1   # The response of zooplankton network indicators to winter
2   # geothermal water warming in shallow reservoirs

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28 **Abstract.** The increase in the temperature of surface waters has been studied for many decades,

29 and various methods have been used to predict the most probable scenarios. The present study

30 was undertaken to test the following research hypothesis: the warming of surface waters in

31 winter (caused by the inflow of geothermal water) significantly modifies the dynamics,

32 significance and type of relationships in zooplankton communities colonizing mine pit

33 reservoirs. These relationships were examined with the use of network graph analysis for three

34 thermal variants: warm winters (WW), moderate winters (MW), and cold winters (CW). The

35 CW network was most cohesive, and it was controlled by eutrophic Rotifera (*Trichocerca*

36 *pusilla, Pompholyx sulcata, Keratella tecta*) and Copepoda, with an equivalent number of

37 positive and negative interspecific relationships. An increase in water temperature in winter led

38 to a decrease in primary production, a decrease in the values of centrality attributes in MW and

39 WW networks, and an increase in the significance of species that communicated with the

40 highest number of species across sub-networks. Moderate winters increased the role of

41 ecologically and functionally diverse species, which contributed to the heterogeneity of the MW

42 network. The WW network was least cohesive, and it was controlled by small-sized

43 psammophilous and phytophilous rotifers (*Monommata maculata*, *Cephalodella* spp.) and

44 littoral cladocerans *Alona* spp. Adults Copepoda were not identified in the network, and the

45 significance of antagonistic relationships decreased, which indicates that the WW network

46 structure was weak and unstable.

47 The results of the impact of warm winters and the flattening of the annual water temperature

48 amplitude on the zooplankton network may be a projection of the expected global changes.

49 These effects are particularly important in water reservoirs exposed to anthropogenic pressure

50 and where changes in the thermal regime can influence future ecosystem services.

51

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1 Introduction

Research on variations in water temperature and their impact on the structure, stability and functions of ecosystems in an era of global warming has been growing in importance in recent years. Temperature is one of the key factors that regulate life processes in the aquatic environment, and it affects gas exchange, saturation levels, and the rates of nutrient and organic matter cycling in water (Lampert and Sommer, 1999, Wrzesiński et al., 2015). Water temperature gradients lead to changes in biocenosis composition and the structure of the food chain (Lewandowska et al., 2014 a; Gutierrez, 2016). In the temperate climate, water bodies are affected by seasonal changes in air temperature and insolation which create diverse thermal regimes (Lampert and Sommer, 1999). Shallow water bodies are particularly susceptible to atmospheric fluctuations because air temperature and the mechanical effects of wind induce frequent changes in thermic and oxygen profiles (Williamson et al., 2009).

The fluctuations and/or permanent changes in the thermal profile of surface waters have been largely associated with the discharge of industrial cooling water (Capuzzo, 1980; Ejsmont-Karabin and Węgleńska, 1988; Zargar and Ghosh, 2006; Vandysh, 2009; Ejsmont-Karabin, 2011). The effects of local geothermal sources have been less frequently investigated, mostly focusing on their local use for therapeutic purposes (balneotherapy) or as tourist attractions (Samsudin et al., 1997; Beriatos and Papageorgiou, 2009; Boekstein, 2014; Menkshi et al., 2019). There is a general scarcity of research on the hydrobiological impact of geothermal water that reaches water bodies, and the few available studies have focused mostly on the tropical regions (Sellami et al., 2009; Dash et al., 2012; Baksir et al., 2022). In recent decades, climatic factors associated with a rise in global temperature, in particular in northern latitudes, have been recognized as an additional driver of changes in the thermal profile of surface water bodies (EEA, 2014; Ptak et al., 2018; IPCC, 2021). A growing temperature gradient can significantly affect the structure and functioning of aquatic biocenoses in the temperate climate, and the

78   sensitivity of aquatic organisms results from evolutionary adaptations to specific thermal

79   regimes (Moore et al., 1996; Richardson, 2008; Wagner and Adrian, 2009; Evans et al., 2020).

80   Zooplankton support important processes in aquatic ecosystems. They play the key role

81   in the food web by integrating primary producers with consumers at higher trophic levels (fish)

82   (Lampert, 1997; Sotton et al., 2014; St-Gelais, 2017). Planktonic animals are the main link in

83   microbial carbon cycling (Bowszys et al., 2020), and they are sensitive bioindicators of changes

84   in abiotic factors (Goździejewska et al., 2016; Zhou et al., 2018; Wang et al., 2021). Due to

85   their taxonomic and functional diversity, different ecological strategies, phylogenetic

86   distinctness, as well as passive and broad dispersion in the environment, zooplankton are highly

87   useful for the development of ecosystem models/forecasts, including in the context of global

88   warming (Richardson, 2008; Chou, 2012; Arlic, et al. 2013; Feitosa et al., 2019; Kruk et al.,

89   2020, 2021; Goździejewska and Kruk 2022). Zooplankton respond directly to water

90   temperature at the physiological (by regulating metabolic, growth and development processes)

91   (Gillooly, 2000; Lewandowska et al., 2014 b) and behavioral level (changes in distribution,

92   population size, species composition and phenology) (Ejsmont-Karabin and Wągleńska, 1988;

93   Carter and Schindler, 2012; Ejsmont-Karabin et al., 2020). In turn, the water temperature

94   indirectly affects the zooplankton communities by determining the availability and quality of

95   food resources (mainly phytoplankton) and the intensity of fish predation (Evans et al., 2020;

96   Wang et al., 2021).

97   Previous research has demonstrated that an increase in mean seasonal/annual water

98   temperature induces similar responses in freshwater zooplankton to accelerated eutrophication,

99   and it involves an increase in total density and biomass, changes in species composition

100   (Williamson et al., 2002; Visconti, 2008; Vandysh, 2009; Arlic et al., 2013), elimination of

101   seasonal succession, including a decrease in the proportion of cold-water species in spring

102   rotifer communities (Ejsmont- Karabin et al., 2020), an increase in the proportion of Copepoda

103   larvae, and accelerated growth of crustaceans characterized by small body size/low biomass

104   (Daufresne et al., 2009; Gutierrez, 2016; Evans et al., 2020; Zhou, 2020). Seasonal shifting

105   caused by, among others, early water warming in spring speeds up the development of

106   thermophilic species and often disrupts their natural life cycle (Edwards and Richardson, 2004;

107   Thackeray et al., 2008; Carter and Schindler, 2012). Particular attention has been paid to

108   phenological changes in temperate ecosystems because the date on which temperatures begin

109   to increase determines reproductive success, emergence from resting stages, generation time,

110   and food availability (Adrian et al., 2006; Costello et al., 2006; Lewandowska et al., 2014 b).

111   Therefore, species-specific responses to changes in the thermal regime are directly reflected by

112   the taxonomic structure and functional attributes of zooplankton communities (Costello et al.,

113   2006; Wagner and Adrian, 2011; Evans et al., 2020). These factors affect the organization of

114   interspecific relationships in zooplankton networks, which involve mostly competition and

115   predation, and they influence successive trophic levels (Hart, 1988; Gliwicz and Pijanowska,

116   1989; Carter et al., 2017). An analysis of the interactions between changing temperatures and

117   the attributes of zooplankton communities provides valuable information for evaluating the

118   condition of aquatic ecosystems and predicting future changes.

