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Epibenthic Cyclopoida in eutrophic, temperate lakes – diversity, abundance and the influence of environmental variables

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ABSTRACT

Epibenthic Cyclopoida in eutrophic, temperate lakes – diversity, abundance and the influence of environmental variables

Predictably, epibenthic Cyclopoida, as part of the meiofauna, have an important role in the secondary production of the zoobenthos. However, studies on the diversity and abundance of epibenthic cyclopoids are still rare. As a result, knowledge regarding distribution of this group under varied environmental conditions is only sketchy. Here we present a comparative study of the community structure of epibenthic Cyclopoida in eutrophic lakes in relation to the physical and chemical characteristics of water and sediments, feeding conditions and grazing pressure from omnivorous fish. Low species diversity coincided with highly variable species composition of epibenthic cyclopoids; 2–9 species occurred in the lakes, but we found a unique species composition of the epibenthic community in each lake. Cyclopoid density ranged from 386 ind/m^2 to 28 526 ind/m^2. Canonical correspondence analysis indicated temperature, bacterioplankton biomass, concentration of total solids and content of organic matter in sediments as variables impacting the density of this group. As these variables are directly and indirectly connected to food recruitment, the results suggest that the taxonomic composition and abundance of epibenthic cyclopoids are regulated primarily by trophodynamics conditions.

Key words: meiofauna, Cyclopidae, freshwater ecosystems, sediments

RESUMEN

Ciclopoides epibentónicos en lagos templados y eutróficos – diversidad, abundancia e influencia de variables ambientales

De manera predecible y como parte de la meiofauna, los copépodos epibentónicos del orden Cyclopoida tienen un rol importante en la producción secundaria del zoobentos. Sin embargo, los estudios de diversidad y abundancia de estos copépodos son escasos. Y, en consecuencia, el conocimiento de su distribución en diferentes condiciones ambientales es poco detallada. En este estudio, comparamos la estructura de la comunidad de copépodos epibentónicos del género Cyclopoida en lagos eutróficos, en relación con las características químicas y físicas del agua y del sedimento, con las condiciones de alimentación y con la presión de pastoreo por parte de las comunidades de peces omnívoros. La baja diversidad de especies coincidió con la alta variabilidad en la composición de especies de la comunidad epibentónica de ciclopoides; 2-9 especies estuvieron presentes en los lagos, pero encontramos una composición única de especies en la comunidad epibentónica en cada lago. La densidad de ciclopoides varió entre 386 ind/m^2 to 28 526 ind/m^2. De acuerdo con el análisis de correspondencia canónica, la densidad de este grupo está afectada por la temperatura, la biomasa de bacterioplancton, la concentración de sólidos totales y el contenido de materia orgánica en los sedimentos. Y como estas variables están relacionadas directa e indirectamente con la captura de alimento, los resultados sugieren que la composición taxonómica y la abundancia en la comunidad de ciclopoides epibentónicos están reguladas principalmente por condiciones tropodinámicas.

Palabras clave: *meiofauna, Cyclopidae, Ecosistemas de agua dulce, sedimentos*

INTRODUCTION

The subclass Copepoda is a very diverse group with about 14 000 described species segregated in nine orders and about 210 family-level groups (Boxhall & Halsey, 2004). They have evolved a high level of diversity in body form and habits and have colonized every aquatic habitat in a wide range of environmental conditions. Copepod species diversity is reflected in their modes of life, which include parasitic and a loosely symbiotic mode. They exhibit a variety of feeding behaviours, from predation to scavenging on detritus (Dussart & Defaye, 2001). Copepods can be also found in every type of habitat, including hot springs, groundwater, cave pools, glacial meltwater pools, ephemeral waterbodies, rock hollows, phytotelmata and leaf litter (Reid, 2001). Calanoida, Cyclopoida and Harpacticoida are three orders of Copepoda that together contain 7750 widespread and primarily free-living species. Calanoids are primarily planktonic, whereas cyclopoids and harpacticoids are generally associated with substrates in benthic habitats (Dussart & Defaye, 2001). As a part of the meiofauna, Copepoda may fulfil an important role, including supplying an ecosystem service, namely the consumption and decomposition of organic matter, nutrient regeneration and energy transfer to higher trophic levels (Schratzberger & Ingels, 2018). The Harpacticoida comprise the major group of benthic Copepoda, for they are typically crawlers, walkers and burrowers, thus they live in interstitial systems (Dahms & Qian, 2004). Approximately 90 % of all species of harpacticoids live in marine environments, where they play an important role in marine food webs (Kennedy & Jacoby, 1999; De Troch *et al.*, 2005). The Cyclopoida, which are generally good swimmers, actively colonize the outer layer of sediments (Dole-Olivier *et al.*, 2000). The species richness of cyclopoids in lake sediments is similar to that of harpacticoids, they commonly achieve lower abundance and biomass (Strayer, 1985), but display more rapid growth and a higher production to biomass ratio (Sarvala, 1979). Thus, the role of the truly epibenthic harpacticoids in marine environments is evidently taken by the cyclopoids in freshwater lakes. Cyclopoids make an important contribution to pelagic-benthic food web coupling due to their life history. They develop from fertilized eggs into a larval stage called nauplii followed by copepodite stages, the last of which is the adult. All these stages may prefer either a pelagic or benthic mode of life. Additionally, some cyclopoids bury themselves in sediments to enter an encysted diapause stage (Dussart & Defaye, 2001). Freshwater cyclopoid densities display marked oscillations. Several hypotheses have been proposed to explain the oscillations observed. The most compelling of these include temperature (Maier, 1989; Abdullahi, 1990), food limitation (Hansen, 1996), predation (Maier, 1998) and mate limitation (Kiørboe, 2006). Notwithstanding the fact that cyclopoids are of great importance in the benthic biotopes of freshwater ecosystems (Sarvala, 1998), most studies on the ecology of this group focus on cyclopoids living in the limnetic zone of lakes, whereas the driving forces behind the distribution of epibenthic species are as yet poorly studied. Additionally, most studies on epibenthic communities derive from the marine environment. Much less is known about the freshwater epibenthos, especially freshwater epibenthic cyclopoids have attracted little interest, considering their diverse and important roles in aquatic systems. Up to this time, this group is only well-described in Finnish lakes where their distribution and abundance is mainly impacted by lake productivity, oxygen conditions and sediment structure (reviewed in Sarvala, 1998).

