1
2   *Running title*:
3   Seasonal dynamics of boreal pelagic rotifers
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Seasonal quantitative dynamics and ecology of

pelagic rotifers in an acidified boreal lake

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33   Tables: 2 and Figures: 8

ABSTRACT

Lake Gjerstadvann is a dimictic, oligotrophic, slightly acidified boreal lake in southern

Norway (northwest Europe). The planktonic rotifer community of this lake was studied

quantitatively during one year in order to investigate the impacts of the local environment and

biotic interactions on seasonal succession and habitat selection. Pure suspension feeders

(mainly *Keratella* spp., *Conochilus* spp., and *Kellicottia longispina*) together with raptorial

graspers or specialised feeders (mainly *Polyarthra* spp. and *Collotheca* spp.) dominated the

rotifer community over prolonged periods, whereas carnivorous/omnivorous species (mainly

Asplanchna priodonta) were extremely uncommon. Low bicarbonate buffering capacity

resulted in a distinctive seasonal oscillating pH between 5.0 and 5.6, defining a special acid-

transition lake category. The pH values were highest in the productive period during summer,

and lowest during ice break-up coinciding with the peak reactive aluminium concentrations of

250-300 μg L^{-1}. As in typical Norwegian boreal perch lakes, the most abundant cladoceran

was *Bosmina longispina* due to perch predation on the genus *Daphnia*. Rotifer community

structure was significantly related to temperature and oxygen (p = 0.001 and 0.022),

illustrating the important effects of the seasonal cycle and vertical density stratification. The

most significant competition indicator species were *B. longispina* and *Eudiaptomus gracilis*

(both with p = 0.001). A variance partitioning indicated that 14% of the total community

composition variance could only be explained by biotic interactions, while 19% of the

variance could be attributed to environmental gradients. Of the variance, 23% could not be

resolved between biotic interactions and environmental gradients, while a residual of 44%

was not explainable by any of the variables. Acid conditions alone cannot account for all the

observed changes in the rotifer community of this lake with low humic content, since resource

limitation and food competition are also important factors shaping rotifer population

dynamics and the community structure.

INTRODUCTION

Pelagic rotifers in North Europe and Northern America are affected to various degrees by anthropogenic acidification processes, which include several abiotic and biotic ecosystem changes (Stenson *et al.*, 1993; Keller *et al.*, 1999; Svensson and Stenson, 2002; Vandysh, 2002; Wærvågen and Nilssen, 2003). The majority of biotic studies in the pelagial of acidified lakes during the last decades has been devoted to pelagic cladocerans, while much less effort has been addressed to pelagic copepods and rotifers. In medium and strongly acidified lakes the major planktonic rotifer species are *K. longispina*, *Polyarthra* spp., *Keratella taurocephala*, and some more rare species are *K. cochlearis*, *Collotheca* spp., *Ascomorpha* spp., and *Keratella serrulata* (Skadovsky, 1926, 1933; Yan and Geiling, 1985; Bērziņš and Pejler, 1987; Morling and Pejler, 1990; Siegfried, 1991; Svensson and Stenson, 2002; Wærvågen and Nilssen, 2003). Most studies focus on non-acidic lakes (Ruttner, 1930; Nauwerck, 1963; Larsson, 1971, 1978; Zimmermann, 1974; Makarewicz and Likens, 1975; Armengol-Díaz *et al.*, 1993; Armengol *et al.*, 1998; Bartumeus and Catalan, 2008; Obertegger *et al.*, 2008), while less is known about acidic lakes. Few studies on rotifer community alterations during acidification are published (Roff and Kwiatkowski, 1977; Hobæk and Raddum, 1980; Mac Isaac *et al.*, 1987; Frost *et al.*, 1998), whereas quantitative seasonal and vertical distribution during acidification is less well known.

Individual species of rotifers display different embryonic development times based on food threshold concentrations influencing interspecific competition (Herzig, 1983; Stemberger and Gilbert, 1985, 1987a, 1987b; Walz, 1995), and consequently affect community species composition during acidification (Wærvågen and Nilssen, 2003). Rotifers often have higher threshold food concentrations than many filter-feeding cladocerans (Duncan, 1989), which makes them inferior competitors at lower food abundance levels. Therefore, when cladocerans

3

84   dominate, raptorial rotifers feed selectively on larger food items (Obertegger *et al.*, 2011).

85   Rotifer community alternations are often caused by changes in ecosystem productivity driven

86   by eutrophication or acidification (Duncan, 1989; Walz, 1995; Stelzer, 2005). Rotifers are

87   usually more productive under eutrophic conditions whereas food limitation is more probable

88   under oligotrophic conditions (Walz, 1995). Nutrient-rich environments therefore support

89   much higher rotifer abundance, characterized by rotifer species with smaller egg sizes and

90   faster development (Herzig, 1983; Orcutt and Pace, 1984; Walz, 1993). Most rotifers produce

91   resting eggs with typical egg-bank characteristics (Nipkow, 1961), and are known for their

92   rapid re-appearance after water chemistry recovery following prolonged acidification

93   (Raddum *et al.*, 1986; Svensson and Stenson, 2002; Wærvågen and Nilssen, 2003).