119   This study proposes a new, structural approach to describing zooplankton's responses

120   to water temperature. Interspecific interactions were examined with the use of the network

121   graph analysis. A network graph model supports the identification and assessment of

122   relationships between species, based on mutualism or neutral coexistence of species in

123   ecological guilds (positive mathematical interactions) or limitation (negative correlations)

124   resulting from predation or competition (Allesina et al., 2005, D'Alelio et al., 2016, Kruk and

125   Paturej, 2020; Goździejewska and Kruk, 2022).

126   Zooplankton were sampled from three artificial reservoirs in the Bełchatów-Szczerców

127   coal strip mine (central Poland) that are supplied with water from various depths, including

128   from geothermal sources. As a result, feedwater differs in temperature. In the studied geological

129   region, the availability of geothermal water is determined by Early Jurassic deposits, where the

130   water table has a stable temperature of ~40-50 °C (Jasnos et al., 2012). As a result, the studied

131   reservoirs differ significantly in mean annual temperature and the annual temperature gradient,

132   in particular in winter. The structures of plankton communities could be compared *in situ* across

133   various thermal conditions, because the examined ecosystems have similar limnological and

134   hydrological parameters and are used in a controlled manner. Zooplankton networks were

135   analyzed between 2014 and 2016 based on the biomass parameters of crustacean, rotifer, and

136   protozoan species. Based on Krebs (2009), we assumed that positive interactions between two

137   taxa are correlated with an increase in their biomass as the effect of consumer guilds, where

138   independent species share resources. In turn, negative interactions between species (their

139   biomass) are indicative of grazing on phytoplankton, predation or interference competition.

140   We hypothesized that water temperature gradient considerably affects food availability,

141   thus influencing the growth and competitive equilibrium of zooplankton species, i.e. the

142   significance of individual taxa and their interactions that determine network cohesion. We

143   assumed that the significance and strength of the interactions between zooplankton species,

144   involving an equal number of positive and antagonistic biocenotic relationships, should be

145   highest in unmodified thermal regimes (cold winters), where zooplankton taxa should form a

146   cohesive central network. In turn, higher water temperatures in winter and the flattening of the

147   annual temperature gradient should be correlated with network decentralization and

148   fragmentation, and it should weaken the interactions between zooplankton species, and the role

149   of crustaceans.

150   The examined reservoirs were created more than 20 years ago, and they are supplied

151   with water with relatively stable physical and chemical parameters (including temperature). The

152   above implies that feedwater influences planktonic biocenoses by acting as a permanent

153   environmental filter, rather than a temporary disturbance. Therefore, the extent to which

154   zooplankton networks are influenced by the water temperature gradient in the compared

155   reservoirs should be examined, and the results can be used to predict changes in aquatic

156   biocenoses resulting from surface water warming under the influence of global climate change.

157   Global warming will affect not only mean temperatures, but it will also increase the frequency,

158   intensity and duration of warm spells, which is why the impact of thermal variations on the

159   structure, stability, and functions of ecological communities is an important consideration

160   (Tuck and Romanuk, 2012, EEA, 2014). A better understanding of the responses of

161   zooplankton communities to long-term environmental changes is vital for predicting the

162   responses of freshwater ecosystems to global climate change.

163

2 Material and methods

2.1 Study area

166   The study was conducted in three artificial reservoirs (CH1, PN, WI) located in the vicinity of

167   the Bełchatów brown coal strip mine in Central Poland (51°24′43.6″N; 19°26′32.9″E). The

168   reservoirs act as dewatering ponds for the open-pit coal mines in Bełchatów and Szczerców

169   (Fig. 1). Their main function is to reduce suspended matter through sedimentation

170   (Goździejewska et al., 2018, 2019). These flow-through reservoirs (with an estimated retention

171   time of 16 h) have a similar structure, shape, area (7.1-8.2 ha), and depth (1.7-2.7 m)

172   (Goździejewska et al., 2018, 2020). Feedwater originates from various depths and differs in

173   temperature. Reservoir CH1 is filled with atmospheric water, meltwater, and capillary water

174   with temperature similar to air temperature. Therefore, reservoir CH1 represents natural

175   seasonal variations in the temperature of shallow water bodies in the temperate climate (Fig. 2).

176   Reservoir WI is supplied with water from a deep dewatering well (up to 350 m) with a stable

177   temperature of >30 °C which is characteristic of geothermal sources (Jasnos et al., 2012;

178   Macuda et al., 2018). Reservoir PN is supplied mainly by deep dewatering wells as well as

179   surface runoffs from a coal yard. Therefore, the temperature of feedwater in reservoir PN

180   corresponds to the mid-range of values describing feedwater in reservoirs CH1 and WI. Water

181   is transported to reservoirs by open concrete channels with a length of 1-1.5 km, which reduces

182   differences in water and air temperature. Despite this, water carried to the warmest reservoir

183   (WI) has a temperature of around 16-18 °C in winter (when air temperature is around 0-4 °C),

184   which results difference between the compared reservoirs is greatest in the coldest season of

185   the year (Fig. 2). In addition, during mild winters, the growing season of aquatic macrophytes

186   is prolonged in reservoir WI, and macrophytic vegetation colonizes the littoral zone as well as

187   well as large portions of the water surface (mainly *Nuphar lutea*), all the year.

188   The influence of water temperature on the interactions between zooplankton species was

189   analyzed in three winter temperature scenarios: cold winters (CW < 6 °C) – reservoir CH1,

190   moderate winters (MW = 6 – 10 °C) – reservoir PN, and warm winters (WW > 10 °C) –

191   reservoir WI.

192

193   **2.2 Sampling and analytical procedure**

194   Zooplankton were sampled monthly, between January and December in 2014 and 2015, and

195   between June and September in 2016. In each reservoir, samples were collected in three sites

196   located in the center, in the coastal zone, and in the vicinity of the filter zone. Samples were

197   collected with a 5 l Patalas trap at an estimated depth of 1 m below the surface. A total of 252

198   zooplankton samples (84 samples from each of the three reservoirs) were collected during the

199   experiment. The sampled material (20 l) was filtered through a plankton net with 30 μm mesh

200   size, preserved with a 4 % formalin solution. Zooplankton were identified under a Zeiss AXIO

201   Imager microscope to the lowest possible taxonomic level (with the exception of Copepoda

202   juvenile stages) using the methods described by von Flössner (1972), Koste (1978), Ejsmont-

203   Karabin et al. (2004), Rybak and Błędzki (2010), and Błędzki and Rybak (2016). Zooplankton

204   abundance (ind l^{-1}) was determined with a Sedgewick-Rafter counting chamber in quantitative

205   analyses. Zooplankton biomass (mg l^{-1}) was determined according to the methods proposed by

206   Bottrell et al. (1976) and Ejsmont-Karabin (1998). The diversity (Shannon's index, H'), species

207   evenness (Pielou's index, J'), and similarity of zooplankton communities (Jaccard's coefficient,

208   P') were analyzed with the use of MVSP 3.22 software (Kovach, 2015).

209   The physical and chemical parameters of water were analyzed in a single site in the

210   center of each reservoir, during each sampling event. Water temperature (°C), pH, and dissolved

211   oxygen (DO, mg l^{-1}) were measured with the YSI 6600 V2 Multi-Parameter Water Quality

212   Sonde. Water transparency (SDT, m) was measured with a Secchi Disk. In the laboratory, water

213   samples were analyzed for color (Hazen scale), turbidity (NTU), total nitrogen (TN, mg l^{-1}),

214   total phosphorous (TP, mg l^{-1}), total organic carbon (TOC, mg l^{-1}), chlorophyll a (Chl a, μg l^{-1}

215   ^{1}), total suspended matter (Tot susp, mg l^{-1}), and iron (Fe, mg l^{-1}) concentrations.

216   Hydrochemical analyses were conducted in accordance with APHA guidelines (1999) (Table

217   1).

