38	30.40 ± 46.74	16.54 ± 13.51
		SUMMER DATA	
Mesotrophy	13.35 ± 8.05	12.21 ± 9.16	20.89 ± 20.38
Meso-eutrophy	10.59 ± 11.99	12.52 ± 12.51	15.92 ± 12.84
Eutrophy	20.49 ± 26.30	21.41 ± 33.71	14.05 ± 13.60
Hypertrophy	12.02 ± 6.60	67.95 ± 110.64	32.20 ± 29.21

Strong differences between chlorophyll *a* contents observed on 18 occassions in hydro- and eupsammon were also reported by Czernaś *et al.* (1991) from different sampling stations of a mesotrophic lake.

Values of chlorophyll concentrations mean for two seasons and three zones and clustered for four trophic groups of lakes (Fig. 3) were practically identical in meso-, meso-eu- and eutrophic lakes (13.1 ± 6.2, 13.0 ± 5.9 and 12.7 μg l^{-1} ± 5.9 μg l^{-1}, respectively) and differences between them were statistically not significant. However, they differed markedly from chlorophyll concentration in hypertrophic lakes, where its mean accounted for 32.5 μg l^{-1} ± 17.8 μg l^{-1}. The difference between mean chlorophyll values for hyper- and mesotrophic lakes was significant at $P = 0.04$, and for eu- and hypertrophic lakes – at $P = 0.01$.

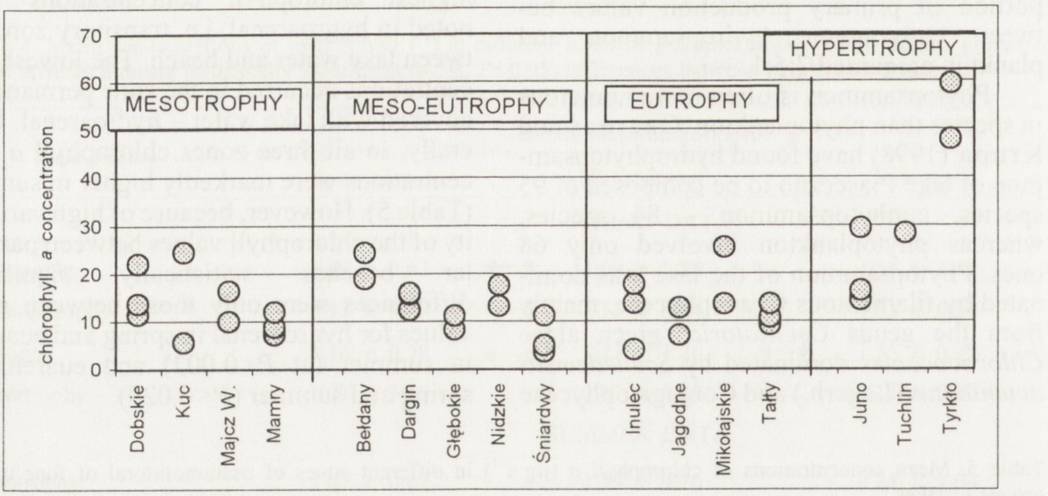

Fig. 3. Concentrations of chlorophyll *a* (in μg l^{-1}) in interstitial water of beaches of lakes of different trophy (see Table 1)

The differences between mean chlorophyll concentrations in trophic groups of lakes compared separately for spring and summer and for three zones of a beach are even stronger. However, because of extremely high deviation of particular results from their mean practically all differences are statistically not significant.

3.1.5. SUSPENDED SOLIDS

The concentrations of suspended solids were markedly higher in spring. Their mean values were then 54.9 ± 70.6 μg l^{-1} in hydroarenal, 82.8 ± 74.7 μg l^{-1} in hygroarenal and 56.3 ± 61.3 μg l^{-1} in euarenal, but the differences between zones were not significant. In summer values of suspended matter were an order of magnitude lower, with mean values of 6.2 ± 3.0 μg l^{-1} in hydro-, 9.2 ± 6.7 μg l^{-1} in hygro- and 10.4 ± 7.6 μg l^{-1} in euarenal and the differences between zones were statistically significant at $P<0.01$.

In spring hygroarenal was generally more abundant in suspended solids than the remaining two zones (Table 6). In summer hygro- and euarenal had the values rather similar and higher than those in hydroarenal.

Psammolittoral of mesotrophic lakes was poorer in suspended matter than all other groups of lakes in spring, but in summer this group of lakes had almost the same values like the remaining trophic groups of lakes (Table 6).

The above-described analysis of concentrations of phosphorus, nitrogen, chlorophyll *a* and suspended solids showed a lack of their statistically significant relationship on trophic state of lake waters. Nevertheless, some tendency to increasing values of chemical parameters with increasing trophy may be seen. To make the tendency better visible a ranking list of parameter's values was established, separately for spring and summer samples. The analysis done also separately for three zones of beaches showed some increase of the values with increasing lake trophy (Fig. 4) in each of the zones. The increase was best

Table 6. Mean concentrations of suspended soilds (mg l^{-1}) in different zones of psammolittoral of four trophic groups of lakes. Arrows indicate statistically significant (t-test, $P<0.05$) differences between neighbouring zones.

Lake trophy	Zones of psammolittoral				
	Hydroarenal		Hygroarenal		Euarenal
SPRING DATA					
Mesotrophy	24.5 ± 18.2	↔	58.8 ± 37.6		34.5 ± 24.0
Meso-eutrophy	83.2 ± 105.1		112.6 ± 120.0		64.1 ± 60.8
Eutrophy	57.2 ± 65.7		70.2 ± 37.1		73.1 ± 92.9
Hypertrophy	45,3 ± 17.2	↔	84.1 ± 32.1	↔	49.0 ± 37.4
SUMMER DATA					
Mesotrophy	7.1 ± 2.7		8.8 ± 5.9		11.6 ± 11.0
Meso-eutrophy	4.8 ± 2.1	↔	8.1 ± 4.7		8.2 ± 4.0
Eutrophy	6.2 ± 3.7		8.3 ± 4.2		11.4 ± 8.4
Hypertrophy	7.4 ± 2.7		13.9 ± 12.5		10.4 ± 4.4

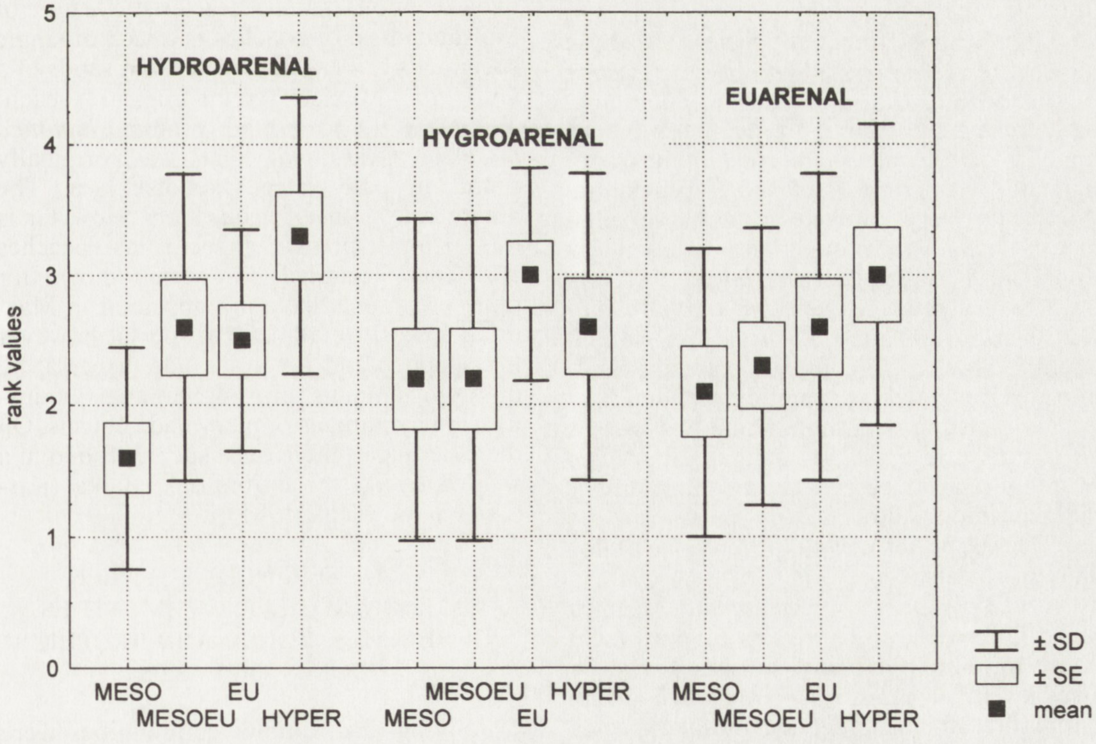

Fig. 4. Physico-chemical characteristics of interstitial waters of beaches in four trophic groups of lakes – ranking list for parameters' values (STATISTICA software; Friedman ANOVA test)

visible in hygroarenal, thus this part of psammolittoral which is under an influence both lake waters and allochtonic matter influx from surrounding lands.