94

95   It is crucial for the understanding of anthropogenic lake acidification and possible trajectories

96   of lake recovery to distinguish between several different categories of acidified lakes (Nilssen

97   and Wærvågen, 2002a; Wærvågen and Nilssen, 2003, 2011), especially chronically acidic

98   lakes and so-called acid-transition lakes (Henriksen, 1979, 1980). In chronically acidic lakes,

99   the bicarbonate buffering capacity is inoperative and pH has stabilised in the low range,

100   usually at 4.4-4.8 (Nilssen, 1982a). Furthermore, all fish species have been eliminated and the

101   new top lake predators are different species of invertebrates, especially pelagic corixids and

102   notonectids (Hemiptera), chaoborids (Diptera), and water beetles (Coleoptera). Acid-

103   transition lakes, including categories between slightly affected and chronically acidified,

104   characterise localities in which the residual bicarbonate buffering capacities are negatively

105   affected with strong pH fluctuations usually between 5.0 and 6.0. In the boreal part of

106   Fennoscandia such lakes were extremely common during the peak acidification period

107   (Henriksen, 1979, 1980), and many organisms, including most fish species, were negatively

108   affected or disappeared altogether (Nyberg *et al.*, 1995). A typical acid-transition lake is

109 dominated by aging fish populations (in southern Norway often Eurasian perch, aged 5-7

110 years on average), while young stages are missing or produce strong cohorts only in years

111 with favourable spring climatic conditions (Kleiven *et al.*, 1990; Linløkken *et al.*, 1991). In

112 acidic, fish-deficient or fishless ecosystems, competition and invertebrate predation are

113 probably of decisive importance in rotifer ecology (Eriksson *et al.*, 1980; Nyman *et al.*, 1985;

114 Yan *et al.*, 1991). The susceptibility of rotifers to invertebrate predators is fairly well

115 documented in non-acidic lakes, however, except for the voracious chaoborid larvae, such

116 knowledge is sparse for acidified lakes (Nyberg, 1984; Yan *et al.*, 1991).

117

118 Aquatic ecosystems have been studied in this region of southern Norway since the early

119 1970s, including both the anthropogenic acidification of aquatic systems and their subsequent

120 recovery during recent years (Nilssen, 1980, 1984; Nilssen and Sandøy, 1990; Nilssen and

121 Wærvågen, 2002a, 2002b, 2003; Wærvågen and Nilssen, 2003, 2010, 2011). The majority of

122 lakes in this area were, at the time of the present study (1980-81), still strongly affected by

123 acid precipitation from a variety of sources in Europe (Drabløs and Tollan, 1980; Nilssen,

124 1980, 1982a, 1982b). The investigated boreal Lake Gjerstadvann (Fig. 1) belonged to a

125 typical acid-transition lake category with pH fluctuating between 5.0 and 5.6. The study was

126 part of a research programme in southern Norway (Fig. 1), which comprised lakes with

127 strongly contrasting chemistry and biology. The aim of the present study was to investigate

128 the seasonal and vertical quantitative distribution of pelagic rotifers in order to relate the

129 rotifer community to abiotic and major biotic factors in a typical boreal acidic-transition lake

130 dominated by Eurasian perch. This may improve our general knowledge concerning the

131 process of acidification and ecosystem structures of anthropogenic acidified lakes and their

132 subsequent recovery, including the ecology, life histories and habitat dynamics of pelagic

133 rotifers in northern boreal lakes.

134

METHODS

Study area

Samples from Lake Gjerstadvann were collected from early February 1980 to mid-March

1981. The lake is situated 31 m above sea level (a.s.l.) ($58^o 53´$ N, $9^o 02´$ E, WGS84 datum) in

a region in southern Norway characterised by a mixture of continental and oceanic climates

(Fig. 1a, b). Lake Gjerstadvann is dimictic with bottom temperatures slightly above 4 °C in

the ice-free period and with a relatively deep mixed layer because of its considerable water

through-flow (Figs. 1d and 2). The seasonal changes in water chemistry are mainly due to

spring snow-melt and seasonal rainfalls in summer and autumn (Figs. 1d and 2), which are

further described in Wærvågen and Nilssen (2010). The lake is situated below the post-glacial

marine limit (i.e. about 100 m a.s.l. in this area), but most of the catchment area of the lake is

situated above the postglacial marine limit, thus draining more acidified water, measured with

mean pH 4.7 in 1980 (Hindar *et al.*, 1984). Lake Gjerstadvann had a mean pH of 5.2 in 1980-

81, was oligotrophic (based on total phosphorus; see Results), and oligo- to mesohumic

(based on the water colour in mg Pt L^{-1}; see Fig. 2). Mean reactive aluminium (RAl)

concentrations were 200-250 µg L^{-1}, and the harmful labile fraction (lAl) at these pH values

was about 40-70 percent of the RAl values (Lydersen, 1998).

Sampling and data collection

Chemical and biological samples were taken simultaneously, approximately at mid-day, every

fortnight during the ice-free period, and circa monthly during the rest of the year. Chemical

samples were collected using a Ruttner sampler at a fixed station at the deepest point (27 m)

of the lake (Fig. 1c), at depths shown in Tab. 1. Water colour expressed as mg Pt L^{-1} was

measured on a Lovibond comparator, primarily representing the amount of aquatic humic

159   substances (Fig. 2). Total organic carbon (TOC) content of the water is closely related to Pt

160   (mg L^{-1}), and usually TOC corresponds to one-tenth of the Pt-value in this North European

161   Fennoscandian region (Degerman, 1987). Chemical analyses were performed according to

162   standard analytical methods, see further details in Wærvågen and Nilssen (2010).