218

2.3 Statistical and network analyses

220   The overall differences in the physical and chemical parameters of water and zooplankton

221   across the analyzed thermal classes were determined by one-way ANOVA (f, $P \leq 0.05$) and

222   Tukey's HSD test. The Kruskal–Wallis non-parametric test (H, $P \leq 0.05$) was used to determine

223   differences in zooplankton biomass between thermal classes (Statistica 13.0 for Windows,

224   Statsoft, Tulsa).

225   The graph theory was applied to compare the parameters of the zooplankton network in

226   three thermal classes and to determine the significance of individual species and interspecific

227   interactions in these networks. The interactions between zooplankton species in three thermal

228   classes were analyzed in the Cytoscape platform (http://www.cytoscape.org/) with the use of

229   MetScape and NetworkAnalyzer applications to determine the correlations between data points.

230   Data were normalized by autoscaling. The correlation matrix was computed in the Correlation

231   Calculator 1.01 program (University of Michigan).

232   In graph theory, the connections (edges) between species (nodes) are examined by analyzing

233   the parameters of the entire network and determining the extent to which the attributes of

234   individual nodes and edges affect the network and centrality measures (Borgatti, 2005). An

235   undirected graph was created to identify all positive and negative interactions between

236   zooplankton species in three thermal classes. Positive interactions denoted co-occurrence

237   patterns or mutualistic relationships between the biomass of zooplankton taxa, whereas

238   negative interactions denoted predatory or competitive relationships (Kruk and Paturej, 2020;

239   Goździejewska and Kruk, 2022). The ranges of correlation coefficient values for the edges were

240   set to ensure that they were significant at $P \leq 0.05$ for sample size in each thermal class. The

241   edge-weighted spring embedded layout was used with correlation coefficients as weights and

242   weight-based heuristics. The absolute values of the correlation coefficients between nodes were

243   used as weights. In weighted graphs, the distance between nodes is defined as the sum of

244   weights (Kamada and Kawai, 1989). The zooplankton network in three thermal classes was

245   compared based on the key network attributes that are applied in ecological studies, including

246   the number of neighbors, closest path, clustering coefficient, network centralization, network

247   density, and network heterogeneity (Pavlopoulos et al., 2011, Kruk and Paturej, 2020;

248   Goździejewska and Kruk, 2022). Four popular node centrality attributes were used to determine

249   the significance of zooplankton taxa in three thermal classes: node degree centrality (NDC)

250   (Pavlopoulos et al., 2011), node closeness centrality (NCC) (Newman, 2005), node betweenness

251   centrality (NBC) (Brandes, 2001), and the clustering coefficient (CCF). The NCC is a measure

252   of how fast information, defined here by significant correlations among taxa, spreads from a

253   given species to other one in the network (Girvan and Newman, 2002). The higher the closeness

254   centrality, the more important the zooplankton species biomass to organizing other interactions

255   in the biocenosis network (Scardoni et al., 2009). NBC denotes the extent to which a given

256   taxon contributes to the network's cohesion by communicating with other clusters (subnets).

257   The global network clustering coefficient measures the degree to which the nodes (species) in

258   the graph tend to cluster together. Each taxon has an individual (local) clustering coefficient

259   (CCF) which denotes the ratio of the actual number of links between a given taxon and its

260   closest neighbors to the possible number of links in a full graph if all possible links (100%) are

261   present in a given cluster (Watts and Strogatz, 1998).

262

3 Results

263   **3 Results**

264   **3.1 Environmental variables and zooplankton distribution along the thermal gradient**

265   Significant differences in the physical parameters of water were noted between the three

266   thermal classes. The analyzed reservoirs differed significantly ($P < 0.05$) in mean annual

267   temperature and mean winter temperature, but significant variations were also observed in DO,

268   chlorophyll a, TOC, TN, and the parameters describing suspended solids (turbidity, color, SDT,

269   Tot susp) (Table 1). Water temperature significantly influenced oxygen concentration, which

270   was confirmed by a significant negative correlation between temperature and DO ($r = -0.555$,

271    $P < 0.05$).

272   The temperature gradient exerted a significant effect on zooplankton species richness.

273   Species diversity was highest in WW ($H' = 2.31$; $J' = 0.824$), and it was significantly lower in

274   MW and CW ($H' = 1.62$ and 1.66; $J' = 0.634$ and 0.605, respectively; Table 1). The zooplankton

275   community comprised 89 taxa in WW, 74 taxa in MW, and 61 taxa in CW. Rotifera dominated

276   in all thermal classes, accounting for 67 % (CW) to 75 % (MW) of total zooplankton species.

277   Greater differences were noted in the taxonomic structure of Crustacea, with a predominance

278   of cladocerans in WW (15 %; 6-10.5 % in the remaining groups) and a predominance of

279   copepods in CW (19 %; 9 % in MW, and 6.5 % in WW). All thermal classes shared 33 (26 %)

280   common taxa and forms, with a predominance of juvenile nauplii and copepodites (100 % CW

281   – 92 % WW and 100 % CW – 50 % MW, respectively), and *Keratella cochlearis* (100 % CW

282   – 50 % MW) (Table S1). The greatest similarities between zooplankton communities, measured

283   by the Jaccard index, were determined between MW and WW (47.8 %). The zooplankton

284   communities in CW and WW were least similar (33.9 %) (Fig. S1).

285   The temperature gradient induced significant differences in the biomass distribution of

286   23 (18 %) zooplankton taxa (Kruskal-Wallis test, $P < 0.05$), including 15 Rotifera, 2 Cladocera,

287   2 Copepoda, and 4 Protozoa. Most of the remaining zooplankton taxa (77 %) were not

288   represented in each thermal class (Table S1). The above led to significant differences in the

289   mean biomass and abundance of zooplankton across thermal classes. These parameters were

290   determined at 28.35 mg/L (CW), 0.73 mg l^{-1} (MW), and 0.094 mg l^{-1} (WW), and at 3903 ind.

291   l^{-1} (CW), 563 ind. l^{-1} (MW) and 45 ind. l^{-1} (WW), respectively (Table 1).

292

3.2 Network structure

294   The compared thermal classes differed in the key metrics describing the structure of the

295   zooplankton species interaction network. The CW network was characterized by the highest

296   cohesion expressed by clustering (0.462), centrality metrics (0.248), the shortest paths (1406),

297   as well as the highest average number of neighbors (6.32) per species (node), i.e. the number

298   of interspecific interactions (Table 2; Fig. 3). Density (0.191) and heterogeneity (0.617) were

299   highest in MW, which suggests that this network was most diverse (Table 2; Fig. 4). The WW

300   network was characterized by the lowest centrality (0.165) and density (0.095) metrics and the

301   lowest parameters of communication paths between taxa, i.e. the shortest total sum of paths

302 (1056) and the longest characteristic path length (3.42), which denote the presence of taxa

303 communicating with the lowest number of species (Table 2; Figs. 5 and 6).

304

305 **3.3 Interspecific interactions in zooplankton networks**

306 Node Degree Centrality (NDC), defined as the number of direct links incident on a taxon

307 (node), is a significant indicator of interspecific relationships. The highest NDC values (more

308 than 10 direct links per taxon) were noted in CW (*Trichocerca pusilla*, *Pompholyx sulcata*, *K.*

309 *tecta,* and copepod nauplii) and MW (*Brachionus calyciflorus, Keratella tecta*, *Ascomorpha*

310 *ovalis*, *Synchaeta* spp., *Ketarella testudo, Filinia longiseta*, cladoceran *Bosmina longirostris*,

311 and protozoan *Codonella cratera*). In WW, cladoceran *Alona quadrangularis* (8), protozoan

312 *Centropyxis aculeata* (8), and rotifer *Trichocerca intermedia* (6) (Table 3) formed the highest

313 number of interspecific relationships.