The group of beaches in mesotrophic lakes took the lowest place in a ranking list, the highest one – in hygro- and euarenal of hypertrophic lakes. The differences between mesotrophic group and all the three remaining trophic groups were statistically significant at $P = 0.05$ (Friedman ANOVA test) in hygroarenal and between mesotrophic and eu- or hypertrophic groups in the remaining two zones.

3.2. STRUCTURE AND ABUNDANCE OF PSAMMON COMMUNITIES OF ROTIFERA IN RELATION TO LAKE TROPHY

3.2.1. SPECIES NUMBER; NEW AND RARE SPECIES

Rotifers were present in all the studied stations. In total, 110 species of Monogononta (i.e. *ca.* 26% of all records of rotifer species in Poland) were found (Table 7) with 22 species occurring exclusively in psammon. As many as 16 species were exclusive for spring samples, whereas 34 species were found in summer ones only. Thus, most of psammon rotifer species can occur both in cold and warm periods of the year. One can easily explain the phemonenon taking into account the fact that all inhabiting psammolittoral rotifers have to stand strong fluctuations of temperature practically every day.

Three most frequent species, i.e. those occurring in all studied lakes (*Lecane closterocerca, L. luna* and *Cephalodella catellina*) are eurytopic forms met in practically all freshwater habitats, but most frequently amongst littoral vegetation. Similarly, very tolerant to environmental stress forms were prevailing among species found in 17 lakes (*Lecane lunaris, Lecane scutata, Lepadella patella Cephalodella gibba* and *Colurella colurus*). From among them *L. scutata* is the only one occurring almost exclusively in psammolittoral and usually co-existing with more numerous species of the genus *Lecane*. In general, 23 species were found in at least half of the total number of lakes under study.

Three species new in rotifer fauna of Poland were discovered (Fig. 5):

– *Cephalodella psammophila,* species described by Koch-Althaus (1962b) from Stechlinsee in Germany. It was found in beaches in as many as 7 Masurian lakes. More often and in higher densities the species occurred in spring. Its highest numbers accounted for 149 individuals per 100 cm^{-2} in hygropsammon of deep, highly eutrophic Lake Jagodne (Table 1).

– *Collotheca wiszniewski*, psammobiotic species, known from a few countries of Central and North Europe. It seems, however, that the species can be more common if its habitat is studied more frequently. At least, it was quite common in the Great Masurian Lakes. It was met exclusively in spring in 10 lakes under study. The highest density of the species was noted in hygropsammon of Mikołajskie Lake (deep and eutrophic lake in a system of the Great Masurian Lakes – see Table 1).

– *Euchlanis dapidula*, psammoxen known from littoral has been found in psammon for the first time; its numbers in polymictic, mesotrophic Lake Śniardwy (Table 1) were low (up to 4 individuals per 100 cm^2) and much higer in hygroareal of deep, mesotrophic Dobskie Lake (33 ind. 100 cm^{-2}) (Fig. 5).

Among rare species one of the most interesting was *Lecane monostyla,* typical for tropical or subtropical waters (Fig. 5), in Poland met previously in two streams surrounded by pine forests in central and north-eastern parts of the country (Ejsmont-Karabin and Kruk 1998).

Nevertheless, it seems (with the above one exception) that a characteristic feature of the studied set of beaches is a lack of single specimens of very rare species. In sands of a Gulf of Mexico (semi-tropical beach) Turner (1993) reported *Notholca japonica kisselevi* (Kutikova) that was originally found in cold-water Okchotsk Sea. The author asks himself a question "How far is too far for dispersal?" It seems lake beaches are better separated, as species known for other continents have not appeared in Masurian Lakes. Small-scale dispersal however may happen and it can include dispersal by migrating animals (birds or mammals), transmission by humans or man-made objects. On the other hand, there exist species found in a single site, like those from Lake Baikal (Kutikova and Arov 1985).

3.2.2. DIFFERENCES BETWEEN PSAMMON ROTIFER COMMUNITIES IN BEACHES, ZONES AND TROPHIC GROUPS OF LAKES

Spring and summer communities were relatively similar in their taxonomic structure (Fig. 6). In both periods rotifer communities were dominated by species of the genera *Lecane*, *Lepadella* and *Cephalodella*. Although the latter two played more important role in spring than summer and were more numerous in hygro- and euarenal, average structure of rotifer communities was similar in all three zones.

Nevertheless, comparison of the species structure of rotifer communities in hi-

Table 7. Rotifer species found in particular lakes in spring (S) and summer (U). Explanations: study lakes are ranked according to the increasing trophy of lake waters. Abbreviations: MA – Majcz Wielki, MM – Mamry, DOB – Dobskie, DAR – Dargin, NDZ – Nidzkie, ŚNR – Śniardwy, GŁB – Głębokie, BŁD – Bełdany, INL – Inulec, MIK – Mikołajskie, CZS – Czos, TLT – Tałty, JGD – Jagodne, TUC – Tuchlin, TYR – Tykło, JUN – Juno, KOC – Kocioł; stars mark psammobionts

SPECIES	LAKES																	
	mesotrophic				mesoeutrophic					eutrophic					hypertrophic			
	MA	KUC	MM	DOB	DAR	NDZ	SNR	GŁB	BŁD	INL	MIK	CZS	TLT	JGD	TUC	TYR	JUN	KOC
Ascomorpha ecaudis Perty													U			U		
Ascomorpha saltans Bartsch			U					U										
Brachionus quadridentatus Hermann											U							
Bryceella tenella Bryce											U							
Cephalodella auriculata (Muller)	S	SU	S		S	S	S	S	S	U	U		S	S		U	S	
Cephalodella catellina (Muller)	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	S	U	SU	SU	SU	SU	SU	U
Cephalodella compacta Wiszniewski*		S	U	SU		S	U	S		U		U	SU					
Cephalodella exigua (Gosse)										U								
Cephalodella gibba (Ehrenberg)	SU	SU	S	SU	SU	SU	SU	SU	SU	SU	S	U	SU	SU	SU	SU	SU	
Cephalodella gracilis (Ehrenberg)		U																
Cephalodella megalotrocha Wiszniewski									S	U	U							
Cephalodella misgurnus Wulfert		S																
Cephalodella psammophila Koch-Althaus*	S		U	SU	S	U				S			S	S			S	
Cephalodella reimanni Donner			SU							U							S	
Cephalodella sterea (Gosse)			U			U					U	U						
Cephalodella tachyphora Myers	S										S							
Cephalodella tenuior (Gosse)		SU	S	S	S				S	SU				U		S		
Cephalodella tenuiseta (Burn)	S	S	S	SU	SU	S	S	S	S	S	S		SU	S	S	SU	S	
Cephalodella ventripes (Dixon-Nuttall)	S			U														
Collotheca ornata (Ehrenberg)											S							
Collotheca wiszniewski Varga*	S	S	S	S		S			S		S		S	S		S		
Colurella adriatica Ehrenberg	S	S		S	S	S	SU	S	S	S	S		S	S		S	S	
Colurella colurus (Ehrenberg)	SU	SU	SU	SU	SU	SU	SU	S	S	SU	SU	U	SU	S	SU	SU	SU	
Colurella hindenburgi Steinecke			U	U	U	SU					S		U					
Colurella obtusa (Gosse)	U	SU	U	S	SU	S	U	S	S	SU	SU	U	SU	SU		U	SU	
Colurella uncinata (Muller)	SU	U	U	U	SU	SU		U	S	U	U	U	U	U		S	SU	

SPECIES (continued)	LAKES																	
	MA	KUC	MM	DOB	DAR	NDZ	SNR	GŁB	BŁD	INL	MIK	CZS	TLT	JGD	TUC	TYR	JUN	KOC
Dicranophorus capucinus Harring i Myers	S		S	S	S	S	S				S		SU					
Dicranophorus edestes Harring i Myers			U															
Dicranophorus forcipatus (Muller)											SU		U	U				
Dicranophorus grandis (Ehrenberg)	S						U						U	U				
Dicranophorus hercules Wiszniewski*	SU		U	S	SU	U	S		U		SU		SU					
Dicranophorus leptodon Wiszniewski*										U								
Dicranophorus luetkeni (Bergendal)	S	U	U		U	SU	U		U		SU		U	U				
Elosa spinifera Wiszniewski*					U													
Elosa woralli Lord													S					
Encentrum diglandula (Zavadowski)*		U	S		U			S					S			S	S	
Encentrum marinum (Dujardin)																	U	
Encentrum sp.										U				U				
Encentrum sutor Wiszniewski*							S	S										
Encentrum uncinatum (Milne)		S														U		
Euchlanis dapidula Parise				U			U											
Euchlanis dilatata Ehrenberg	U					U	U		SU		U	U	S	U				
Euchlanis oropha Gosse	U						U		S		S		SU	S			S	
Euchlanis triquetra Ehrenberg													S					
Keratella cochlearis (Gosse)			SU		U		SU		SU	U	S		SU	S		U		
Lecane aculeata (Jakubski)										S								
Lecane arcuata (Bryce)		SU	S	SU	SU		S		SU	SU	SU			S			SU	
Lecane arcula Harring														U				
Lecane bulla (Gosse)	SU	U			U	S			S	U					S			
Lecane clara (Bryce)													S					
Lecane closterocerca (Schmarda)	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU
Lecane flexilis (Gosse)	S	SU	S	SU	SU		U	U		U	S			S		S	U	
Lecane furcata (Murray)		U	U	U	U						U			U	U			
Lecane gwileti (Tarnogradski)		U			U				U							S		
Lecane hamata (Stokes)	S	U	U	U	SU	S		S	SU	SU			SU	SU	SU	S		
Lecane intrasinuata (Olofsson)		U						U										
Lecane levistyla (Olofsson)*	SU		SU	U					SU		SU		SU					
Lecane luna (Muller)	SU	SU	SU	U	U	SU	SU	U	SU	SU	U	U	SU	SU	SU	S	SU	
Lecane lunaris (Ehrenberg)	SU	SU	SU	SU	SU	S	SU	S	SU	SU	S	U	SU	SU	SU	S	SU	