163

164   Duplicate quantitative zooplankton samples were collected in Lake Gjerstadvann using a 15

165   litre Patalas/Schindler device (Schindler, 1969), with an attached net with mesh size 45 μm.

166   The volume proportions (Tab. 1) were calculated from a volumetric curve used to convert the

167   total and mean population abundance at different depths of all species to individuals per m^3

168   (Bottrell *et al.*, 1976). Most metazoan zooplankton (Tab. 2) were identified to species level

169   and counted (Rylov, 1963; Flößner, 1972; Ruttner-Kolisko, 1972; Einsle, 1975; Kiefer, 1978).

170   Preserved with Lugol's solution, identification was primarily based on morphological

171   characteristics included the lorica, foot, and anterior projections (Ruttner-Kolisko, 1972;

172   Koste and Voigt, 1978; Pontin, 1978; Nogrady *et al.*, 1993). Due to Lugol's-induced

173   retraction, especially within the genera *Conochilus*, *Synchaeta*, *Polyarthra* and *Ascomorpha*,

174   body size measurements were, in addition, performed under the microscope. Rotifers can be

175   categorized as suspension feeders (*Keratella* spp., *K. longispina*, *Conochilus* spp.), raptorial

176   graspers or specialised feeders (*Polyarthra* spp., *Synchata* spp., *Ascomorpha* spp., *Collotheca*

177   spp.), and carnivorous/omnivorous species (*Asplanchna* spp., *Ploesoma* spp.) (Nogrady *et al.*,

178   1993; Walz, 1995, 1997; Obertegger *et al.*, 2011). Cladocerans, copepods, and fish species

179   present in Lake Gjerstadvann are presented in Tab. 2.

180

181   *Statistical analyses*

182   Rotifer community structure was investigated by non-metric multidimensional scaling

183   ordination (NMDS; Minchin, 1987) using a Bray-Curtis dissimilarity measure calculated from

184 fourth root-transformed rotifer abundances and the metaMDS function in the vegan package

185 (Oksanen *et al.*, 2013). We excluded one sample, where no rotifers were detected, from the

186 analysis. We also excluded two rotifer species (*Asplanchna priodonta* and *Keratella*

187 *ticinensis*) with low occurrence (less than 20% of the samples). Relationships between rotifer

188 community ordination axes and explanatory variables were investigated by permutation tests

189 using the envfit function of the vegan package. The first two axes of a principal component

190 analysis (PCA) of scaled and centered environmental variables explained 58% of the total

191 variance. Based on the PCA biplot (Fig. 3) we chose temperature, oxygen, pH, and reactive

192 aluminum (RAl) to represent the major environmental gradients. The first two represented the

193 major seasonal and vertical gradients in the lake, while the latter two served as acidification

194 indicators. We represented a second group of biotic explanatory variables as the fourth root-

195 transformed abundances of two potential predators, *Chaoborus flavicans* (see *C. flavicans* in

196 Fig. 8) and "Cyclopoids" (the sum of Cop IV-adult stages of all cyclopoid copepods) (see Fig.

197 8 and Tab. 2). Furthermore, we included two potential competitors, *B. longispina* and *E.*

198 *gracilis* (as the sum of all its stages). Finally, we used the varpart function of vegan (Borcard

199 *et al.*, 1992) to identify fractions of total redundancy analysis variance that could be explained

200 uniquely by either environmental gradients or biotic interactions.

201

202 **RESULTS**

203 The annual mean pH in Lake Gjerstadvann was 5.2, but dropped slightly below this value

204 during the spring ice breakup and autumn and summer rain periods (Figs. 1d and 2). The

205 epilimnetic oxygen content fluctuated around 100 percent during most of the year, with an

206 oxygen deficit close to the lake bottom during periods of stagnation (Fig. 2), most probably

207 due to accumulation of allochthonous organic material. The epilimnetic colour of the lake

208 water was 10-30 mg Pt L^{-1} ($\approx$ 1-3 mg TOC L^{-1}), and increased considerably ($\approx$ 10-15 mg

209   TOC L^{-1}) above the bottom sediments (Fig. 2). The close correlation between Pt and iron (Fe)

210   in Fig. 3 indicates Fe-colour contribution to TOC under oxygen deficit close to the bottom. In

211   1980-81, the following mean concentrations were recorded: ca. 2.0 mg L^{-1} Ca^{2+}, 8 μg L^{-1} total

212   phosphorus (TP), 6 mg L^{-1} sulphate, 2.2 mg L^{-1} chloride, and 230 μg L^{-1} reactive aluminium

213   (RAl); specific conductivity, expressed as K_{25}, was 2.7 mS m^{-1} and the ANC value was −6.7

214   μekv L^{-1}.

215

216   The majority of the *Conochilus* population in Lake Gjerstadvann was identified as *Conochilus*

217   *unicornis*, with some very few *Conochilus hippocrepis* specimens in addition. The colonial *C.*

218   *unicornis* was most abundant in the upper water masses during summer (slightly above 100

219   ind. L^{-1}), but was also present under ice cover (Fig. 4a). The other species, *C. hippocrepis* was

220   recorded in small numbers at all depths in the autumn overturn, but was not found during the

221   spring overturn (Fig. 4a). *Polyarthra* spp. also displayed the largest population abundance

222   during the ice-free period (close to 50 ind. L^{-1}), and much lower during winter (Fig. 4b). The

223   most abundant species were *Polyarthra minor* and *Polyarthra vulgaris*, whereas *Polyarthra*

224   *dolichoptera* was recorded in small numbers in the upper water masses during late

225   autumn/early winter. The individual *Polyarthra* species relative to seasonal and vertical

226   abundance are indicated in Fig. 4b, where *P. minor* was the predominant summer species and

227   *P. vulgaris* was prevalent during the rest of the year.