314   The strongest and the most numerous interspecific relationships were formed in MW.

315 Positive relationships with the highest values of the correlation coefficient were established

316 between *Polyarthra longiremis* and *Trichocerca tigris* (0.961), *Bosmina longirostris* and

317 *Ascomorpha ovalis* (0.932), and *Asplanchna priodonta* and *Keratella valga* (0.907), whereas

318 negative relationships were formed between *Brachionus calyciflorus* and *Synchaeta* spp. (-

319 0.821), *Brachionus calyciflorus* and *K. valga* (-0.754), and *B. longirostris* and *K. testudo* (-

320 0.701). Under extreme conditions, both positive and negative correlations were somewhat

321 weaker, and they were observed between *A. ovalis* and *Notholca squamula* (0.837; CW),

322 *Brachionus angularis* and *Polyarthra vulgaris* (0.779; WW), *Brachionus calyciflorus* and *K.*

323 *tecta* (-0.671; CW), and *Cephalodella* spp. and *P. vulgaris* (-0.582; WW) (Figs. 3, 4, 5; Table

324 S2).

325 Node closeness centrality (NCC), which ranks nodes based on their distance to other nodes and

326 identifies nodes whose effect rapidly spreads to most nodes in the network, decreased with a

327   rise in temperature (CW – NCC >0.5; MW– NCC >0.4; WW – NCC >0.3). The number of taxa

328   with the above NCC values was similar in each thermal class (8, 8, and 9, respectively), but the

329   species composition of these groups differed in 75-88 % (Table 3). The rotifers *Trichocerca*

330   *pusilla* and *Pompholyx sulcata* were characterized by the highest centrality attribute values in

331   CW (Fig. 3). The highest centrality attribute values were observed for *Ascomorpha ovalis* and

332   *Keratella testudo* in MW, and for cladoceran *Alona quadrangularis* and rotifer *Trichocerca*

333   *intermedia* in WW (Figs. 4, 5).

334   The taxa in the WW network played a more important role in network cohesion,

335   measured by node betweenness centrality (NBC), than the taxa in other thermal classes because

336   this attribute favors taxa that connect with sub-networks (clusters). Thus, when a network is

337   less cohesive and more fragmented, taxa (nodes) that communicate with other network clusters

338   play a more important role than the taxa within the network. The phytophilous taxa of

339   *Cephalodella* spp. and *Monommata maculata* were characterized by the highest values of NBC

340   (>0.250) in the WW network, but high betweenness centrality (>0.200) values were also noted

341   for *Alona quadrangularis*, *Brachionus angularis*, and *T. intermedia*. The most cohesive and

342   centralized network (CW) favored mostly *Trichocerca pusilla* (0.253), whereas the most

343   heterogeneous network (MW) favored mostly *Ascomorpha ovalis* (0.205) (Table 3).

344   The MW network was most heterogeneous, and it contained taxa with a high tendency

345   to form clusters. These taxa were bound by the highest number of links with neighbors (CCF

346   >0.9), and they represented all higher-rank groups: Rotifera (*Notholca acuminata, K. valga,*

347   *Asplanchna priodonta*), Cladocera (*Daphnia cucullata*), Copepoda (Harpacticoida), and

348   Protozoa (*Arcella discoides*). Taxa with the smallest number of links also formed a large cluster

349   (CCF <0.2) (Figs. 4, 7).

350   The CW network was most centralized, and it contained a much higher number of

351   interspecific links with moderate values and no links with extreme values (CCF = 0 or 1) (Fig.

352   8). The CW network was characterized by the highest CCF value and the highest cohesiveness

353   (Table 2; Fig. 3).

354   **4 Discussion**

355   Various methodologies and research hypotheses have been proposed for investigating and

356   predicting changes in plankton biocenoses under the influence of rising water temperatures

357   (Hessen et al., 2007; Tuck and Romanuk, 2012; Ingleton and McMinn, 2012; Ejsmont-Karabin

358   et al., 2020). Graph theory opens new possibilities for analyzing the structure of zooplankton

359   networks across temperature gradients by focusing on biomass distribution as an indicator of

360   interspecific interactions. In ecosystem ecology, all interspecific relationships are associated

361   with the flow of energy (biomass), and the type and strength of these processes are largely

362   dependent on changes in temperature and insolation (Currie, 1991). Temperature is a physical

363   factor that modifies the energy of water, and the thermal gradient determines the intensity and

364   direction of these processes (Lampert and Sommer, 1999; Hessen et al., 2007).

365   The studied reservoirs differed mainly in winter water temperature (the difference

366   between CW and WW = 9.7 °C), which significantly affects the annual temperature gradient

367   (Fig. 2). In the coldest reservoir (CW), more energy was needed to heat water to a similar

368   temperature within the same period of time (winter – summer), which led to changes in the rate

369   of physical and chemical (element cycling) processes and biomass accumulation. As a result,

370   organic matter cycling was rapidly intensified due to an increase in water temperature after

371   winter (by 19.2 °C in CW), when heat energy was absorbed by the surface layer and distributed

372   to the bottom (the examined reservoirs are shallow) by convection or mechanical motion. The

373   above contributed to rapid phytoplankton growth. However, when the water temperature

374   gradient is flattened (water temperature increased by 13.1 °C in MW and 9.2 °C in WW;

375   therefore, less energy was generated), phytoplankton is produced at a slower rate and algal

376   blooms are less frequent (Wollrab et al., 2021). When the accumulated matter is continuously,

377   but less rapidly cycled in heated reservoirs (in particular in WW), surface water can be

378   colonized by macrophytes that effectively utilize the available nutrients (TN and TOC levels

379   decreased in WM and WW) and compete for food with phytoplankton (Vanderstukken et al.,

380   2011). These energy transformations create trophic conditions which exert the greatest

381   influence on species composition and function, as well as biomass and the type and strength of

382   interspecific interactions in zooplankton communities (Kruk et al., 2021; Goździejewska and

383   Kruk, 2022).

384   The natural, for temperate climate, thermal regime of surface waters (CW) promoted

385   the development of the most cohesive zooplankton network with an equal number of strong

386   positive and negative interspecific relationships. These relationships (node centrality; NCC >

387   0.5) were formed mainly by rotifers with a diverse food base, i.e. detritophagous and

388   bacteriophagous *Pompholyx sulcata* and *Brachionus angularis*, phytophagous *Keratella tecta*

389   and *K. valga* (Ejsmont-Karabin et al., 2004), as well as raptorial *Polyarthra vulgaris* and

390   *Trichocerca pusilla*. In the CW network, these species formed numerous (NDC >10) and strong

391   relationships with other taxa, mostly copepods. In the CW network, the above Rotifera node

392   species were characterized by higher biomass than in warmer classes, and these taxa could be

393   regarded as effective bioindicators (Ejsmont-Karabin, 2012; Goździejewska et al., 2018) of

394   good food conditions (eutrophic) in class CW. The above observation was confirmed by the

395   highest values of primary productivity (Chl *a*), organic carbon (TOC), and nitrogen in CW in

396   comparison with the remaining thermal classes. In the CW network, total zooplankton biomass

397   was more than 40 and 300 higher than in MW and WW, respectively. This result differs from

398   the predictions based on the correlations between increasing water temperature and biomass

399   accumulation in the food chain (Visconti et al., 2008; Vandysh, 2009), but it confirms that

400   energy processes in ecosystems (their significance and effects) are related to the amplitude of

401   water temperature.