Here we present a comparative study of the community structure of epibenthic Cyclopoida copepods in six eutrophic lakes located in a temperate climate. We also examine the role of environmental factors on the diversity and abundance of epibenthic cyclopoids. Our specific goal is to determine whether differences exist in communities of benthic Cyclopoidae in a group of neighbouring lakes and to assess which environmental variables influence the taxonomic composition and abundance of epibenthic cyclopoids.

MATERIALS AND METHODS

Study area

The study was carried out in six lakes (Białe Sosnowieckie, Czarne Sosnowickie, Domaszne, Dratów, Krzczeń, Skomielno) located between 51° 33’ 92"–51° 53’ 11" N and 22° 94’ 64"–23° 04’ 75" W in the Łęczyńsko-Włodawskie Lake District (Eastern Poland, Fig. 1). In 1961 the lakes were connected by a canal supplying waters rich in nutrients from agricultural runoff (Dawidek *et al.*, 2004). As a result of this supply of nutrient-rich waters from the canal, originating from the Wieprz River, all the lakes present with a eutrophic status. The lakes differ in surface area, depth and cover of submerged macrophytes (Table 1). The dimictic, deep Lake Czarne Sosnowickie (max. depth 15.6 m) is the most natural (forest catchment) whereas the other lakes are shallow (max. depth 3.1–5.2 m) and polymictic, with agricultural catchments. In Lakes Krzczeń and Domaszne, perennial blooms of toxigenic cyanobacteria occur (Pawlik-Skow-

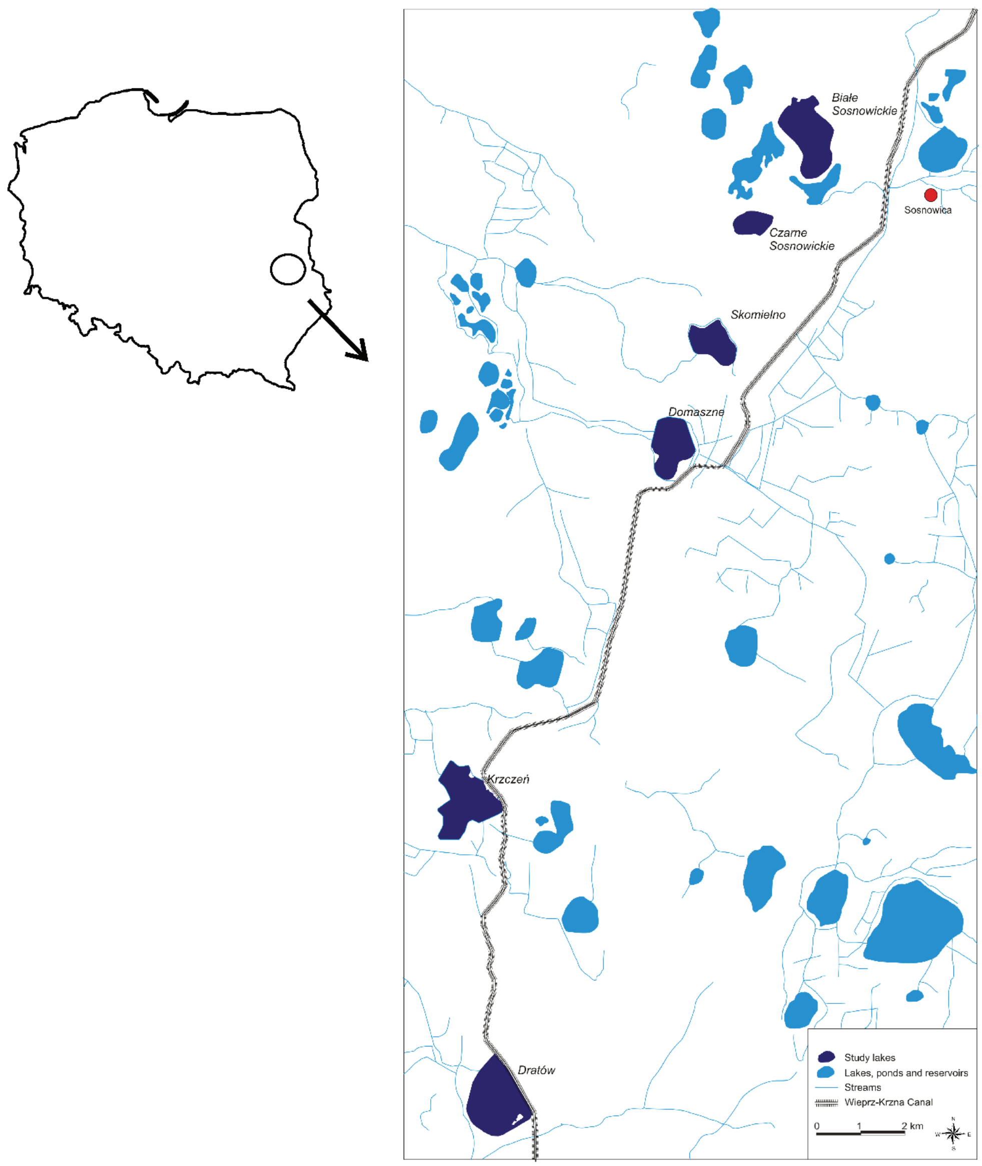

Figure 1. Study area. *Área de estudio.*

rońska & Toporowska, 2016). The lakes are systematically stocked with fry. Roach (*Rutilus rutilus*), bleak (*Alburnus alburnus*), rudd (*Scardinius erythrophthalmus*) and perch (*Perca fluviatilis*) are the dominant fish species in the lakes (Adamczuk *et al.*, 2015).