SPECIES (continued)	LAKES																	
	MA	KUC	MM	DOB	DAR	NDZ	SNR	GŁB	BŁD	INL	MIK	CZS	TLT	JGD	TUC	TYR	JUN	KOC
Lecane monostyla (Daday)	U																	
Lecane opias Harring i Myers			U			U	S											
Lecane psammophila (Wiszniewski)*	SU	SU	SU	SU	SU	SU	SU		SU	SU	SU	U	SU	SU	SU	SU	SU	
Lecane pyriformis (Daday)				U														U
Lecane scutata (Harring i Myers)	SU	SU	SU	SU	SU	SU	U	U	SU	SU	U	U	SU		U	SU	SU	U
Lecane stenroosi (Meissner)		U		U						S				U			S	
Lecane subtilis Harring i Myers		U			S													
Lecane tenuiseta Harring	U	U	SU	SU	SU									U	S	S		
Lepadella acuminata (Ehrenberg)	S								S	S			S				S	
Lepadella elliptica Wulfert																S		U
Lepadella ovalis (Muller)	S				S	S								S				
Lepadella patella (Muller)	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	SU	U	SU	SU	SU	SU	SU	
Lepadella quadricarinata (Stenroos)	SU	SU	S	SU	SU	U	SU		S	SU	SU	U	SU	SU		SU	SU	
Lepadella triptera Ehrenberg					U		S							U				
Lindia janickii Wiszniewski*	S			S				U					S		U		S	
Lindia torulosa Dujardin		S			U			S		S		U			U	S		
Lindia truncata (Jennings)			S		S	S			S	SU		U	S		S	S		
Lophocharis oxysternoon (Gosse)					U													
Lophocharis salpina (Ehrenberg)			U															
Monommata astia Myers			S															
Myersinella tetraglena (Wiszniewski)*	SU	U	SU	S		S	U		S	SU			S		S	U		
Mytilina mucronata (Muller)					U				S									
Mytilina ventralis (Ehrenberg)			U						S									
Notholca foliacea (Ehrenberg)									S									
Notholca squamula (Muller)													S	S				
Notommata aurita (Muller)		U																
Notommata cyrtopus Gosse	SU	SU	SU	U			U		S	SU	SU	U	S	U			U	
Notommata doneta Harring i Myers					U													
Notommata tripus Ehrenberg					U													
Pompholyx sulcata Hudson			U				U		U	U	U		U	U		U	U	
Proales minima (Montet)			U							U								
Proales wesenbergi Wulfert		U																
Scaridium longicaudum (Muller)					U													

SPECIES (continued)		LAKES																	
		MA	KUC	MM	DOB	DAR	NDZ	SNR	GŁB	BŁD	INL	MIK	CZS	TLT	JGD	TUC	TYR	JUN	KOC
Synchaeta kitina Rousselet				S															
Synchaeta stylata Wierzejski								SU		S									
Testudinella patina (Hermann)						U													
Testudinella truncata (Gosse)					U													U	
Trichocerca intermedia (Stenroos)*		S	SU		S	U				S	U	U		SU			SU	SU	
Trichocerca musculus (Myersi)				U		U		U											
Trichocerca myersi (Myersi)*		U			S			U		S	U			S		U	U	U	
Trichocerca pusilla (Lauterborn)														U					
Trichocerca similis (Wierzejski)														U					
Trichocerca taurocephala (Hauer)*		SU	S	SU	SU	U	U	SU	S	SU	SU	SU	U	SU	SU		U	SU	
Trichocerca tenuior (Gosse)			U	SU	S	U			SU	S	U	S	U					S	
Trichocerca tigris (Muller)				U	S						S	S			S			SU	
Trichocerca weberi (Jennings)			SU	S	S			U			U								
Trichotria pocillum (Muller)						U		U			U								
Trichotria tetractis (Ehrenberg)		U																	
Wierzejskiella sabulosa (Wiszniewski)*		U	U	SU	S			U			U	SU		SU					
Wierzejskiella velox (Wiszniewski)*		S	SU	SU	S	SU	U	U		SU	SU	SU		S	U		U		
Wigrella depressa Wiszniewski*		SU						U											
TOTAL NUMBER OF SPECIES	SPRING	35	28	32	31	26	24	21	17	38	27	30		39	24	14	24	27	
	SUMMER	26	36	37	28	40	19	32	12	19	27	27	20	31	26	14	20	22	6

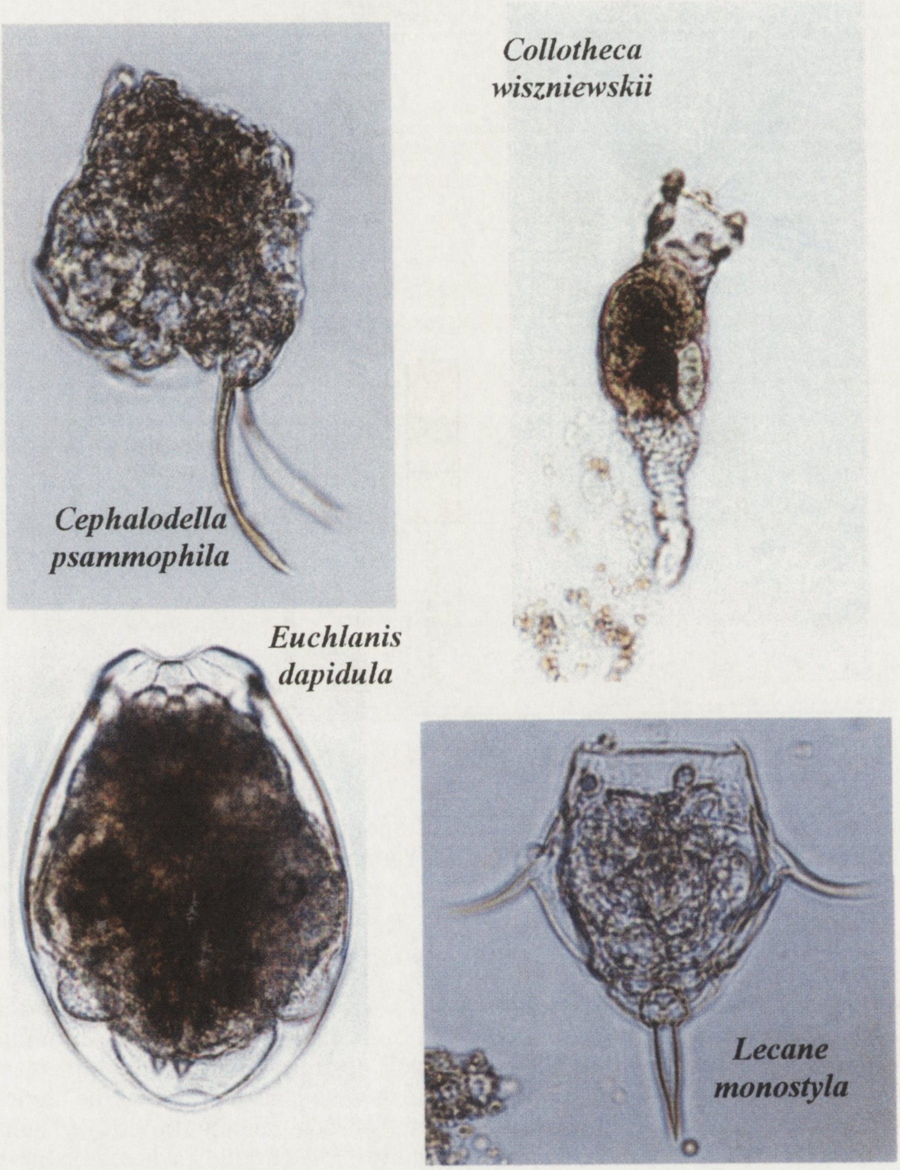

Fig. 5. New in rotifer fauna of Poland and rare rotifer species found in the study lake beaches

gropsammon of particular beaches (Fig. 7) shows high diversity of sub-dominants and less numerous species. It is often observed that species structure of rotifer communities from beaches of the same lake is very different (like in lakes Juno, Nidzkie and Tyrkło), whereas beaches of two different lakes have nearly identical rotifer assemblages (compare Dobskie 3, Kuc 3, Majcz 1, Inulec 3). It seems that all trophic groups of lakes are relatively similar as regards species structure of rotifer communities with rotifers of the genus *Lecane* playing most important role (Fig. 8).