402   In the coldest reservoir (CW), an increase in trophy levels probably also contributed to

403   a higher content of mineral suspensions. Suspended particles form a substrate that is readily

404   colonized by algae, bacteria and protozoa, and they contribute to the accumulation of organic

405   matter (greater availability of food resources) and its effective cycling (Boenigk and Novarino,

406   2016; Goździejewska et al., 2019; Goździejewska and Kruk, 2022). According to Bonecker et

407   al. (2013), the concentration of mineral suspensions is highly correlated with the concentration

408   of chlorophyll *a* which is an important predictor of increased rotifer biomass and copepod

409   diversity in lotic ecosystems. The results of the present study confirm the above observation

410   because copepods were represented by diverse species characteristic of astatic habitats and

411   small water bodies (*Microcyclops varicans*, *Cryptocyclops bicolor*), eurytopic species (*Cyclops*

412   *vicinus*, *C. strenuus*, *Thermocyclops crassus*) as well as benthic Harpacticoida (Błędzki and

413   Rybak, 2016). These species were characterized by low values of centrality attributes in CW,

414   but they contributed to the formation of valuable antagonistic (predator-prey) relationships.

415   According to Currie (1991) and Schmitz and Trussell (2016), predatory behavior is crucial for

416   maintaining high interspecific cohesion because it prevents competitive exclusion and loss of

417   biodiversity.

418   The abundance and diversity of food resources in CW were responsible not only for the

419   strength, but also for the closeness of interspecific relationships which was expressed by the

420   highest number of the shortest communication paths between taxa. A similar dependency

421   between high primary production (organic matter), high total zooplankton biomass, short path

422   length, and high network cohesion was reported by Goździejewska and Kruk (2022) in a study

423   of environmental gradients (turbidity). Kruk et al. (2021) also found that network cohesion and

424   the strength of interspecific interactions increased with a rise in salinity which was correlated

425   with trophy levels in coastal lakes.

426   In the present study, an increase in water temperature led to changes in the species

427   composition of zooplankton communities, including that with the highest centrality attribute

428   values, and similar observations were made by Richardson (2008), Arlic et al. (2013), and

429   Carter et al. (2017). Similarly to CW, Rotifera made the greatest contribution to network

430   centrality also in warmer reservoirs (MW and MM), but their ecological and functional structure

431   was clearly modified. Only a few studies have investigated Rotifers' responses to changes in

432   water temperature, pointing to their lower sensitivity, i.e. tolerance of a wider range of

433   temperatures (Bērzinš and Pejler, 1989), and a correlation between their lower reactivity vs.

434   lower biomass and lower activity, compared with crustaceans (Xu et al., 2008). Most rotifers

435   are eurythermal species, therefore the results of studies analyzing species-specific responses,

436   such as migration patterns in vertical temperature and food gradients in deep lakes (Obertegger

437   and Flaim, 2018; Goździejewska et al., 2021), cannot be used to formulate far-reaching

438   conclusions about global changes in the environment. According to Obertegger and Flaim

439   (2018), changes in water temperature affect the structure of the relationships between rotifer

440   species that are based on feeding and predation, which is consistent with the present findings.

441   In the MW network, raptorial rotifers (*Ascomorpha ovalis* and *Synchaeta* spp.), rotifers

442   grazing on selected algae (*Keratella testudo*, *K. quadrata* and *Brachionus calyciflorus*), and

443   predatory rotifers (*Asplanchna priodonta*) were characterized by the highest values of network

444   centrality attributes (Moreira et al. 2016; Obertegger and Flaim 2018). At the same time, these

445   species established the highest number of strong positive and antagonistic relationships,

446   predominantly with the cladoceran *Bosmina longirostris*. These observations point to lower

447   trophy levels in MW (resulting from the energy transfer described above), including lower

448   phytoplankton production and lower food availability (Goździejewska et al. 2018). In a study

449   by Goździejewska et al. (2018), the chemical parameters of sediments in reservoir PN

450   (represented by class MW in the present study), resulted phosphorus concentration decrease in

451 water. Lower phosphorus levels inhibited the development of more demanding phytoplankton

452 groups and led to the dominance of diatoms, including large *Pennales* species. Due to the

453 specificity of the available food resources, only consumer species with functionally specialized

454 roles (*Notholca* spp., *A. ovalis, K. testudo*) and species relying on other food resources, such as

455 animal protein (*A. priodonta*), were able to maintain high biomass (May, 1980; Ejsmont-

456 Karabin et al., 2004). The MW network was highly fragmented (divided into sub-networks), as

457 demonstrated by the highest values of opposing attributes – density and heterogeneity (i.e. the

458 tendency to form concentrating nodes - clusters). Loosening of the network structure, i.e. a

459 decrease in the values of centrality attributes, increased the significance and number of taxa

460 communicating with two sub-networks (NBC; Table 3, Fig. 4). The heterogeneity of the MW

461 network was manifested by high fragmentation and the formation of large groups with the

462 highest and lowest number of interspecific relationships (Fig. 7). The largest clusters (CCF ~

463 1) with many positive and negative relationships contained effective filter feeders, including

464 cladoceran *Bosmina longiostris* and *Daphnia cucullata*, predatory benthic copepods of the

465 order Harpacticoida, phytophilous rotifers *K. valga* and *Notholca acuminata*, and protozoan

466 *Arcella discoides*. These observations point to the dynamic character of zooplankton

467 communities in MW, which can be attributed to their taxonomic and functional diversity

468 (feeding strategy, habitat ecology). Taxa with high CCF values (>0.5) played a crucial role

469 because they formed numerous antagonistic relationships (correlation coefficient > -0.5; Table

470 S2) which were important for maintaining this rich, but unstable (due to a very weak second

471 sub-network) network structure (Schmitz and Trussell 2016).

472   Warm winters and small differences in water temperature between seasons significantly

473 affected the rate of physical (decrease in saturation) and biochemical processes

474 (accumulation/immobilization of organic matter in macrophyte tissues) and decreased

475 phytoplankton production in the warmest reservoir (WW). The above weakened interspecific

476   interactions, including negative relationships, and compromised the cohesiveness of the

477   zooplankton network relative to colder reservoirs (CW and MW). Network attributes (NCC and

478   NBC) were determined by phytophilous and psammophilous rotifers *Cephadella* spp.,

479   *Monommata maculata,* and *Trichocerca intermedia* (Ejsmont-Karabin et al., 2004), littoral

480   cladocerans *Alona* spp., small eurytopic *Chydorus sphaericus* and *Bosmina longirostris*

481   (Błędzki and Rybak, 2016), and protozoa. Therefore, zooplankton species characterized by

482   smaller size, lower weight and lower nutritional requirements contributed to an increase in

483   biomass. Ejsmont-Karabin et al. (2020) also reported a positive correlation between

484   psammophilous-epiphytic Rotifera and an increased and stable water temperature in heated

485   lakes. Other authors observed that the growth of small crustacean species was accelerated by

486   an increase in water temperature (Daufresne et al. 2009, Gutierrez 2016, Evans et al. 2020,

487   Zhou 2020). In the present study, zooplankton growth was also promoted by the development

488   of macrophytes which colonized a large part of reservoir WW and created a supportive

489   habitat/refugium for the diverse group of Cladocera.

490   Small littoral cladocerans *Alona* spp. were characterized by the highest values of NCC

491   and NBC (Figs. 5, 6), and were responsible for the highest number of individual links (NDC),

492   mostly negative competitive interactions (Table S2). According to Martín González et al.