Field studies

Sediment samples were collected in spring (April), summer (July) and autumn (November) of 2014–2015. Separate samples for Copepoda analyses and chemical analyses were taken in the same area of a lake, from nine sites (three samples per site) in each lake. Samples were taken with a gravity corer (UWITEC Ltd., Australia) equipped with a 59 mm inner diameter tube. Immediately after sampling the upper 3 cm layer was separated by means of a sediment slicer and stored at 4 °C until further analysis. In the laboratory the samples were agitated in beakers with tap water and sieved to remove larger pieces of detritus. Target samples were washed and examined under a binocular microscope to collect live copepods, including larval (nauplii), juvenile (copepodites) and adult individuals. All copepods found in the sediment were non-encysted. They were transferred into vials filled with water and preserved with a few drops of acid lugol solution. Density was expressed as number of individuals per m^2 (ind/m^2). The dominance structure of cyclopoids was expressed as average percentage of the density of each species compared to the total density of cyclopoids in each lake. Species with an abundance higher than 10 % of total abundance were considered dominant.

At the same time as biological studies were conducted, selected physical and chemical parameters of lake water were measured. Transparency (SD) was estimated using a Secchi disc. Temperature, conductivity (EC), pH and dissolved oxygen (DO) were determined *in situ* with a YSI 556 MPS multiparameter probe. Other environmental variables were estimated in the laboratory: total suspended solids (TSS), surface active agents (SUR), chemical oxygen demand (COD) and biological oxygen demand (BOD) using the PASTEL UV spectrophotometer; total phosphorus (TP_w) and dissolved ortho-phosphorus ($P\text{-}PO_4$) with a Specord 40 Analityk Jena spectrophotometer (by the molybdate method after mineralization with a mixture of HNO_3 and H_2SO_4); nitrate nitrogen $N\text{-}NO_3^-$ by the sodium salicylate method and $N\text{-}NH_4$ by Kjeldah's method. For total solids (TS), water samples were evaporated in a pre-weighed vessel and dried to constant weight at 104 °C. The mass of TS was determined by difference in mass of

Table 1. Differences in morphometric characteristics, trophic status, macrophyte cover and fish management between the lakes. The lakes are sorted according to TSI values. Macrophyte cover according to: a – Sender (2012), b – Mieczan *et al.* (2016), c – Sender (2016). *Diferencias en las características morfométricas, el estado trófico, la cobertura de micrófitos y la gestión de los peces entre los lagos. Los lagos son ordenados en función de los valores de TSI. Cobertura de macrófitos de acuerdo con: a – Sender (2012), b – Mieczan* et al. *(2016), c – Sender (2016).*

	Krzczeń	Dratów	Białe Sosnowickie	Domaszne	Czarne Sosnowickie	Skomielno
Area (ha)	174	168	114.8	85.5	38.8	75
Volume (10^3 m^3)	2630	4166	2018	2208	1968	1019
Maximum depth (m)	5.1	3.2	2.7	3.1	15.6	3.5
Mean depth (m)	1.5	2.5	1.7	2.6	5.1	1.4
$TSI_{SD + TPw + chl\text{-}a}$	80	77	74	67	65	51
Submerged macrophyte cover (% of lake area)	28[b]	11[b]	7[b]	39[b]	9[c]	33[a]

the vessel. Using the values of SD, TP_W and chlorophyll-*a* (chl-*a*), a classic trophic state index for the lakes ($TSI_{SD + TP + chl\text{-}a}$) was calculated (Carlson, 1977).

Chemical analyses of sediments included the percentage of organic matter (OM), concentration of carbonates and concentration of total phosphorus (TP_S). Concentration of OM was analysed using the ignition loss method (Dean, 1974). Concentrations of carbonates from Ca and biogenic silica were determined according to Krause *et al.* (1983) and computed as percentage of dry mass of sediments. TPs was analysed using the molybdenum blue method with a Specord 40 Analityk Jena spectrophotometer.

Abundance of food resources were estimated based on biomass of total organic carbon (TOC), chl-*a*, bacteria and heterotrophic nanoflagellates (HNF). TOC was determined using the PASTEL UV spectrophotometer. Chl-*a* was determined spectrophotometrically (Specord 40 Analytik Jena) after extraction with ethanol. Concentration of chl-*a* was used as a proxy to estimate the biomass of phytoplankton (Huont *et al.*, 2007). The abundance and biomass of bacteria and HNF were determined with DAPI (4´6-diamino-2-phenylindole) (Porter & Feig, 1980). A 10 mL volume of water was preserved in formaldehyde to a final concentration of 2 % and kept in darkness at 4 °C. Preparations were made within 24 h of sampling. Subsamples of 2 mL were condensed on polycarbonate filters (0.2 µm pore size) dyed with Irgalan black and enumerated using an epifluorescence microscope. The biomass of bacteria and HNF was estimated by assuming geometric shapes and converting to carbon using the following conversion factor: 1 $\mu m^3 = 5.6 \times 10^{-7}$ mgC (Gilbert *et al.*, 1998). Predatory pressure on Copepoda, expressed as the biomass of omnivorous fish in each lake, was calculated using data from Adamczuk *et al.* (2015).