The thesis on high differences between psammon rotifer communities from beaches of the same lake may be well illustrated by means of the Index of Percentage Similarity of the Community (*PSC*, Whittaker and Fairbanks 1968). The index calculated for randomly chosen 36 pairs of beaches from the same lake (Fig. 9A) and for beaches of different lakes (Fig. 9B) was 41.8 ± 27.0 in the former and 40.9 ± 24.9 in the latter case. It reveals that having very similar list of dominants the studied beaches are strongly differentiated as regards quantitative relations

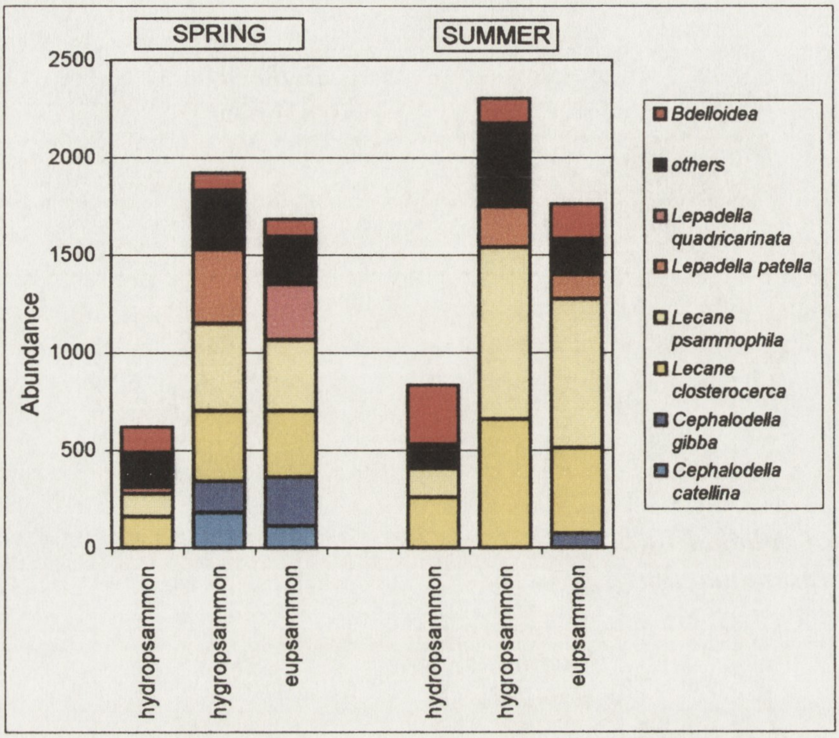

Fig. 6. Mean numbers (ind. 100 cm $^{-2}$) of dominating rotifer species in three zones of psammolittoral in spring and summer

between the species. Similarly, Pennak (1951) described strong differences between particular beaches of the same lake.

The observed strong differences between the fauna in particular beaches are caused rather by exchange of species from the same frequency group. The most common species, i.e. those occurring in more than 75% of the study lakes (*Cephalodella auriculata, C. catellina, C. gibba, C. tenuiseta, Colurella adriatica, C.colurus, C. obtusa, C. uncinata, Lecane closterocerca, L. luna, L. lunaris, L. psammophila, L. scutata, Lepadella patella, L. quadricarinata, Trichocerca taurocephala*) constitute the overwhelming majority of individuals forming rotifer communities of all beaches (Fig. 10). Medium (from 25–75% of beaches) and low (<25%) frequency species play unimportant role in rotifer abundance both in spring and summer. Also differences between beaches from four trophic groups of lakes are very low in this respect (Fig. 10).

Species very common in sand beaches (those met in more than 75% of the studied lakes) constitute as many as *ca.* 93% of total abundance in rotifer communities. Forms specific for just 1 to 5 lakes constitute as little as 0.6% of their abundance, but this group of species decides on faunistic originality of the communities. Consequently, the index of originality is related to number of species met in a given beach (Fig. 11). The relationship is very significant (R = 0.91) thus number of species explains 84% of the original variability of the index.

Trophic state of lakes seems to influence the originality of psammon communities as well. Rotifer communities of mesotrophic lakes were characterised by the highest values of species number and Index of Faunal Originality (*IFO*) (Fig. 11), whereas in hypertrophic lakes both the indices had the lowest values. The indices for communities of meso-eutrophic and eutrophic lakes were distributed more or less randomly in a full range of values.

3.2.3. SPECIES DIVERSITY OF PSAMMON ROTIFER COMMUNITIES

Generally, psammon communities of Rotifera were characterised by relatively high species diversity. Spring communities were markedly higher diversified than summer ones in all three zones studied. However, differences between values mean for summer and spring were statistically significant (*P* = 0.002 and 0.009; t-test) only for zones of hydro- and euarenal. When put together for the three zones, the values of the index varied be-

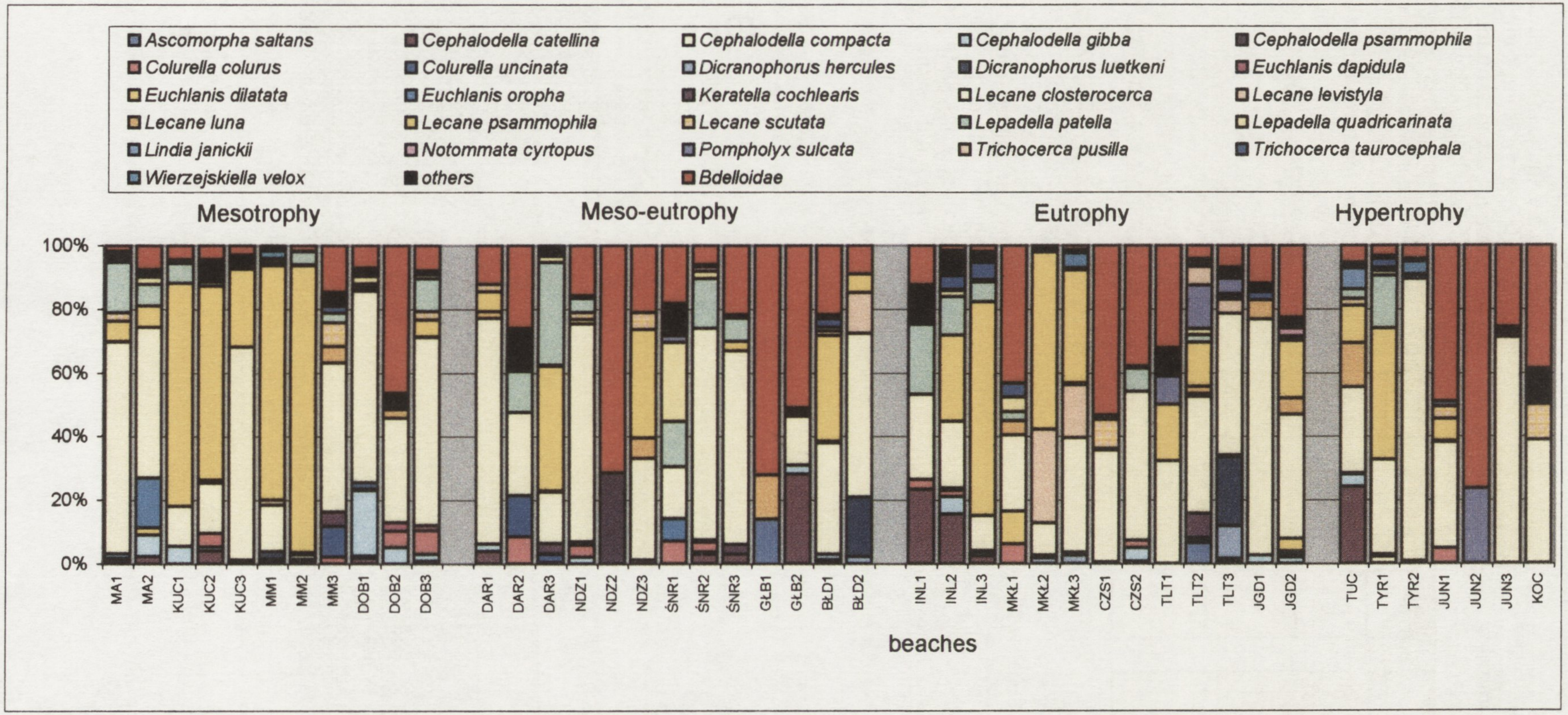

Fig. 7. The share of dominating species in total abundance of the rotifer communities from hygroarenal in summer (abbreviations of lake names like in Table 7)

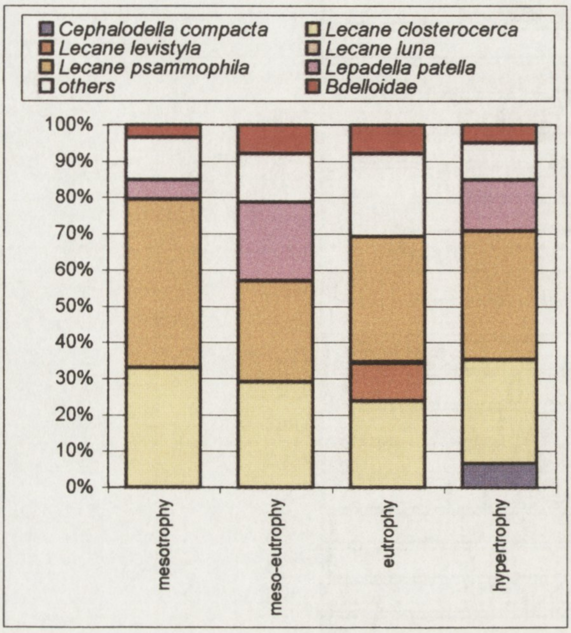

Fig. 8. Mean percentage of rotifer species dominating in their total numbers in hygropsammon of trophic groups of lakes in summer

tween 0.0 and 3.3 (with mean value of 2.1 ± 0.7; n = 111) in spring, whereas in summer the maximum value was 3.04 (mean 1.6 ± 0.7; n = 132).