493   (2010), species with high NCC and NBC values play a special role in zooplankton networks

494   because network structure disintegrates more rapidly when these species are selectively

495   eliminated. The ratio of positive to antagonistic relationships also plays an important role

496   (Schmitz and Trussell 2016), and this parameter was not optimal in the WW network. Despite

497   the above, the WW network was characterized by the co-existence of the highest number of

498   rotifer and cladoceran taxa, as well as the highest taxonomic diversity of zooplankton relative

499   to colder reservoirs. Macrophyte habitats probably played an important role in this process.

500   Macrophytes promote microbial carbon cycling and increase the bioavailability of carbon for

501   small zooplankton species when phytoplankton resources are scarce (Bowszys et al. 2020).

502   In warmer reservoirs, a decrease in copepod biomass was followed by the disappearance

503   of most taxa noted in CW. Smaller differences in temperature and low food availability in warm

504   reservoirs induced long-term disruptions in Copepoda phenology. The absence of clear seasonal

505   fluctuations in the temperature of warmer reservoirs could have disrupted the life cycle of

506   copepods (no diapause), which decreased the body size and biomass of adult individuals

507   (Adrian et al. 2006; Costello et al. 2006; Rybak and Błędzki 2010). According to Santer and

508   Hansen (2006), when algal food resources are scarce, Copepoda can skip diapause and develop

509   directly into adults. This observation was validated by the present study where a decrease in

510   copepod biomass weakened the WW network because Copepoda play an important role in

511   predatory interspecific relationships.

512   **5 Conclusions**

513   The network graph analysis enabled a comprehensive visualization of the changes in plankton

514   communities induced by a rise in the temperature of surface water reservoirs. The applied

515   method elucidated the position and role of taxa in the biocenotic network and the ecological

516   mechanisms that are usually difficult to identify and interpret with the application of

517   conventional structural and multidimensional analyses, especially in *in situ* studies.

518   In the natural thermal regime (cold winters), the network of interspecific interactions

519   was characterized by the highest cohesion and the highest centrality attributes of taxa utilizing

520   shared and abundant food resources. The network featured an equal number of positive and

521   negative relationships that were controlled by eutrophic rotifers, with very high values of

522   centrality attributes (NCC > 0.5). An increase in water temperature in winter and the flattening

523   of the annual temperature gradient decreased primary production and affected the availability

524   of food resources for zooplankton. The values of centrality attributes decreased, which led to

525   the disintegration of MW and WW networks into clusters (sub-networks). In MW, diverse

526   ecological and functional groups of rotifers (raptorials, phytophiles and predators) made the

527   greatest contribution to the network's cohesion and interspecific communication. In the

528   warmest environment (WW) colonized by macrophytes, small littoral cladocerans and small

529   psammophilous-epiphytic rotifers formed a network with the lowest values of centrality

530   attributes. Warm winters disrupted the phenology of Copepoda and diminished their importance

531   in the biocenosis, leading to a decrease in their biomass and in the number of antagonistic

532   relationships responsible for the network's functionality.

533

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815

816 **Author contributions**
817 A.M.G. designed the research, conducted fieldwork, analyzed the zooplankton samples and
818 water samples, planned and wrote the main manuscript text and prepared Figs. 1, 2 and S1.
819 M.K. prepared network graph analysis of zooplankton structure, interpreted results and
820 prepared Figs. 3 - 8.

Competing interests

The authors declare that they have no conflict of interest.

Figure captions

Figure 1. Location of the study area. Abbreviations: O-MB – opencast mine in Bełchatów, O-MS – opencast mine in Szczerców; reservoir CH1 represents CW class, reservoir PN represents MW class; reservoir WI represents the WW class. Modified, see Goździejewska and Kruk (2022).

Figure 2. Mean monthly water temperature in the analyzed thermal classes in 2014-2016.

Figure 3. Network graph analysis of the interactions between zooplankton species in the CW network with an analysis of node closeness centrality (NCC), node betweenness centrality (NBC), and edge betweenness centrality (EBC) values. Node size is proportional to the NCC measure, node color on the blue (dark) – orange (bright) color scale is proportional to the NBC measure, and edge thickness is proportional to the EBC measure. Sign of the relationship: bright orange edges denote positive relationships between nodes, whereas dark blue edges denote negative relationships.

Figure. 4. Network graph analysis of the interactions between the zooplankton species in the MW network with an analysis of node closeness centrality (NCC), node betweenness centrality (NBC), and edge betweenness centrality (EBC) values. Refer to the legend and explanations in Fig. 3 (CW).

Figure. 5. Network graph analysis of the interactions between the zooplankton species in the WW network with an analysis of node closeness centrality (NCC), node betweenness centrality (NBC) and edge betweenness centrality (EBC) values. Refer to the legend and explanations in Fig. 3 (CW).

Figure 6. Clustering coefficient distribution in the WW zooplankton network. Node size is proportional to the Clustering coefficient measure in the range 0 – 1, showed by arrows. For node and edges color explanations see the legend in Fig. 3.

Figure 7. Clustering coefficient distribution in the MW zooplankton network. Node size is proportional to the Clustering coefficient measure in the range 0 – 1, showed by arrows. For node and edges color explanations see the legend in Fig. 3.

Figure 8. Clustering coefficient distribution in the CW zooplankton network. Node size is proportional to the Clustering coefficient measure in the range 0 – 1, showed by arrows. For node and edges color explanations see the legend in Fig. 3.

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Figure 1

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Figure 2

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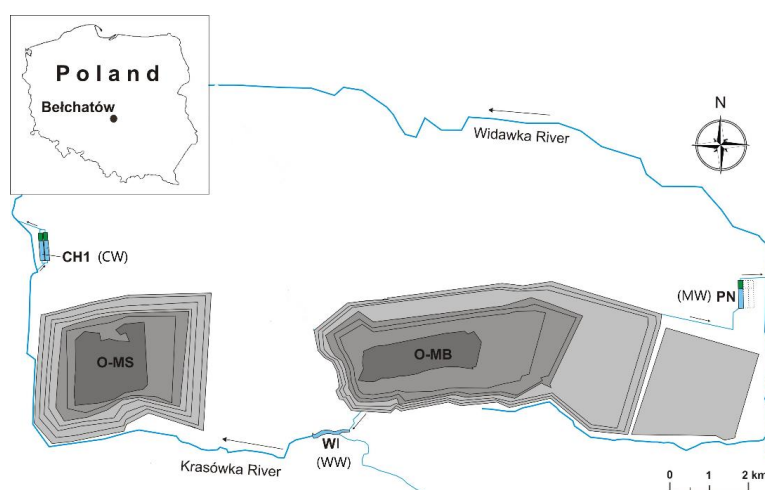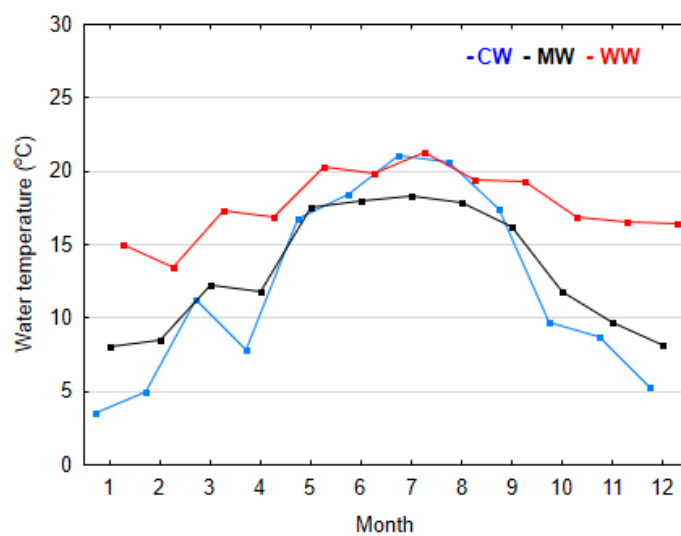
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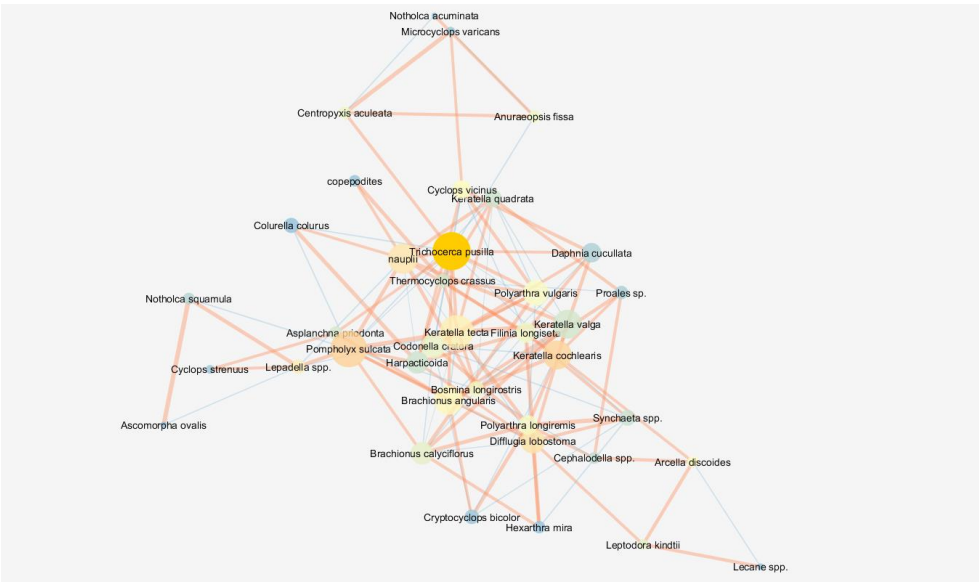
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864 **Figure 3**