Statistical analysis

Differences in species number and density of cyclopoids among lakes and seasons were

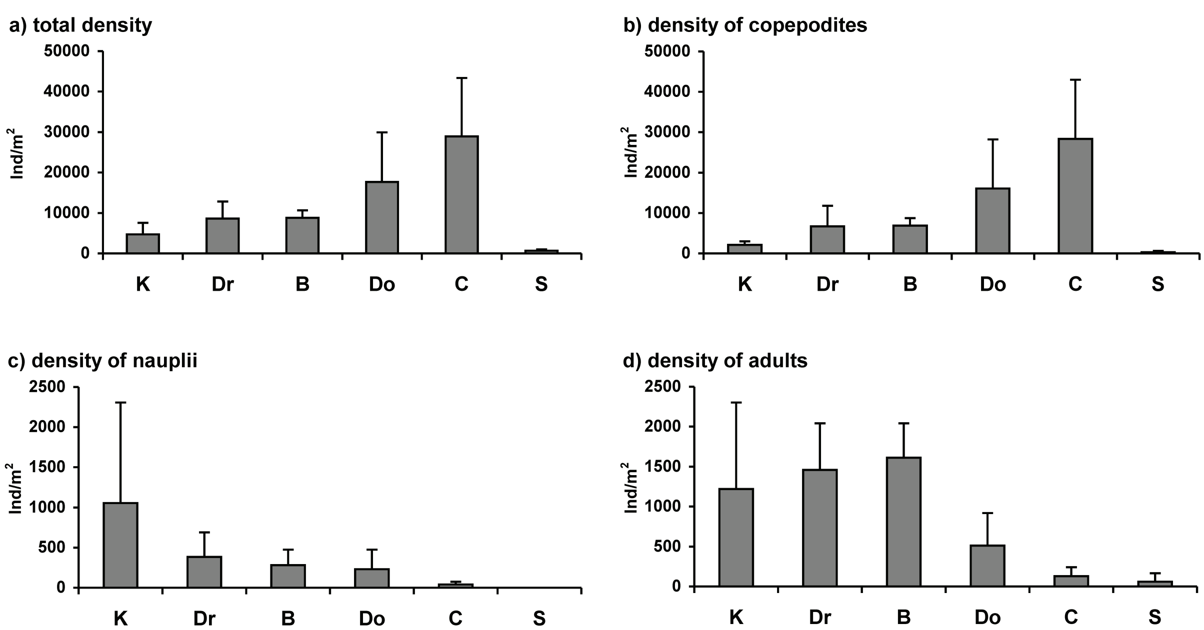

Figure 2. Density (± standard deviation) of epibenthic Cyclopoida in the studied lakes. Abbreviations: K – Lake Krzczeń, Dr – Lake Dratów, B – Lake Białe Sosnowickie, Do – Lake Domaszne, C – Lake Czarne Sosnowickie, S – Lake Skomielno. *Densidad (± desviación estándar) de la comunidad epibentónica de Cyclopoida en los lagos estudiados. K – Lake Krzczeń, Dr – Lake Dratów, B – Lake Białe Sosnowickie, Do – Lake Domaszne, C – Lake Czarne Sosnowickie, S – Lake Skomielno.*

analysed using a series of two-way analysis of variance (ANOVA) (factor 1: lake; factor 2: season; factor 3: interaction lake x season). Differences in the physical and chemical parameters of water samples (14 variables: SD; pH; temperature; EC; concentration of DO; TS; TSS; SUR; TP_W; $N\text{-}NO_3$; $N\text{-}NH_4$; $P\text{-}PO_4$; COD; BOD) and potential food abundance (TOC; chl-*a*; bacteria; HNF) were also analysed using a two-way ANOVA. As the season is too short to display changes in TP_S, OM or carbonates in lake sediments, or the biomass of potential predators (omnivorous fish), these variables were analysed using a one-way ANOVA (factor: lake). Post hoc comparisons (Tukey HSD) among the lakes were performed. All the analysis and statistical tests described above were carried out using the Statsoft Statistica package for Windows. Ordination techniques were used to describe the relationships between the abundance of particular species of epibenthic cyclopoids and environmental variables. The indirect multivariate method, Detrended Correspondence Analysis, was used to measure and illustrate gradients of Cyclopoidae. Due to the length of the gradient with a range > 4 standard deviations (SD), we used Canonical Correspondence Analysis (CCA) to explore the relationships between the abundance of species of Cyclopoida and the environmental variables studied. Before running the analyses, we evaluated correlation coefficients among environmental variables and employed forward selection to detect and remove from the analysis variables that were highly correlated. We found two groups of variables correlating with each other. The first group comprised TP_W, TP_S and OM; the second group comprised EC and TS. Thus TP_W, TP_S and EC were removed from the analysis. CCA analysis was performed on log-transformed data. A Monte Carlo analysis with 499 permutations was used to determine the most important variables ($P < 0.05$). The proportion of variance explained by each environmental variable was quantified using variance partitioning. The ordination analysis was performed in CANOCO 4.5 software for Windows (ter Braak & Šmilauer, 2002).

RESULTS

Structure of benthic Cyclopoida

The number of benthic species of Cyclopoida ranged from two in Lake Czarne Sosnowickie to nine in Lake Dratów. All species found belonged to the Cyclopidae family and were represented mainly by those from the genera *Acanthocyclops* Kiefer, 1927, *Diacyclops* Kiefer, 1927, *Eucyclops* Claus, 1893, *Macrocyclops* Claus, 1893, *Microcyclops* Claus, 1893, *Megacyclops* Kiefer, 1927 and *Paracyclops* Claus, 1893.