228

229   The only typical perennial species recorded was *K. longispina*, showing distribution at all

230   depths (Fig. 5a). Mean abundance of this species was lowest during winter with about 2-4 ind.

231   L^{-1}, and it displayed two population peaks during early summer and early autumn at 8 and 10

232   ind. L^{-1}, respectively (Fig. 5a). The highest abundance approached 50 ind. L^{-1} in summer

233   epilimnion and close to metalimnion during early autumn. Egg production took place at most

234 water depths during the ice-free period, and at deeper water layers during the period with ice

235 cover (Fig. 5a).

236

237 The typical cold-water species, *Keratella hiemalis*, displayed autumn and winter population

238 peaks (Fig. 5b). Its abundance peaked close to the sediment with maximum mean abundance

239 of about 1 ind. L^{-1} and with an absolute maximum of 20 ind. L^{-1} during February 1980.

240 *Keratella hiemalis* carried eggs at depths close to the sediment surface during most of the

241 year. *Keratella cochlearis* had relatively low abundance in Lake Gjerstadvann, with a

242 maximum mean slightly above 1 ind. L^{-1} (Fig. 5c). It displayed population peaks in the deeper

243 parts of the lake later than the periods of maximum abundance for most other rotifer species.

244 It also produced eggs in that period of the year, whereas winter reproduction was almost

245 absent.

246

247 *Collotheca libera* occurred in all water masses in a very restricted period during autumn (Fig.

248 5d), with a mean abundance of about 3 ind. L^{-1}, whereas *Collotheca liepetterseni* showed

249 maximum abundance during late winter and spring (Fig. 5d). *Ascomorpha ecaudis* (Fig. 5e)

250 and the genus *Lecane* spp. (Fig. 5f) both showed three separate peaks during the ice-free

251 period, with maximum mean abundance of 0.2 and 0.6 ind. L^{-1}, respectively. The *Lecane* spp.

252 were identified as *Lecane mira*, *L. bulla*, *L. lunaris*, *L. scutata* and *L. closterocerca.*

253

254 Some of the rotifer species with least abundance are summarised in Fig. 6. *Keratella serrulata*

255 was nearly perennial while *K. ticinensis* showed autumn and winter population peaks, both

256 were recorded close to the sediment surface. Population maxima for *Synchaeta* gr. *tremula-*

257 *oblonga* occurred in summer and winter/spring, but also with minor perennial presence.

258 Population numbers of the carnivorous/omnivorous species *A. priodonta* peaked in a

259 restricted period during autumn with a mean abundance of about 0.3 ind. L^{-1}. The most

260 abundant rotifer species in Lake Gjerstadvann are shown together with major ecological

261 factors such as temperature and food; algae (usually well below 200 mm^3 m^{-3}) and organic

262 matter were calculated as TOC in mg L^{-1} (Fig. 7).

263

264 The converged NMDS ordination had relatively high stress (0.22) for 2 axes. Including 3 or 4

265 axes reduced the stress to 0.15 and 0.10, respectively, but Procrustes tests showed that all

266 solutions were very similar in the first 2 axes (vegan protest function, all with p = 0.001 on

267 999 permutations). The NMDS ordination diagram (Fig. 8) appears to capture the seasonal

268 cycle with *C. liepetterseni* and *K. hiemalis* as winter species, being replaced by *K. longispina*,

269 *Polyarthra* spp., *C. unicornis* and *Lecane* spp. in summer (June-August). *Ascomorpha ecaudis*

270 and *Synchaeta* gr. *tremula-oblonga* have higher abundances in spring and late

271 summer/autumn, while *K. cochlearis* is characteristic of the autumn/winter transition. The

272 least common species included in the analysis, *K. serrulata* seemed to have no distinct

273 environmental or seasonal preferences. The explanatory variables fitted to the ordination are

274 represented by gray arrows in Fig. 8. Among the environmental gradient indicators there were

275 significant effects of temperature and oxygen (p = 0.001 and 0.022), but not of the

276 acidification indicators (pH and RAl: p = 0.214 and 0.156, respectively). Among the biotic

277 variables, none of the predation indicators were significant (p = 0.410 and 0.493 for *C.*

278 *flavicans* and "Cyclopoids", respectively), while both the competition indicators *B. longispina*

279 and *E. gracilis* were highly significant (both with p = 0.001). Temperature, which had the

280 highest correlation to the ordination axes among the environmental variables, was mainly

281 associated with the first NMDS axis, while oxygen had stronger associations with the second

282 NMDS axis. The highly significant competition indicators (*B. longispina* and *E. gracilis*)

283 were also mainly associated with first NMDS axis. A variance partitioning sensu Borcard *et*

284 *al.* (1992) indicated that biotic interactions could explain 14% of the total community

285 variance uniquely, while 19% of the variance could be attributed to environmental gradients.

286 Twenty-three percent of the variance could not be resolved between biotic interactions and

287 environmental gradients, while a residual of 44% could not be explained by any of the

288 variables.