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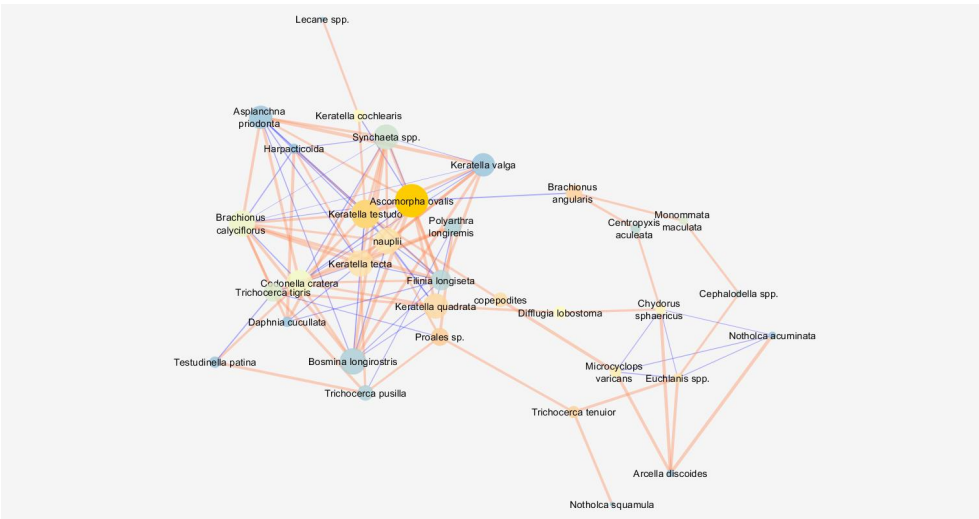
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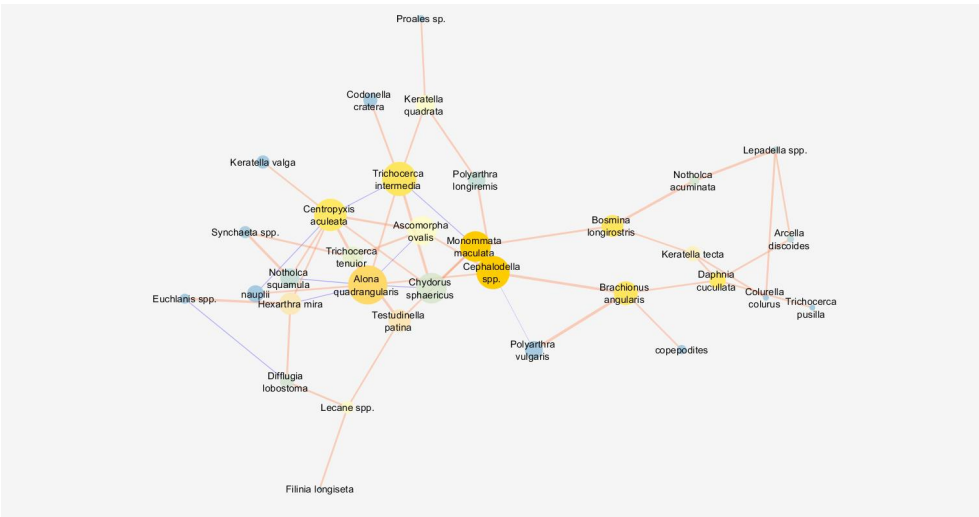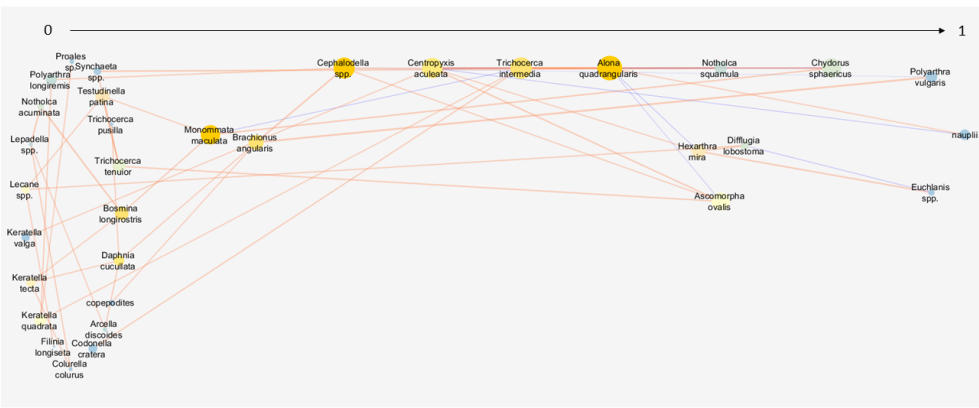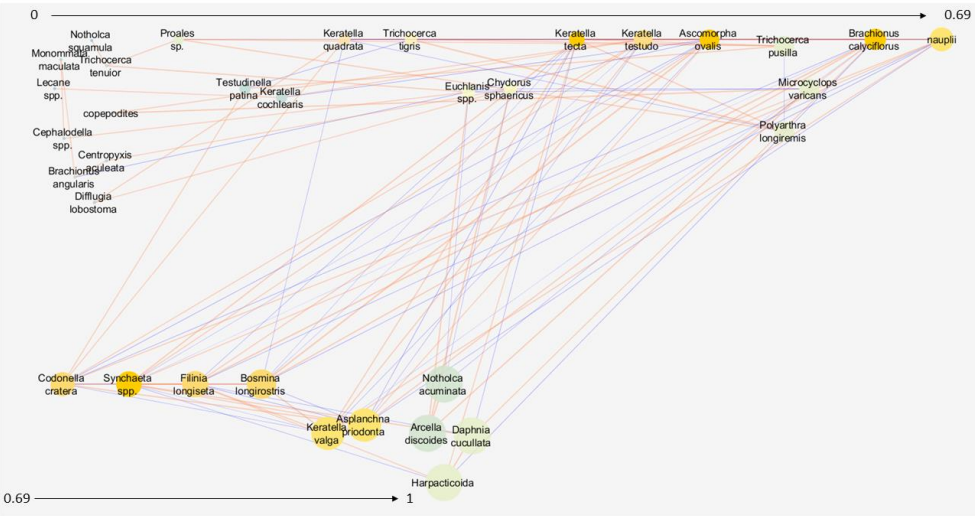
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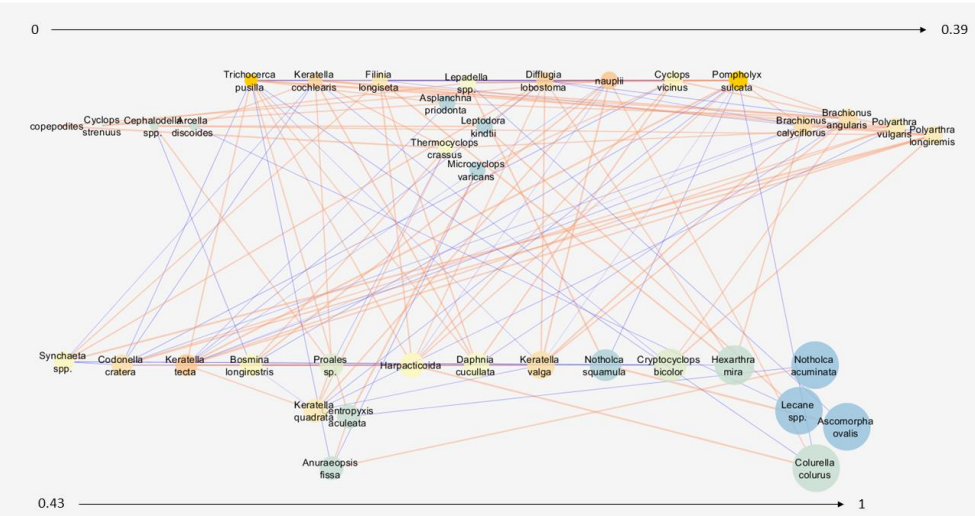
Figure 6