The density of cyclopoids ranged from 386 ind/m^2 in Lake Skomielno to 28 526 ind/m^2 in Lake Czarne Sosnowickie (ANOVA, $F_{1,5} = 8.9$, $P < 0.05$) (Fig. 2a). Juvenile individuals (copepodites) constituted from 46 % (Lake Skomielno) to 98 % (Lake Czarne Sosnowickie) of total density of cyclopoids (Fig. 2b) and their densities differed significantly among lakes (ANOVA, $F_{1,5} = 5.1$, $P < 0.05$). Larval stages of cyclopoids (nauplii) constituted between 0 % (Lake Skomielno) and 22 % (Lake Krzczeń) of total cyclopoid density but densities did not differ significantly among lakes (Fig. 2c). The density of adult stages of epibenthic cyclopoids ranged from 183 ind/m^2 in Lake Skomielno to 4841 ind/m^2 in Lake Białe Sosnowickie (ANOVA, $F_{1,5} = 4.5$, $P < 0.05$) (Fig. 2d). Differences in the abundance of nauplii, copepodites and adult cyclopoids both among seasons and seasons x lakes were statistically insignificant. Analysis of the structure of dominance revealed that *Eucyclops serrulatus* (Fisher, 1851), *Diacyclops bicuspidatus* (Claus, 1857) and *E. macruroides* (Lilljeborg, 1901) were most commonly found to be dominant in the lakes. Another three species had densities of above 10 % of total density of benthic cyclopoids, including *E. macrurus* (Sars, 1863), *D. nanus* (Sars, 1863) and *Paracyclops fimbriatus* (Fisher, 1853). Lake Skomielno differed from the other lakes in terms of structure of dominance since *Megacyclops latipes* (Lowndes, 1927) and *M. viridis* (Jurine, 1820) were dominant in this lake (Table 2).

Environmental variables

The lakes differed significantly from each other

Table 2. Structure of dominance of epibenthic Cyclopoida in the studied lakes. *Estructura de dominio de la comunidad de copépodos epibentónicos del género Cyclopoida.*

	Krzczeń	Dratów	Białe Sosnowickie	Domaszne	Czarne Sosnowickie	Skomielno
Acanthocyclops einslei (Mirabdulalyev and Defaye, 2004)	2.1%					
Cyclops abyssorum (G. O. Sars, 1863)	2.5%					
Cyclops scutifer (G. O. Sars, 1863)	5.3%					
Cyclops vicinus (Uljanin, 1857)			1.3%	6.3%		
Diacyclops bicuspidatus (Claus, 1857)	2.9%	17%	23%	33%		
Diacyclops disjunctus (Thallwitz, 1927)				5.7%		
Diacyclops nanus (G. O. Sars, 1863)					66.6%	
Eucyclops macruroides (Lilljeborg, 1901)	78.4%	21.3%	19.4%	26.7%		
Eucyclops macrurus (G. O. Sars, 1863)	3.1%		11.1%			
Eucyclops serrulatus (Fisher, 1851)		34%	45.2%	7.1%	33.4%	
Macrocyclops albidus (Jurine, 1820)		2.1%				
Megacyclops gigas (Claus, 1857)	5.7%	2.5%		6.7%		
Megacyclops latipes (Lowndes, 1927)		2%				33.5%
Megacyclops viridis (Jurine, 1820)						66.5%
Metacyclops minutus (Claus, 1863)		2.2%				
Microcyclops rubellus (Lilljeborg, 1901)		12.8%				
Paracyclops fimbriatus (Fisher, 1853)				14.5%		
Paracyclops imminutus (Kiefer, 1929)		6.1%				

in most physical and chemical parameters, including SD, TS, TSS, SUR, $N\text{-}NH_4$, COD, BOD (ANOVA, $F_{1,5}$ = 9.1–108.7, $P < 0.01$) and DO, TP_w (ANOVA, $F_{1,5}$ = 3.2–3.5, $P < 0.05$); Tukey HSD post hoc comparisons indicated Lake Czarne was significantly different in terms of the majority of water parameters (Table 3A). Temperature was the sole parameter that differed significantly among seasons (ANOVA, $F_{1,2} = 83.6$, $P < 0.01$). Lake Krzczeń had significantly higher concentration of OM in sediments (ANOVA, $F_{1,5} = 46.8$, $P < 0.01$), whereas the concentration of carbonates in sediments was significantly higher in Lake Domaszne (ANOVA, $F_{1,5} = 11.5$, $P < 0.01$) (Table 3B). Among potential food sources, concentration of TOC was significantly higher in Lake Czarne Sosnowickie (ANOVA, $F_{1,5} = 11.1$, $P < 0.01$), bacterial biomass was the highest in Lake Dratów (ANOVA, $F_{1,5} = 2.1$, $P < 0.05$) and chl-*a* exhibited the highest concentration in Lake Krzczeń (ANOVA, $F_{1,5} = 48.4$, $P < 0.01$) (Table 4A). The biomass of potential predators was highest in Lake Białe Sosnowickie and lowest in Lake Czarne Sosnowickie (ANOVA, $F_{1,5} = 8.9$, $P < 0.01$). Tukey HSD post hoc comparison tests showed that both these lakes differed significantly from the other lakes (Table 4B).

Epibenthic Cyclopoida versus environmental variables

The CCA analysis showed that axis 1 and axis 2 accounted for 30.1 % and 24.6 %, respectively, of variability in the abundance of epibenthic Cyclopoida. CCA showed that feeding conditions were of highest significance, namely biomass of bacteria ($F = 1.85$; $P = 0.013$) and OM in sediments

($F = 1.3$, $P = 0.023$), which explained 28 % and 9 % of total variance in epibenthic cyclopoid abundance, respectively. Among physical and chemical variables, temperature ($F = 1.5$, $P = 0.032$) and TS ($F = 1.15$, $P = 0.038$) also seemed to be important, as they explained from 4 % (TS) to 7 % (temperature) of total variance in benthic cyclopoid abundance. TS correlated with the abundance of *Eucyclops* and *Diacyclops* species, as well as *M. latipes* and *M. viridis*. OM in sediments correlated