289

290 **DISCUSSION**

291 Lake Gjerstadvann forms part of an investigated region of small lakes with a variety of

292 pelagic fish, invertebrate predation and acidification (Nilssen, 1980, 1984; Fjerdingstad and

293 Nilssen, 1982). Many are oligotrophic perch-lakes (Demmo, 1985; Næss, 1985), such as Lake

294 Gjerstadvann (Linløkken, 1985, 1988), but also meso- and eutrophic lakes with low fish

295 predation dominated by large-sized *Daphnia* spp. (Larsen, 1982; Nilssen and Wærvågen,

296 2002a; Wærvågen and Nilssen, 2003). A small group of strongly acidified, fishless lakes have

297 communities dominated by pelagic rotifers during the whole year (Sandøy, 1984), probably a

298 consequence of intensive predation of *Chaoborus* spp. larvae on crustaceans (Nyberg, 1984).

299 Rotifers are normally controlled by a combination of factors: the physiological relationship to

300 their ambient environment, available food (bottom-up), invertebrate and vertebrate predation

301 (top-down), and interspecific competition with cladocerans (especially large-sized *Daphnia*

302 spp.), herbivorous stages of copepods (such as *E. gracilis*), as well as between rotifer species

303 (Herzig, 1987; Gonzalez and Frost, 1992; Arndt, 1993; Kirk, 1997a, 1997b; Brandl, 2005;

304 Sarma *et al.*, 2005).

305

306 Rotifers are commonly sub-divided into assemblages and species groups related to their

307 quantitative and vertical distribution, where season, temperature and oxygen are important

308 factors (Carlin, 1943; Larsson, 1971; Zimmermann, 1974; Elliott, 1977; Hofmann, 1987;

309   Mikschi, 1989). Usually, perennial epilimnetic forms are considered eurytherms, while

310   perennial hypolimnetic forms and summer-surface forms are mainly viewed as cold-

311   stenotherms and warm-stenotherms, respectively (Larsson, 1971). The above classifications

312   are often helpful, but seasonal and vertical distributions of rotifers may also be strongly

313   influenced by hatching events in the benthic egg-bank (Nipkow, 1961; Sandøy, 1984; Herzig,

314   1987), as indicated by e.g. *Ascomorpha*, *Synchaeta*, *Collotheca* and *Asplanchna* in the present

315   study. Thus, the same species can show contrasting seasonal and vertical distributions

316   between neighbouring lakes, and even between years in the same lake (Elliott, 1977; Larsen,

317   1982; Synnes, 1982; Sandøy, 1984; Herzig, 1987). As in many other studies, we found the

318   majority of *K. cochlearis* in the deeper lake regions (Demmo, 1985; Næss, 1985; Hofmann,

319   1987). Further, we found *K. hiemalis* and *P. dolichoptera* to be cold-water species, the latter

320   also having been thusly characterised by Bērziņš (1976). Stenson (1983) found that *P.*

321   *vulgaris* replaced *P. dolichoptera* following an interplay of available food when fish were

322   eliminated from the system. In the oxygen-depleted zone close to the sediments of Lake

323   Gjerstadvann, a zone which often contains high abundance of detritus-associated bacteria

324   (Hessen, 1998), we found high abundances of *Conochilus*, *Polyarthra*, and most *Keratella*

325   species.

326

327   ***Rotifer species response to physiological factors***

328   Lake Gjerstadvann was a typical acid-transition lake with low pH and high concentration of

329   toxic aluminium species especially during spring, but with pH increasing to above 5.5 in the

330   upper water masses during summer periods with less acid rain. We found no significant

331   effects of the acidification indicators pH and RAl on the total rotifer community, even though

332   some individual species may be affected. Lake Gjerstadvann was oligo- to mesohumic, which

333   may be a possible reason for the lack of such acidification response, since humus is known to

334   de-toxify poisonous heavy metals and Al in acidic lakes (Degerman, 1987; Lydersen, 1998).

335   The strong relationship between rotifer community ordination axes and temperature and

336   oxygen illustrates the important effects of seasons and vertical stratification. Rotifer

337   assemblages in Lake Gjerstadvann were similar to communities of other acid-transition lakes

338   in southern Norway (Hobæk and Raddum, 1980; Wærvågen and Nilssen, 2003), with no or

339   few carnivorous/omnivorous species of rotifers such as *A. priodonta* and *Ploesoma hudsoni.*

340   Correspondingly, no omnivorous species of rotifers were found in the strongly acidified Lake

341   Gårdsjön in Sweden, but were observed in larger numbers following aquatic recovery

342   (Svensson and Stenson, 2002). Few studies, mostly *in situ*, have been devoted to the

343   physiological tolerance of rotifers against changes in water chemistry (Havens and De Costa,

344   1988; Havens and Heath, 1989; Keller *et al.*, 1992), so many questions are still to be

345   answered.

346

347   *Conochilus unicornis* was the most abundant rotifer species in Lake Gjerstadvann. The

348   species is usually absent in chronically acidified lakes (Almer *et al.*, 1974; Holopainen, 1992;

349   Wærvågen and Nilssen, 2003), and rarely observed in high abundance below a pH of 5.0-5.2

350   in other acidic regions (Roff and Kwiatkowski, 1977; Havens and De Costa, 1988; Marmorek

351   and Korman, 1993). *Conochilus hippocrepis* was a minor species in Lake Gjerstadvann, but

352   was abundant in many other acid-transition lakes with pH below 5.0-5.2 in this region

353   (Nilssen and Wærvågen, 2001). The two closely related species probably display slightly

354   contrasting relationships to their ambient environment, and may serve as a good niche

355   differentiation indicator genus (Wærvågen and Nilssen, 2003; also see Hampton, 2005). Other

356   dominant rotifers in Lake Gjerstadvann were *Polyarthra* spp. and *K. longispina*, which are

357   commonly found in both chronically acidic and acid-transition lakes in southern Norway

358   (Hobæk and Raddum, 1980; Nilssen, 1980; Sandøy, 1984; Wærvågen and Nilssen, 2003).