Data on species diversity index for particular beaches under study are very differentiated (Fig. 12). However, some tendency might be seen for lower diversity of psammon rotifer communities of hypertrophic lakes (mean 1.63 ± 0.84). The highest values of diversity index occurred in eutrophic lakes (2.06 ± 0.69) (Table 8).

3.2.4. ECOLOGICAL CATEGORIES OF PSAMMON COMMUNITIES

According to Wiszniewski (1934a, b, 1953) psammon rotifers may be separated into three categories: psammobiotic ones (species occurring only in sand), psammophilic (species occurring both in sand and open water) and psammoxenic (rotifers that are not able to survive in sands).

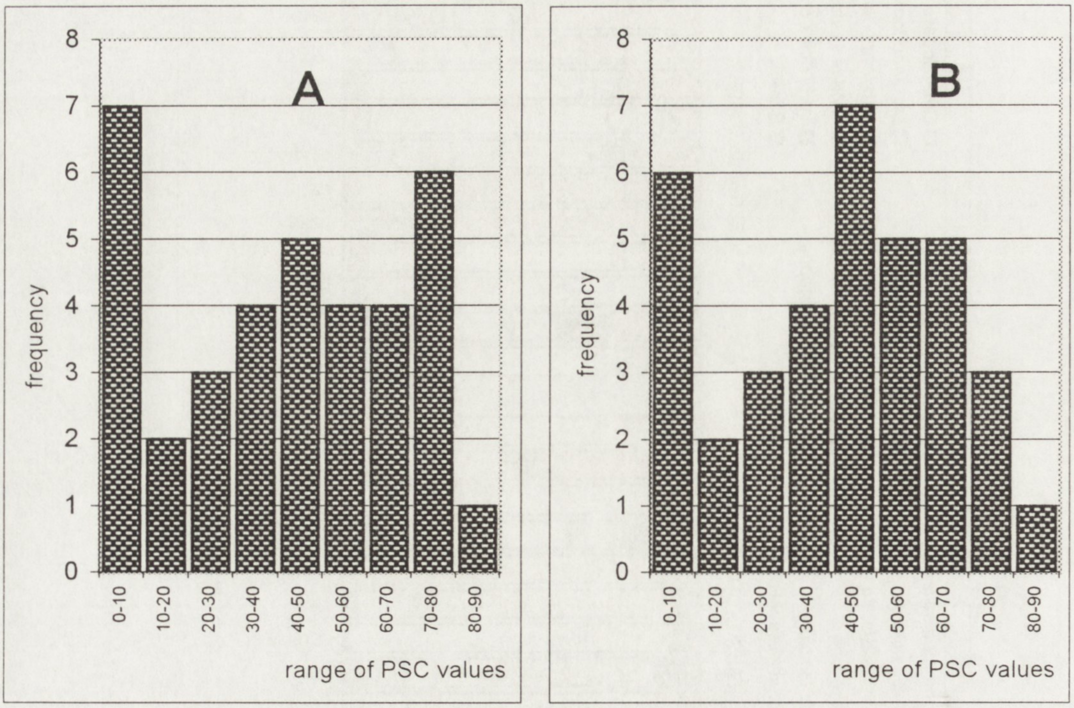

Fig. 9. Comparison of PSC (Percentage Similarity of Community) values for pairs of hygropsammon communities of rotifers from the same lake (A) and for pairs from different lakes (B).

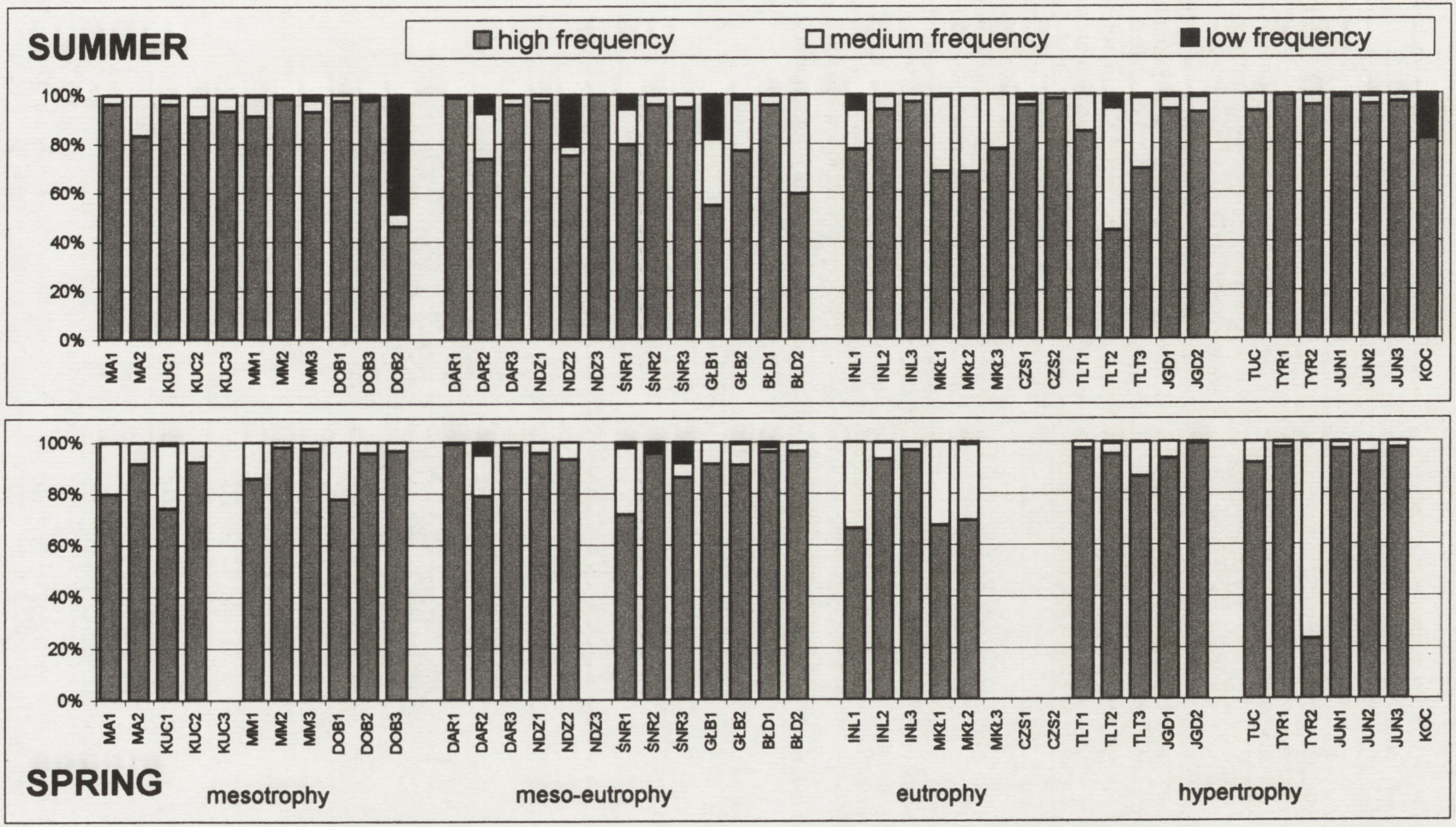

Fig. 10. The role of high, medium and low frequency species in total abundance of psammon rotifers of particular beaches(abbreviations of lake names like in Table 7)

Similarly to lake psammon a group of "obligatory" interstitial rotifers was recognised by Turner and Palmer (1996) in Goose Creek (USA). The authors included *Brycella* sp., *Wierzejskiella velox, Lecane pyriformis, Proales minima* and *Trichocerca taurocephala* into the group. In Arov's (1985) studies in Lake Baikal only two species (*Wierzejskiella sabulosa* and *Notholca kozhovi*) were classified as psammobiotic forms. The community was dominated by psammophilic and psammoxenic species.