Table 3. Mean values (± standard deviation) of environmental parameters of water in the studied lakes. Different letters indicate statistically significant differences between lakes (Tukey HSD after one-way ANOVA). *Valores medios (± desviación estándar) de los parámetros ambientales del agua en los lagos estudiados. Las letras diferentes indican diferencias en la significancia estadística entre lagos (Tukey HSD después de ANOVA de una vía).*

	Krzczeń	Dratów	Białe Sosnowickie	Domaszne	Czarne Sosnowickie	Skomielno	*F*	*P*
A) Lake water	Range of mean values ± standard deviation among seasons						ANOVA	
Transparency (m)	^{A} 0.42 ± 0.25	^{A}0.47 ± 0.25	^{A}0.53 ± 0.2	^{A}0.72 ± 0.19	^{B} 1.1 ± 0.25	^{C}3.13 ± 0.32	108.7	< 0.01
pH	8.6 ± 0.1	8.5 ± 0.3	8.5 ± 0.6	8.5 ± 0.2	8 ± 0.4	8.3 ± 0.2		
Temperature (°C)	14.5 ± 4.7	14.5 ± 4.8	14.7 ± 5.7	14.8 ± 4.9	14.9 ± 4.8	14.9 ± 5.3		
EC (µS/cm)	263.7 ± 37.5	303.7 ± 56.6	388 ± 8.7	351 ± 4.4	318 ± 23.5	274.7 ± 31.6		
DO (mg/dm^3)	^{A}12.1 ± 2.8	^{AB}11.2 ± 2.8	^{A}13 ± 2.2	^{AB}50.3 ± 69.8	^{B} 9.1 ± 2.5	^{AB}10.5 ± 1.6	3.5	< 0.05
TS (mg/dm^3)	^{A} 37.4 ± 26.2	^{AB}26 ± 18.8	^{B}19.8 ± 12.2	^{B} 8.9 ± 1.3	^{B}4.2 ± 1.2	^{B}1.3 ± 0.7	9.1	< 0.01
TSS (mg/dm^3)	^{A}29 ± 15.3	^{A}21.8 ± 11.6	^{A}23.7 ± 9.6	^{A}9.4 ± 3.3	^{B} 108.7 ± 20.7	^{A}2.6 ± 0.1	29.5	< 0.01
SUR (mg/dm^3)	^{A}2.7 ± 0.2	^{A}3.1 ± 0.3	^{A}2.8 ± 0.3	^{A}1.9 ± 0.1	^{B} 13.9 ± 2.2	^{A}1.5 ± 0.1	2.5	< 0.01
TP_w (mg/dm^3)	0.216 ± 0.116	^{C} 0.144 ± 0.095	^{a} 0.130 ± 0.09	^{B} 0.046 ± 0.034	^{aBCd} 0.188 ± 0.135	^{d} 0.065 ±0.028	3.2	< 0.05
N-NO_3 (mg/dm^3)	0.101 ± 0.103	0.111 ± 0.112	0.170 ± 0.090	0.137 ± 0.068	0.393 ± 0.264	0.212 ± 0.283		
N-NH_4 (mg/dm^3)	^{A}0.096 ± 0.011	^{A}0.137 ± 0.039	^{A}0.117 ± 0.021	^{A}0.072 ± 0.005	^{B} 0.552 ± 0.151	^{A}0.106 ± 0.012	30.5	< 0.01
P-PO_4 (mg/dm^3)	0.03 ± 0.014	0.042 ± 0.03	0.021 ± 0.03	0.046 ± 0.024	0.06 ± 0.057	0.03 ± 0.022		
COD (mg O_2/dm^3)	^{A}15.1 ± 2.1	^{A}15.8 ± 2.4	^{A}13.1 ± 2.4	^{A}10.7 ± 1.3	^{B}39.7 ± 4	^{A}12.8 ± 1.1	18.5	< 0.01
BOD (mg O_2/dm^3)	^{A}8.1 ± 0.9	^{A}8.7 ± 1.2	^{A}7.2 ± 1.2	^{A}5.8 ± 0.6	^{B} 24.2 ± 2.7	^{A}6.7 ± 0.4	37.6	< 0.01
B) Lake sediments	Range of mean values ± standard deviation							
TP_s (g/kg dry mass)	4.389 ± 1.147	3.958 ± 2.981	0.919 ± 0.678	1.069 ± 0.274	2.918 ± 2.096	1.154 ± 0.434		
OM (% dry mass)	^{A}59.3 ± 8.4	^{A}22.7 ± 3.5	^{B}20.1 ± 0.8	^{A}14.2 ± 1.2	^{C}33.4 ± 1.6	^{D}38.6 ± 4.7	46.8	< 0.01
carbonates (% dry mass)	^{AC}15 ± 10.5	^{C}21.1 ± 16.8	^{AC}52.6 ± 1.3	^{B}58.8 ± 1.4	^{AC}29.1 ±1.5	^{BC}41.5 ± 7.1	11.5	< 0.01

Table 4. Mean abundances (± standard deviation) of potential food sources and predators. Different letters indicate statistically significant differences between lakes (Tukey HSD after one-way ANOVA). WPUE – weight per unit effort (12 hours). *Abundancias medias (± desviación estándar) de las fuentes potenciales de alimento y de predadores. Las letras diferentes indican diferencias en la significancia estadística entre lagos (Tukey HSD después de ANOVA de una vía).*