359

The low abundance of *K. cochlearis* in Lake Gjerstadvann may demonstrate its physiological

vulnerability to acidified waters, but food availability could also play a decisive role (Havens

and De Costa, 1988; Gonzalez and Frost, 1994). It is recorded in very acidic environments in

western Sweden and Finland (Arvola *et al.*, 1986; Hörnström and Ekström, 1986; Bērziņš and

Pejler, 1987; Morling and Pejler, 1990), but never recorded in high abundance at low pH in

Norway (Hobæk and Raddum, 1980; Wærvågen and Nilssen, 2003). Wærvågen and Nilssen

(2003) found that *K. cochlearis* increased significantly with increasing pH in many lakes in

southern Norway. In North America *K. cochlearis* was recorded at both low pH (Roff and

Kwiatkowski, 1977) and at higher pH levels (Orcutt and Pace, 1984; Siegfried *et al.*, 1984;

Carter *et al.*, 1986; Mac Isaac *et al.*, 1987). As observed in *K. cochlearis,* the apparently

contrasting ability of tolerance and relationship towards acidic waters may be explained by

the existence of populations with different ecological adaptations (Pejler, 1977; Hofmann,

1980; Dumont, 1983; Cieplinski *et al.*, 2016).

373

Exploitative competition and/or bottom-up relations

Pelagic freshwater food webs are in general based upon phytoplankton production, especially

in clear-water lakes. Consumers in humic lakes may also, by a similar degree, be subsidised

by detritus-associated bacterial food (Hessen, 1998). Phytoplankton was a scarce food source

in Lake Gjerstadvann, usually well below 200 mm^3 m^{-3}, comparable to chronically acidified

lakes (Hindar and Nilssen, 1984; Raddum *et al.*, 1986). Further, the amount of particulate and

dissolved humic substances in Lake Gjerstadvann was also limited compared to other oligo-

to mesohumic lakes (Salonen *et al.*, 1990; Sarvala *et al.*, 1999; see also Brett *et al.*, 2009;

Brett *et al.*, 2012; Brett *et al.*, 2017). Resource limitation and food competition may therefore

be important factors shaping rotifer populations in Lake Gjerstadvann. Efficient filter-feeder

cladocerans can monopolise shared food resources and suppress rotifers (Gilbert, 1988; Mac

Isaac and Gilbert, 1989; Sanni and Wærvågen, 1990). The only cladoceran with sufficient

abundance to potentially suppress rotifer species in Lake Gjerstadvann was *B. longispina*,

which is found in both fertilised and acidic lakes (Brettum *et al.*, 1984; May, 1995). The

omnivorous copepod species *E. gracilis* was relatively common in Lake Gjerstadvann

(Wærvågen and Nilssen, 2010), and could also be able to compete with rotifers during

specific parts of the year. The highly significant associations between rotifer community

ordination axes and abundances of both *B. longispina* and *E. gracilis* could be taken as

indications of such competitive relationships. In Lake Gjerstadvann, we found mostly

suspension feeders (*Conochilus* spp., *K. longispina* and *Keratella* spp.) following the

phytoplankton level maxima in spring and autumn. Furthermore, in the mid-summer and early

autumn, the levels of raptorial species (*Polyarthra* spp., *A. priodonta* and *Ascomorpha* spp.)

peak in near coincidence with TOC-peaks (mostly allochtonous organic matter). Even with

some succession overlap, the raptorial *Polyarthra* spp. peaked together with a cladoceran (*B.*

longispina) in Lake Gjerstadvann, as was also found by Obertegger *et al.* (2011).

Furthermore, algal and detrital food abundance was low in the water masses during June,

which could be due to grazing by *B. longispina* at peak abundance.

Keratella cochlearis avoids most rotifers in time and space in Lake Gjerstadvann, probably

due to a higher threshold food concentration than the other pure suspension feeders, such as

C. unicornis and *K. longispina* (Gilbert and Bogdan, 1984). *Kellicottia longispina* has a lower

threshold food concentration than *K. cochlearis* (Walz, 1997), which indicates that *K.*

longispina is a superior competitor at lower food levels (Stemberger and Gilbert, 1985).

These species can apparently coexist in lakes with sufficient food (Salonen *et al.*, 1990;

Sarvala *et al.*, 1999), while under eutrophic conditions *K. cochlearis* was found to be a better

409   competitor than *K. longispina* (Zimmermann, 1974; Sterzynski, 1979; Lair and Oulad Ali,

410   1990). In other non-acidic neighbouring lakes, *K. cochlearis* was among the dominant rotifer

411   species (Larsen, 1982; Demmo, 1985; Næss, 1985), and outside South Norway it was the

412   dominant rotifer in many non-acidic lakes (Pejler, 1961; Larsson, 1971; Zimmermann, 1974;

413   Eloranta, 1982; Laxhuber, 1987; Andrew and Andrew, 2005; May and O' Hare, 2005). The

414   abundance of rotifers in Lake Gjerstadvann was relatively low compared with a neighbouring

415   lake with similar food availability and very low cladoceran abundance (Sandøy, 1984), in

416   accordance with the highly significant relationship between rotifer community composition

417   and abundance of both *B. longispina* and *E. gracilis*.