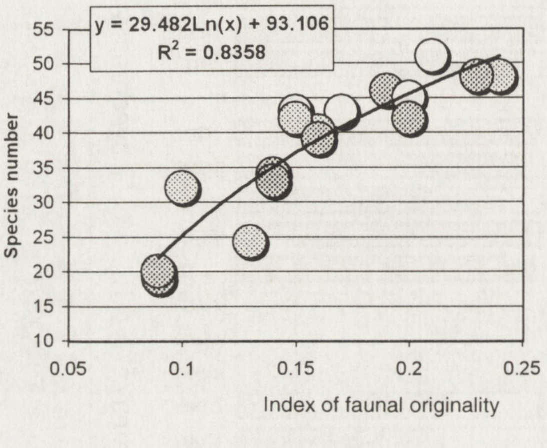

Fig. 11 Relationship between number of species and index of faunal originality in psammon rotifer communities of lakes of different trophy. Explanations: white circles – mesotrophic lakes, light grey – meso-eutrophic, grey – eutrophic and dark grey – hypertrophic ones.

Psammophilic forms were also the dominating ecological group of psammon rotifers in all the studied lakes, both in spring and summer (Fig. 13). The role of psammoxenic species seems to be more important in more eutrophicated lakes, whereas markedly more psammobionts were observed in mesotrophic lakes. Psammobionts constituted from 1% of rotifer numbers in hydropsammon of hypertrophic lakes to 40% in eupsammon of mesotrophic lakes. Psammoxenic species were even less important constituting from 5% to 20%. Psammophilic rotifers decidedly dominated with maximum value of 88% of rotifer abundance in hydropsammon of hypertrophic lakes.

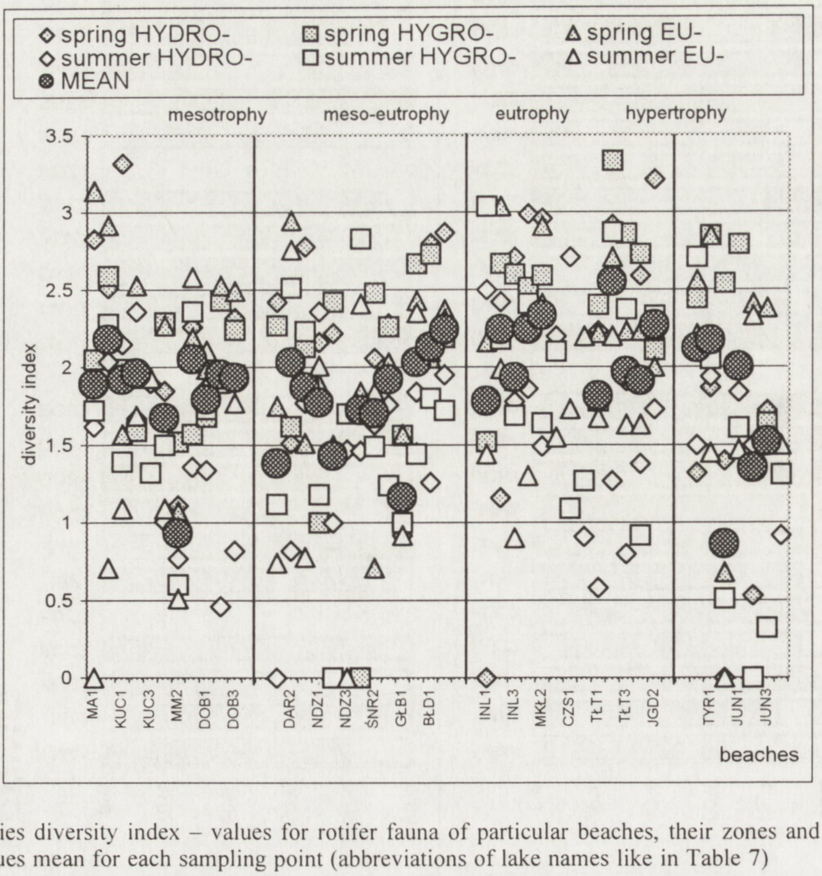

Fig. 12. Species diversity index – values for rotifer fauna of particular beaches, their zones and two sampling dates and values mean for each sampling point (abbreviations of lake names like in Table 7)

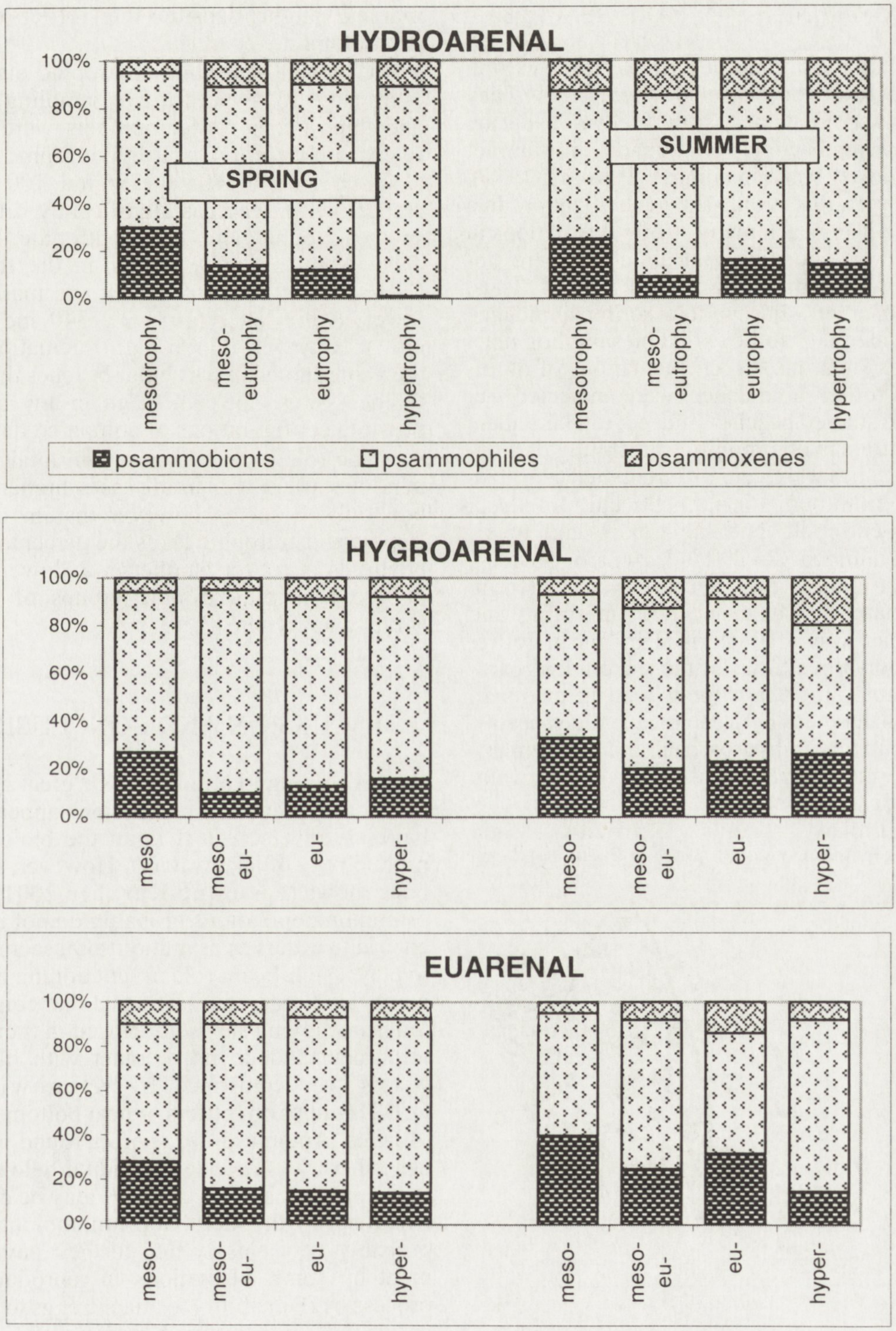

Fig. 13. The percentage of ecological groups of psammon rotifers in total numbers of the community (mean for trophic groups of lakes)

3.2.5. DENSITIES OF ROTIFER COMMUNITIES IN LAKE BEACHES

Sand communities of Rotifera exhibit some kind of seasonal succession. They dissapear in winter, slowly develop during the spring, become very abundant in summer and slowly wane in autumn (Pennak 1951). However, this is only the generalization. In a single lake beach many strong fluctuations in rotifer composition and abundance are observed (Ejsmont-Karabin 1998). Thus, the observed values of total rotifer abundance depended into some extent on sampling date. In this situation strong fluctuations of psammon rotifer abundance were expected between studied beaches. Indeed, total numbers of rotifers in communities inhabiting particular beaches were very differentiated (Fig. 14). Both minimum (7 ind. 100 cm^{-2} in deep, meso-eutrophic Nidzkie Lake), and maximum numbers (24 290 ind. 100 cm^{-2} in deep, hypertrophic Lake Tyrkło) were noted in hygroarenal. This zone both in spring and summer was characterised by mean rotifer numbers three times of those from hydroarenal and somewhat higher than in euarenal. The differences between mean values of rotifer numbers in hydroarenal and two remaining zones were in all cases statistically significant at $P<0.05$.

Similarly, in Radwan and Bielańska-Grajner (1998) studies eu- and higropsammon rotifer communities had markedly higher densities than rotifers of hydropsammon.