	Krzczeń	Dratów	Białe Sosnowickie	Domaszne	Czarne Sosnowickie	Skomielno	*F*	*P*
A) Potential food sources	Range of mean values ± standard deviation among seasons						ANOVA	
TOC (mg/dm^3)	^{A}5.8 ± 0.7	^{A}6.2 ± 0.8	^{A}5.3 ± 0.9	^{A}4.1 ± 0.4	^{B}18.9 ± 3.1	^{A}4.6 ± 0.3	48.4	< 0.01
chl-*a* (µg/dm^3)	^{A}149.7 ± 88.1	^{B}74.1 ± 49.7	^{BC}55 ± 17.4	^{BC}45.7 ± 30.1	^{BC}18.4 ± 3.7	^{C}4.29 ± 1.1	11.1	< 0.01
bacteria (mg/dm^3)	^{A} 2 ± 1	^{B}3.7 ± 2.4	^{A} 3.2 ± 1.2	^{A} 1.4 ± 0.6	^{A} 1.8 ± 1.5	^{A} 1.3 ± 1.1	2.1	< 0.05
HNF (ng/ml)	47.9 ± 16.8	40.3 ± 27.1	56.1 ± 27.1	57.4 ± 34	38.8 ± 26.1	42.3 ± 21.2		
B) Potential predators	Range of mean values ± standard deviation among samples						ANOVA	
total biomass (kg WPUE)	^{AC}2.4 ± 1.1	^{A}3.6 ± 1.1	^{B}5.3 ± 2.6	^{A}2.7 ± 1	^{C}0.25 ± 0.1	^{AC}1.7 ± 1.4	8.9	< 0.01

positively with *Acanthocyclops*, *Paracyclops* and *Diacyclops disjunctus* Thallwitz, 1927. Biomass of bacteria seemed to be beneficial mainly for the development of *M. albidus*, *Metacyclops minutus* (Claus, 1863), *Paracyclops imminutus* (Kiefer, 1929) and *Microcyclops rubellus* (Lilljeborg, 1901). The locations of larval and juvenile stages of cyclopoids as well as *Megacyclops gigas* (Claus, 1857) on the ordination plot suggest none of the environmental variables included in the analysis had a direct impact on their density (Fig. 3).

DISCUSSION

According to the literature, the species richness of epibenthic copepods in lake sediments ranges between 3 and 12 species (Strayer, 1985). We only found two species in Lake Czarne Sosnowickie. This lake is polymictic and much deeper than the other lakes, it also differs from the other lakes in environmental variables. In the remaining, shallower lakes the number of species ranged from three to nine. Interestingly, a unique group of epibenthic cyclopoids was found in each lake. In Lake Skomielno large carnivorous cyclopoids were dominant whereas in the other lakes medium-sized and small cyclopoids were more common. Despite high densities of adult cyclopoids, larval (nauplii) and juvenile (copepodites) developmental stages were most numerous in all the lakes. The density of nauplii is usually higher or similar to the density of copepodites in planktonic species of Cyclopoida (Kobari & Ban, 1998; Ferrari & Dahms, 2007). However, remarkably, we found that the density of copepodites in sediments was several hundred times higher than the density of nauplii. Additionally, in some periods of sampling we did not find nauplii in the samples taken from Lakes Czarne Sosnowickie, Domaszne, Dratów and Krzczeń and we did not record nauplii stages in Lake Skomielno during the whole period of study. High densities of epibenthic cyclopoids may partly result from diapause in the sediments of an advanced copepodite instar of limnetic species (Hansen & Hairston, 1998). Our results also indicate that

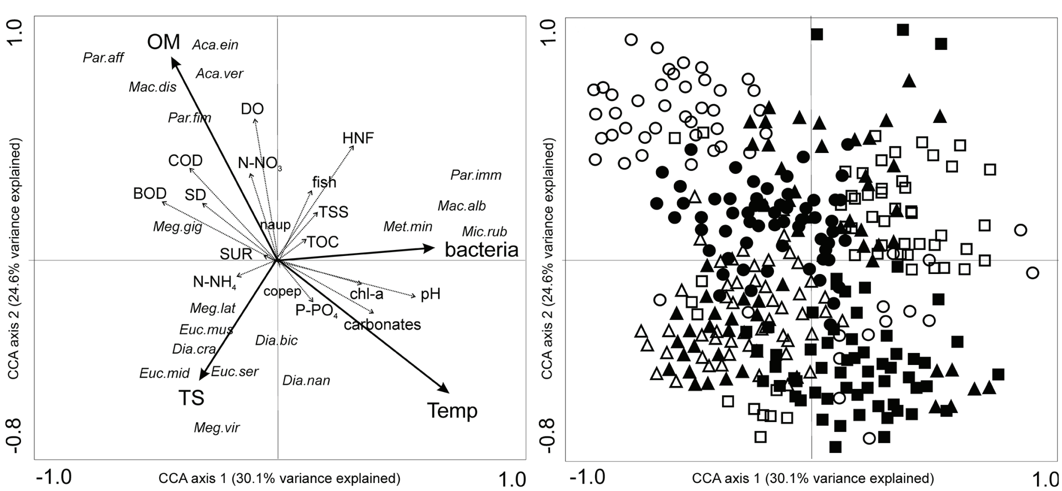

Figure 3. CCA analysis biplot showing distribution of epibenthic Cyclopoida in relation to environmental variables. Solid arrows indicate variables significant at $P < 0.05$ in Monte Carlo Permutation Test. Species codes: *Aca.ein – Acanthocyclops einslei, Aca.ver – Acanthocyclops vernalis,* copep – copepodites, *Dia.bic – Diacyclops bicuspidatus, Dia.cras – Diacyclops crassicaudis, Dia.nan – Diacyclops nanus, Euc.mus – Eucyclops macrurus, Euc.mid – Eucyclops macruroides, Euc.ser – Eucyclops serulatus, Mac.alb – Macrocyclops albidus; Dia.dis – Diacyclops disjunctus, Meg.gig – Megacyclops gigas, Meg.lat – Megacyclops latipes, Meg.vir – Megacyclops viridis, Met.min – Metacyclops minutus, Mic.rub – Microcyclops rubellus,* naup – nauplii, *Par.aff – Paracyclops affinis, Par.fim – Paracyclops fimbriatus, Par.imm – Paracyclops imminutus*. Sample codes: ○ Lake Krzczeń, ● Lake Dratów, □ Lake Białe, ■ Lake Domaszne, Δ Lake Czarne Sosnowickie, ▲Lake Skomielno. *Biplot del análisis análisis de correspondencia en el que se muestra la distribución de copépodos epibentónicos del género Cyclopoida con relación a las variables ambientales. Las flechas continuas indican las variables significativas a* P *< 0.05 con la prueba de permutación de Monte Carlo.*