Figure 7

Figure 8

TABLES

Table 1 Water quality and zooplankton parameters across the studied thermal classes (mean ±
SD). Abbreviations: DO – dissolved oxygen, Chl *a* –chlorophyll *a*, TOC – total organic carbon,
TP – total phosphorus, TN – total nitrogen, SDT – Secchi depth transparency, Tot susp – total
suspended solids, Fe – iron. Differences in the analyzed parameters were determined by
ANOVA ($P \leq 0.05$); values with different superscripts differ significantly across reservoirs in
Tukey's HSD test.

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	CW		MW		WW		ANOVA
	$\bar{x}$	± SD	$\bar{x}$	± SD	$\bar{x}$	± SD	*P*
Physical and chemical parameters of water							
Temperature (°C)	13.61[a]	6.58	14.69[a]	3.91	18.49[b]	2.21	0.000
Winter temperature (°C)	5.63[a]	2.19	8.60[b]	0.76	15.35[c]	1.41	0.000
DO (mg l⁻¹)	9.36[a]	1.35	9.33[a]	1.33	7.59[b]	0.97	0.000
pH	7.80	0.39	7.80	0.24	7.69	0.29	>0.05
Chl *a* (µg l⁻¹)	5.10[a]	2.86	4.32[a]	3.74	1.99[b]	4.42	0.000
TOC (mg l⁻¹)	3.85[a]	3.37	1.98[b]	0.71	1.63[b]	0.62	0.000
TP (mg l⁻¹)	0.125	0.175	0.109	0.048	0.122	0.068	>0.05
TN (mg l⁻¹)	0.299[a]	0.124	0.238[ab]	0.077	0.220[b]	0.126	0.034
Turbidity (NTU)	17.30[a]	7.08	12.56[b]	7.53	9.74[b]	5.14	0.006
SDT (m)	0.756[a]	0.168	0.919[a]	0.166	1.46[b]	0.32	0.000
Color (Hazen)	15.00[a]	7.09	10.04[b]	3.91	7.39[b]	2.71	0.000
Tot susp (mg l⁻¹)	6.13	4.28	3.98	3.04	4.28	2.88	>0.05
Fe (mg l⁻¹)	0.165[ab]	0.098	0.255[a]	0.204	0.138[b]	0.062	0.042
Zooplankton measures							
Biomass (mg l⁻¹)	28.25[a]	33.1	0.730[b]	0.999	0.094[c]	0.064	0.000
Abundance (ind. l⁻¹)	3903.1[a]	3933.5	563.2[b]	1119.2	45.03[c]	25.12	0.000
Av. number of species (ind.)	16	5	15	5	17	5	>0.05
Total number of species (ind.)	61		74		89		-
Shannon's biodiversity index *H'*	1.66[a]	0.37	1.62[a]	0.54	2.31[b]	0.37	0.000
Pielou's eveness index, *J'*	0.605[a]	0.128	0.634[a]	0.206	0.824[b]	0.085	0.000

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909   Table 2 General attributes of the zooplankton network in the compared thermal classes.
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Attribute	Thermal class		
	CW	MW	WW
Clustering coefficient	0.462	0.437	0.191
Network centralization	0.248	0.216	0.165
Shortest paths (100 %)	1406	1122	1056
Characteristic path length	2.37	2.64	3.42
Average number of neighbors	6.32	6.29	3.03
Network density	0.171	0.191	0.095
Network heterogeneity	0.518	0.617	0.577

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950 Table 3 Zooplankton taxa with the highest net attribute. Abbreviations: NCC - node closeness
951 centrality, NBC – node betweenness centrality, NDC - node degree centrality,
952 CCF - clustering coefficient.
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	CW				MW				WW			
	NCC	NBC	NDC	CCF	NCC	NBC	NDC	CCF	NCC	NBC	NDC	CCF
Rotifera												
Brachionus angularis	0.521		9			0.116			0.333	0.204	4	
Polyatrhra vulgaris	0.500											1
Keratella valga	0.521		9		0.446		10	0.911				
Trichocerca pusilla	0.578	0.253	15									
Keratella cochlearis	0.521	0.123	10									
Pompholyx sulcata	0.569	0.127	13									
Keratella tecta	0.552		11		0.465		13			0.103		
Keratella testudo					0.478	0.164	11					
Brachionus calyciflorus			9		0.465		13					
Keratella quadrata					0.458	0.106	8					
Synchaeta spp.					0.458		12					
Asplanchna priodonta					0.446		10	0.911				
Proales sp.						0.123						
Filinia longiseta							11					
Ascomorpha ovalis				1	0.507	0.205	13		0.360		4	
Trichocerca intermedia									0.386	0.203	6	
Cephalodella spp.									0.381	0.265	5	
Monommata maculata									0.368	0.254	4	
Hexarthra mira				0.833					0.327	0.119	4	
Lecane spp.				1								
Colurella colurus				1								
Euchlanis spp.												1
Notholca acuminata				1				1				
Crustacea												
Alona quadrangularis									0.410	0.244	8	
Chydorus sphaericus									0.368		4	0.666
Bosmina longirostris							11	0.818		0.195		
Daphnia cucullata								1		0.168	4	
Harpacticoida								1				
nauplii	0.529		11				10					1
Protozoa												
Codonella cratera			9				11					
Centropyxis aculeata									0.376	0.146	8	
Arcella discoides								1				
Difflugia lobostoma			10									

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