418

419   ***Predation influence or top-down relations***

420   Cyclopoid copepods generally exert negative influence on rotifers (Anderson, 1970; Monakov

421   *et al.*, 1972; Vardapetyan, 1972; Gilbert and Williamson, 1978; Karabin, 1978; Brandl and

422   Fernando, 1979; Stemberger, 1985; Plassmann *et al.*, 1997). There is a certain controversy

423   regarding which species of pelagic rotifers are vulnerable to predatory cyclopoid copepods,

424   and whether this applies mainly to soft-bodied forms without lorica (e.g. *Synchaeta* spp.)

425   (Monakov *et al.*, 1972; Vardapetyan, 1972; Plassmann *et al.*, 1997; and ref. herein), or all

426   sorts of smaller forms irrespective of body structure and the presence of lorica (Karabin,

427   1978; Walz, 1995; and ref. in all). The predation indicator from "Cyclopoids" was not

428   significant (p = 0.493) in Lake Gjerstadvann, probably due to the relatively small cyclopoid

429   populations. The abundance of the summer-active, mainly epilimnetic species *Thermocyclops*

430   *oithonoides* and *Mesocyclops leuckarti* (both winter diapausing) was relatively low in Lake

431   Gjerstadvann (Wærvågen and Nilssen, 2010) and several other Norwegian lakes (Nilssen and

432   Wærvågen, 2000). *Cyclops scutifer* was perennially present in the plankton in Lake

433   Gjerstadvann (Wærvågen and Nilssen, 2010). Despite this, we found no significant predation

434   effects of this species which is known to predate upon rotifers (Monakov *et al.*, 1972;

435   Vardapetyan, 1972). Furthermore, its predatory instars were present in high numbers mainly

436   following ice break when few rotifers normally are present in the plankton. The coloniality

437   tendency in *Conochilus* probably protects individuals from predation by copepods and

438   carnivorous/omnivorous rotifers (Anderson, 1977; Stemberger and Gilbert, 1987a; Matveeva,

439   1989; Diéguez and Balseiro, 1998), as for *C. unicornis* in this study. Finally, Lake

440   Gjerstadvann was in a process of continuous acidification at the time of sampling, and some

441   of the cyclopoid species were suffering (Wærvågen and Nilssen, 2010), as was also found in

442   nearby upstream lakes (Sandøy and Nilssen, 1987).

443

444   In fishless ecosystems Stenson (1982) found that the abundance of suspension feeders within

445   the rotifers decreased strongly. Under low fish predation, and a potentially high abundance of

446   *Chaoborus* spp. as a consequence, the latter may exert a strong predation influence on the

447   relative abundance and spatial distribution of their preferred prey rotifers in addition to the

448   total zooplankton community (Nyberg, 1984; Yan *et al.*, 1991; Moore *et al.*, 1994). In Lake

449   Gjerstadvann, such larvae represented the most important fish food item during most of the

450   year (Linløkken, 1988; Vethe, 1988), although they were very seldom collected in the

451   quantitative zooplankton samples (Wærvågen, 1985). We found no significant predation

452   indicator from *C. flavicans* (p = 0.410) in Lake Gjerstadvann. The species resided mainly in

453   the sediment during daytime, and migrated into the hypolimnion during the night where it was

454   highly selected by both Eurasian perch and brown trout (Vethe, 1988).

455

456   **CONCLUSIONS**

457   The major ecological factor influencing rotifer abundance and seasonal occurrence in Lake

458   Gjerstadvann was the perennial low abundance of food, which indicates that resource

limitation and food competition are important factors in structuring rotifer seasonal

population dynamics. The lake has both relatively low allochtonous input of organic matter

and low autochtonous pelagic algae production, and therefore the basis for high abundance

levels of rotifers in Lake Gjerstadvann was therefore not fulfilled. But, Lake Gjerstadvann

still had several common rotifer species present, and possible reasons may be the fact that we

found no significant effects of the acidification indicators pH and RAl on the total rotifer

community in this lake, even though some individual species may have been affected.

Furthermore, we found no significant predation indicator from *C. flavicans* or predator stages

of cyclopoid copepods (Cop IV-adult stages). The most significant competition indicator

species were *B. longispina* and *E. gracilis*, in good accordance with the their dominance as

cladoceran and copepod species in Lake Gjerstadvann, respectively (Wærvågen and Nilssen,

2010, 2011). Among the highly significant environmental gradient indicators were

temperature and oxygen, illustrating the important effects of the seasonal cycle and vertical

density stratification in the rotifer community.

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Tab. 1. Sampling depths of chemical and quantitative zooplankton samples in Lake

Gjerstadvann 1980/81. The representative layers given in % and volume proportions.

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Sample depths (m)	Representative layer (m)	Proportion (%)	of total volume (m^3 x 10^6)
1	0-2	13	1.83
3	2-4	12	1.68
5	4-6	10	1.52
7	6-8	10	1.42
10	9-12	17	2.54
15	12-18	22	3.15
20	18-22	10	1.52
25	22-27	6	0.88
Mean depth: 15.3 m	Max. depth: z_m = 27 m		Total volume: 14.54 x 10^6 m^3

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Tab. 2. List of all metazoan species collected in the pelagial of Lake Gjerstadvann in

1980/81. Relative abundance within each group of animals is indicated as: XXX =

dominating, XX = frequent, X = few specimens and R = rare.