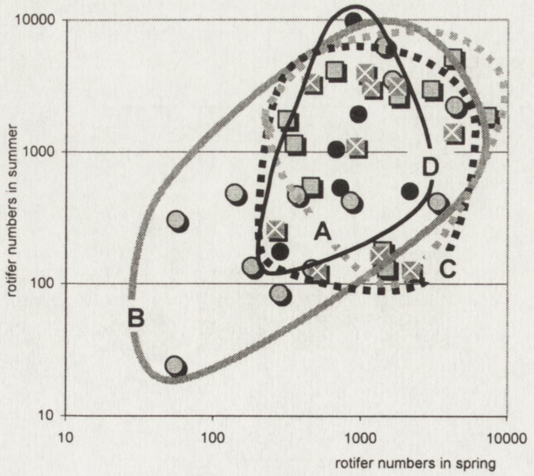

Fig. 14. Mean for zones abundance (ind. 100 cm^{-2} of sand area) of psammon rotifer communities in lakes of different trophy in spring and summer. Explanations: line A and grey squares – mesotrophic lakes, line B and grey circles – meso-eutrophic lakes, line C and crossed grey squares – eutrophic and line D and black circles – hypertrophic ones.

Grouped according to trophic state of lakes (Fig. 15) mean for two sampling dates and three zones rotifer numbers were relatively similar in eu- and hypertrophic lakes (1588 ± 884 and 1405 ± 1796 ind. 100 cm^{-2}, respectively), whereas significantly differed in mesotrophic and meso-eutrophic lakes. They were markedly higher in the former (2016 ± 1514 ind. 100 cm^{-2}), and markedly lower in the latter (1081 ± 1340 ind. 100 cm^{-2}). However, due to high fluctuations of the values noted in particular beaches the differences were not significant in any of the possible configurations of compared data.

The role of monogononts in total numbers of rotifers was in all cases higher than bdelloids. It seems however that in mesotrophic and eutrophic lakes the percentage of bdelloids in rotifer numbers was lower than in two remaining trophic groups of lakes (Fig. 15 and Table 8).

4. DISCUSSION AND CONCLUSIONS

According to Neel (1948) "great development of psammon populations appears to have an adverse effect upon the biological productivity of lake waters". However, it has been shown (Ejsmont-Karabin 2001) that psammon populations probably do not influence lake waters as psammolittoral seems not to play a significant role in functioning of the whole lake ecosystem. The fact that communities occupying sands are closed in their environment and do not contact with littoral waters was confirmed by Klimowicz's (1972) studies on rotifers of near bottom zone of lakes. Among rotifer species found in the zone there was no one individual belonging to the psammobionts' group. It may be easily explained by the fact that psammobionts are probably very closely tied to their environment by some adaptations in reproduction process by their ability to attache eggs to sand grains (Neiswestowa-Shadina 1933).

The opposite relationship however can be expected, i.e. some effect of lake waters on psammolittoral communities. High species diversity of the psammon communities, expressed as both total number of all found species and number of species in particular beaches seems to support this thesis. Sand

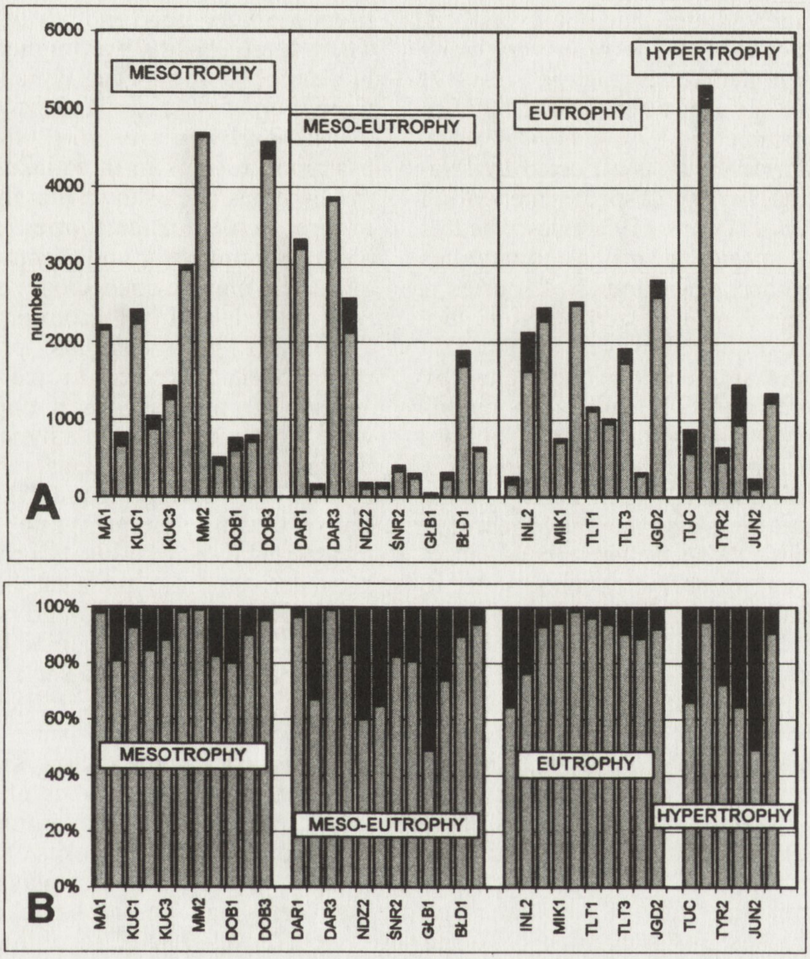

Fig. 15. Total abundance (A, ind. 100 cm^{-2} of sand area) and percentage (B) of monogonont (grey coloured) and bdelloid (black) rotifers in psammolittoral (mean for three zones) of lakes grouped according to their trophy (abbreviations of names like in Table 7).

Table 8. General characteristics of psammon rotifer communities in four trophic groups of lakes – summary of data (mean values of parameters ± SD)

Parameter	Lake trophy			
	Meso-	Meso-eu-	Eu-	Hyper-
Total number of species in a lake (mean for trophic groups)	46 ± 5	37 ± 9	44 ± 4	29 ± 8
Number of species in particular beaches (mean for trophic groups)	20 ± 6	15 ± 6	19 ± 7	14 ± 4
Index of faunal originality	0.18 ± 0.03	0.16 ± 0.05	0.17 ± 0.05	0.12 ± 0.03
The percentage of ecological groups in community numbers:				
Psammobionts	30.5 ± 5.4	15.7 ± 6.1	18.5 ± 7.7	13.7 ± 8.2
Psammophiles	61.8 ± 4.2	74.0 ± 6.7	70.8 ± 9.5	74.7 ± 11.7
Psammoxens	7.7 ± 3.2	10.3 ± 3.6	10.7 ± 3.1	11.7 ± 4.9
Species diversity index	1.82 ± 0.68	1.75 ± 0.71	2.06 ± 0.69	1.63 ± 0.80
Mean abundance (ind. 100 cm^{-2})				
Monogononta	1895 ± 1521	1050 ± 1337	1388 ± 883	1385 ± 1829
Bdelloidea	121 ± 59	103 ± 113	137 ± 144	248 ± 149

habitats are rather simple and not diversified, so they are not expected to offer very many niches. Thus, high diversity may be a result of penetration of the sandy beach zone by littoral and pelagic species.

This high diversity is reflected by relatively high total list of 122 species met during the study. Also Myers (1936) described as many as 144 species in rotifer communities of acidic beaches. The number of species is probably dependent upon some abiotic factors like wind action and waves. Perhaps that is the reason that species richness cited by Schmid-Araya (1998) from papers by different authors was not so high. It ranged from 11 to 34 in marine beaches, from 19 to 145 in lake beaches and from 21 to 27 in river sands. The community was also markedly poorer in Pawłowski's (1958) studies carried out in river Grabia and water-bodies connected to it. The author has found only 73 psammon species of Rotifera with only 7 psammobionts and 18 psammophiles.

Lists of species found in particular lake beaches were much shorter: 17–24 species in a mesotrophic lake, 10–14 and 9–10 in two eutrophic lakes and 9–23 in hypertrophic lake in Łęczyńsko-Włodawskie Lakeland, East Poland (Radwan *et al.* 1998). Bielańska-Grajner (2001) found in summer communities of psammon rotifers of soft-water and mesotrophic lakes in Pomeranian Lakeland 24, 26 and 10 species (respectively). Thus, number of species found in psammon communities of Masurian lakes (Table 8) were comparable to those cited above and similar to number of species usually observed in homogenic pelagic waters, but lower than number found in littoral, i.e. 25–50 rotifer species in one sample (Ejsmont-Karabin, unpublished data from different lakes and water-bodies connected with rivers).

This discrepancy between number of all species met in the whole set of the studied lakes and number found in particular lakes can be explained by the fact, that the basic part of the list is consisted of common forms with high frequency – the same in all beaches, whereas psammoxenic and at the same time not frequent species are different in different lakes. This phenomenon may give a long list of all met species and short lists of species from one sampling point.

In Karabin's (1985) studies on the role of trophic state of lake waters in determining composition and abundance of pelagic communities of rotifers it has been shown that rotifers are very good indices of lake trophy. Their total density was higher in lakes of higher trophy and species typical for different trophic types of lakes were discovered.