larval stages of epibenthic cyclopoids may conduct a planktonic mode of life, whereas copepodites may be more bound to a substrate. The lack of larval stages in Lake Skomielno may result from a species structure dominated by carnivorous species that exhibit cannibalism and attack other copepods, including larval and juvenile stages (Dussart & Defaye, 2001; Hwang & Martens, 2011).

In Finnish lakes the density of epibenthic cyclopoids vary between 1000 and 13 000 ind/m^2 (Särkkä, 1995; Sarvala, 1986) and their abundance and diversity are negatively correlated with the trophic state of lakes. Experimental studies on the effect of nutrient enrichment on the abundance of benthic organisms reveal that epibenthic copepods reach a maximum at intermediate nutrient levels (Ristau *et al.*, 2012). In the lakes studied the density of adult individuals of epibenthic cyclopoids ranged from 183 to 4841 ind/m^2 and, with larval and juvenile stages included, reached nearly 30 000 ind/m^2. Additionally, a higher number of species of epibenthic cyclopoids settled sediments in lakes with a TSI close to hypereutrophy. Discrepancies in the observed relations between the diversity and abundance of epibenthic cyclopoids and trophic status of lakes may suggest that trophy may not be the primary factor influencing the distribution of this group.

Variation partitioning based on CCA revealed that environmental factors played important roles in structuring the aquatic communities by explaining 54.7 % of their variation. Among all the factors measured, the biomass of bacteria, organic matter (OM), total solids (TS) and temperature were the variables that significantly influenced the density of epibenthic species. Concentration of OM, TS and biomass of bacteria were probably linked to the trophodynamics of epibenthic cyclopoids. There is a little exact information on the feeding ecology of the various epibenthic cyclopoids. In the literature, *Megacyclops* species are classified as carnivores that feed on other copepods and various other benthic species and may even attack fish larvae (Fryer, 1957; Hartig & Jude, 1988). *Diacyclops* and *Acanthocyclops* are primarily carnivorous (Roche, 1990; LeBlanc *et al.*, 1997; Munschial *et al.*, 2008), *Eucyclops* feed on detritus, phytoplankton and small zooplankton (Monakov, 2003), whereas *Paracyclops* are detritus feeders and scavengers (Karaytug, 1999; Dussart & Defaye, 2001). The density of representatives of these genera correlated either to concentrations of OM or TS. OM and TS may indicate the amount of detrital particles in the studied lakes. It may suggest that, despite apparent differences in feeding preferences, all these species are able to use detrital particles as sources of nourishment and/or may benefit from organic and inorganic matter serving as a medium for bacterial development (Weiss *et al.*, 1996). Some studies have reported that more than half of the bacterioplankton in aquatic ecosystems can be attached to particulate matter (Riemann *et al.*, 2000; Carrias *et al.*, 2002). Thus, such particles could be an important non-algal food source for epibenthic cyclopoids, since phytoplankton alone do not satisfy all of the nutritional requirements of cyclopoids (Marzolf, 1990; Adrian & Frost, 1993). CCA analysis indicated that the density of a group of epibenthic cyclopoids was strongly impacted by the biomass of bacteria. This agrees with other reports revealing that some cyclopoids are omnivorous but selective in their feeding and their diet can abound in bacteria and detritus (Desvilletes *et al.*, 1997). Notwithstanding, a bulk of species showed weak correlations with the studied trophic variables. It may result in part from the fact that the considered food sources did not allow for Rotifera. That group of preys is an important food source in the diet of Copepoda (Brandl, 2005; Meyer *et al.*, 2017), thus it may significantly influence abundance and distribution of epibenthic cyclopoids. Surprisingly, we did not find correlations between the density of epibenthic cyclopoids and abundance of omnivorous fish. Larger epibenthic cyclopoids from the *Macrocyclops* and *Megacyclops* genera often form a considerable proportion of the diet of omnivorous fish. (Donald *et al.*, 2001; Knapp *et al.*, 2001). Our results suggest that the differences in densities of epibenthic species among lakes were more readily explained in terms of the distribution of food than of predation. The abundance of epibenthic cyclopoids was also influenced by temperature; a variable that is regarded as one of the most important factors explaining oscillations in copepod populations, since temperature controls the timing of reproduction and ontogenic development (Dell *et al.*, 2011).

CONCLUSIONS

Our study, which was conducted in a group of eutrophic lakes, revealed great variability in species structure and density of epibenthic Cyclopoida. We found that temperature, amount of bacterioplankton, organic matter stored in sediments and total solids had significant impact on the diversity and abundance of epibenthic cyclopoids. As the above variables are directly and indirectly related to the trophodynamics of cyclopoids, feeding conditions seem to be the most significant factor impacting the distribution of epibenthic Cyclopoida. The relationship between quantity of food and structure of epibenthic cyclopoids suggests that this group plays an important role in the food web. By combining knowledge about the distribution of this group in eutrophic lakes with data relating to their environmental conditions, we believe that our study adds to field studies on the ecology of epibenthic Cyclopoida. However, further detailed studies are required in order to learn more about the structure and role of epibenthic species and analyse the variables that modulate them in order to predict future changes in a world increasingly impacted by anthropogenic and climatic changes.

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