In Radwan's *et al.* (2001) studies on psammon rotifers in three lakes of different trophy it has been shown that the occurrence of three ecological categories (i.e. psammobiont, psammophilic and psammoxenic ones) of rotifers may be connected with the trophic type of the lake. In a mesotrophic lake (Lake Piaseczno) psammobionts prevailed and psammoxens were very scarce. In eutrophic and hypertrophic lakes psammophilic species were more important. In a hypertrophic lake psammobionts occurred as residuals. Also Pejler (1995) suggested that the role of specialists (psammmobionts) might be different in different types of lakes. His conclusion had been derived from the fact that Ruttner-Kolisko (1953, 1954) found no psammobionts in the oligotrophic alpine lake, whereas in more eutrophic Swedish lake the author found typically psammic rotifers. However, results described in this paper of investigations carried out on a large set of beaches from different trophic types of lakes do not support this hypothesis. Psammobionts seem to be more numerous in lakes of lower trophy and psammoxenic species play more important role in highly eutrophic lakes.

On the other hand, according to results of Myers's (1936) studies, the number of psammophilic species found in hygropsammon was dependent on the proximity of the submerged macrophytes. It would have suggested that littoral rotifers played significant role in psammon communities. Their income to psammolittoral zone should increase diversity of an invaded community. However, species diversity of psammon communities is similar (or lower) to that observed in pelagic communities (Ejsmont-Karabin and Karabin 1999) rather than littoral. Its values were also higher in spring when macrophyte biomass was still low, and lower – in summer at maximum development of submerged vegetation.

The question arises: "Why specialists (i.e. psammobionts) are less numerous than generalists (here: psammophilic forms)?" Psammobionts should have prevailed in the community being the forms best adapted to very harsh life in this variable environment.

Pejler (1995) believed that the rotifers inhabiting the most extreme environments were mostly closely related to some common species and even those being specialists were closely related to decidedly euryecious species. He suggested that specialists were derived from very variable in morphological and biological respect generalists.

It seems that domination of psammophilic forms, thus forms present also in other than sand environments (mainly littoral with abundant vegetation) means that psammolittoral is the zone suffering frequent disasters. Thus it undergoes permanent colonisation by new inhabitants what results in domination of opportunistic species, r-strategists. This may explain extremely high maximal densities achieved by these communities. Pontin (1989) has observed similar phenomena in rotifer communities colonising young ponds. Initial colonisers included species which were common in temporary ponds and which could multiply rapidly. It that case the main factor influencing rotifer abundance and structure in the studied beaches may be sampling time or, more strictly – time since last catastrophe like heavy rain, strong wind or extreme temperatures. This factor, however, was reduced due to rather constant weather conditions. Nevertheless, some of observed differences between particular communities might be related to weather history.

The observed differences between beaches may be also a consequence of the fact that amounts of organic material disposed by waves are not constant either in quantity or location. Neel (1948) suggests that large quantities of autochthonous and allochthonous interstitial organic debris and the relationship of zones of primary production and decomposition are probably the main reason of high productivity of sands. However the productivity is highly influenced by water movements. On the other hand, supply of detrital food has not been found (Pennak 1951) to be a limiting factor as large populations are often found at low content of organic matter and small populations can be found at high amount of the matter.

The hypothesis on advantageous influence of high trophy of lake waters on abundance of psammon communities of Rotifera cannot be supported by results of this work. In lakes of moderate trophy (from meso- to eutrophy) trophic state of lake waters does not seem to influence psammon communities. In hypertrophic lakes this impact is observed, but it seems to be rather unfavourable for psammon rotifers. The communities in hypertrophic lakes are poorer in species, less diversified and less original. The groups of animals developing well in this group of lakes are bdelloids. The above results do not support Pennak's (1951) conclusion that there is some evidence that poorer faunas occur in beaches washed by cold waters containing little organic matter, whereas more productive lake beaches contain more than 30 species.

However, particular beaches are so differentiated as regards chemistry of their interstitial waters and quantitative and qualitative structure of inhabiting them rotifers that possible impact of trophic state of lake waters may be concealed. On the other hand, psammon rotifer communities consist of euryecious forms that are not especially sensitive to strong fluctuations in their habitat.

Species structure and abundance of psammon communities of rotifers seem to be rather determined by many different factors, lake trophy being only one of them and probably not the main one. A character of inhabited soils, and especially the size of sand grains may be another important factor influencing existence of psammon communities (Arov 1990).

5. SUMMARY

Rotifer communities inhabiting wet sands of lake beaches are dependent in their functioning on permanent input of organic matter from neighbouring sites. The aim of the study is to test the hypothesis, that abundance in nutrients of interstitial and/or lake waters may influence densities and structure of psammon communities of Rotifera.

Studies were carried out in hydro-, hygro- and euarenal of 44 beaches in 18 lakes of different trophy (Table 1 and Fig. 1) in summer 1999 (since 2 till 17 July) and 38 beaches in 16 lakes in spring 2000 (since 10 till 23 May). Psammon was sampled always between 10 a.m. and 2 p.m. at similar weather conditions (no shadow, rains and strong winds).

Values of pH in interstitial waters of the studied stations were (with one exception) above 7.0 (Fig. 2). Hydroarenal waters were always more alkaline than euarenal ones, both in spring and summer. Interstitial waters always contained less oxygen than lake ones and oxygen concentrations decreased upward water line (Fig. 2). Very high variability of phosphate P content (Table 2) made differences between trophic groups of lakes not significant. Similarly, concentrations of P total (Table 3) were more or less similar in all trophic groups of lakes under study and relatively

weak differences between them were always not significant statistically at $P = 0.05$. Total nitrogen values were increasing from meso-eutrophic to hypertrophic lakes in spring, whereas this trend was not observed in summer, although the concentration was always lower in hygro- and euarenal of mesotrophic than eutrophic and hypertrophic lakes (Table 4). Chlorophyll *a* concentrations were practically identical in meso-, meso-eu- and eutrophic lakes and differed markedly from chlorophyll concentrations in hypertrophic lakes. Extremely high variability of the chlorophyll values was noted between particular beaches (Table 5; Fig. 3). The concentrations of suspended solids (Table 6) were markedly higher in spring and at that time psammolittoral of mesotrophic lakes was poorer in suspended matter than all other groups of lakes in spring. In summer this group of lakes had almost the same values like the remaining trophic groups of lakes. Despite of the lack of significant correlations between above-described parameters and lake trophy some tendency to increasing values of chemical parameters with increasing trophy may be seen if their ranking list is compared (Fig. 4).

Rotifers were present in all studied stations. In total, 110 species (i.e. *ca*. 26% of all records of rotifer species in Poland) were found with 22 species occurring exclusively in psammon (Table 7). Three species new in rotifer fauna of Poland were discovered – *Cephalodella psammophila, Collotheca wiszniewski* and *Euchlanis dapidula* (Fig. 5).

Spring and summer communities were relatively similar in their taxonomic structure (Fig. 6). In both periods rotifer communities were dominated by species of the genera *Lecane*, *Lepadella* and *Cephalodella*. However, species structure of rotifer communities of particular beaches showed high diversity of sub-dominants and less numerous species. Generally all trophic groups of lakes were relatively similar as regards species structure of rotifer communities with rotifers of the genus *Lecane* playing most important role (Figs 7 and 8). The index of Percentage Similarity of Community calculated for randomly chosen 30 pairs of particular beaches from the same lake and for beaches of different lakes was in both cases almost identical (Fig. 9).

Species of high frequency, i.e. those occurring in more than 75% of the study lakes constitute the overwhelming majority of individuals forming rotifer communities of all beaches (Fig. 10). Forms specific for 1 to 5 lakes decide on faunistic originality of the communities. The relationship between species number and the index of originality is very significant (Fig. 11). Although data on species diversity index for particular beaches under study are very differentiated (Fig. 12) some tendency is seen for lower diversity of psammon rotifer communities in hypertrophic lakes.

Psammobionts constituted only 20% of the community numbers in all lakes and all zones of the beaches, psammoxenic species were even less important (10%), whereas psammophilous rotifers decidedly dominated (70%) (Fig. 13).

Grouped according to trophic state of lakes mean for two sampling dates and three zones rotifer numbers were relatively similar in eu- and hypertrophic lakes, and different in mesotrophic and meso-eutrophic lakes (Table 8). They were markedly higher in the former and lower in the latter. However, due to high fluctuations of the values noted in particular beaches the differences were not significant in any of the possible configurations of compared data (Figs 14 and 15).

The hypothesis on advantageous influence of high trophy of lake waters on abundance of psammon communities of Rotifera cannot be supported by results of this work. In lakes of moderate trophy (from meso- to eutrophy) trophic state of lake waters does not seem to influence psammon communities. In hypertrophic lakes this impact is observed, but it seems to be rather unfavourable for psammon rotifers. The communities in hypertrophic lakes are poorer in species, less diversified and less original. Quantitative and qualitative structure of psammon communities of rotifers seem to be rather determined by many different factors, lake trophy being only one of them and probably not the main one. A character of inhabited soils, and especially the size of sand grains is suggested to be another important factor influencing existence of psammon communities.

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