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Rotifera:		Cladocera:	
Conochilus unicornis Rousselet,1892	XXX	*Bosmina longispina* Leydig, 1860	XXX
Conochilus hippocrepis (Schrank, 1803)	R	*Holopedium gibberum* Zaddach, 1855	XX
Polyarthra minor Voigt, 1904	XXX	*Diaphanosoma brachyurum* (Liéven, 1848)	XX
Polyarthra vulgaris Carlin, 1943	XX	*Polyphemus pediculus* (Linnaeus, 1761)	X
Polyarthra dolichoptera Idelson, 1925	R	*Bythotrepes longimanus* Leydig, 1860	X
Kellicottia longispina (Kellicott, 1879)	XXX	*Ceriodaphnia quadrangula* (O.F. Müller, 1776)	X
Keratella hiemalis Carlin, 1943	XX	*Leptodora kindti* (Focke, 1844)	X
Keratella cochlearis (Gosse, 1851)	XX	Chydoridae spp. Stebbing, 1902	X
Keratella serrulata (Ehrenberg, 1838)	X	*Scapholeberis mucronata* (O.F. Müller, 1776)	R
Keratella ticinensis (Callerrio, 1920)	X	*Sida crystallina* (O.F. Müller, 1776)	R
Keratella testudo (Ehrenberg, 1832)	R	*Daphnia lacustris* G.O. Sars, 1862	R
Collotheca libera (Zacharias, 1894)	X		
Collotheca liepetterseni Bērziņš, 1951	X		
Ascomorpha ecaudis Perty, 1850	X	**Insecta:**	
Lecane spp. Nitzsch, 1827	X	*Chaoborus flavicans* (Meigen, 1830)	X
Asplanchna priodonta Gosse, 1850	X		
Synchaeta gr. *tremula-oblonga*	X		
Euchlanis dilatata Ehrenberg, 1830	R	**Copepoda:**	
Trichocerca spp. Lamarck, 1801	R	*Eudiaptomus gracilis* (G.O. Sars, 1863)	XXX
Gastropus stylifer Imhof, 1891	R	*Heterocope saliens* (Lilljeborg, 1863)	R
Gastropus minor (Rousselet, 1892)	R		
		Cyclops scutifer G.O. Sars, 1863	XXX
		Mesocyclops leuckarti (Claus, 1857)	XX
Fish:		*Thermocyclops oithonoides* (G.O. Sars, 1863)	X
Perca fluviatilis Linnaeus, 1758	XXX	*Cyclops abyssorum* G.O. Sars, 1863	R
Salmo trutta Linnaeus, 1758	XX	*Diacyclops nanus* (G.O. Sars, 1863)	R
Coregonus lavaretus (Linnaeus, 1758)	X	*Diacyclops bicuspidatus* (Claus, 1857)	R
Salvelinus alpinus (Linnaeus, 1758)	R	*Megacyclops gigas* (Claus, 1857)	R

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Figure legends

Fig. 1. Lake Gjerstadvann and its catchment area. a) Geographical position in southern Norway; b) Catchment area climate (as mean monthly air temperature); c) Depth map with sampling station (*); d) Streamflow as specific discharge ($L\ s^{-1}\ km^{-2}$) of the dominating inlet River Storelva (-------- ; no available data before November 1980) and a neighbouring, continuously monitored River Stigvasså i (——— ; used as a proxy for River Storelva in 1980).

Fig. 2. Isoplots for temperature (°C), pH, oxygen (%) and water colour Pt ($mg\ L^{-1}$) in Lake Gjerstadvann 1980-1981. Ice covers are shown in real dimensions as black bars here and in similar figures.

Fig. 3. Principal Components biplot of physical and chemical water quality parameters, based on variables that have been centered and scaled to zero means and unit standard deviations. Arrows represent loadings of the different parameters while dots represent scores of individual samples, colour coded according to sample depth (see top left in this Fig. and Tab. 1). PC1 and PC2 represented 39% and 19% of the total variance, respectively. Key to environmental parameters: Temp (temperature), O2 (% oxygen), pH, K25 (conductivity as K_{25}), RAl (reactive aluminium), TN and TP (total N and P), Fe and Mn (total Fe and Mn), SiO2 (SiO_2), UV254 (organic matter as UV-absorption at 254 nm), KMnO4 (organic matter determined by oxidation with $KMnO_4$), Pt (water colour expressed as mg Pt L^{-1}, closely related to TOC) and finally the ions Ca (Ca^{2+}), Mg (Mg^{2+}), Na (Na^+), K (K^+), SO4 (SO_4^{2-}), Cl (Cl^-), NO3 (NO_3^-), NH4 (NH_4^+).

840 Fig. 4. Population abundance (logaritmic scale) and vertical distribution of the two most

841 abundant rotifer species in Lake Gjerstadvann during 1980/1981. a) *Conochilus unicornis* and

842 some few specimens of *Conochilus hippocrepis* recorded at all depths in the autumn overturn

843 (marked in the graph); b) *Polyarthra* spp., where *Polyarthra vulgaris* was the most abundant

844 species during late summer epilimnion, early autumn, and the whole winter, whereas

845 *Polyarthra minor* dominates most of the summer season. *Polyarthra dolichoptera* was

846 recorded in small numbers in the upper water masses during late autumn/early winter. The

847 font sizes indicate the individual species abundance.

848

849 Fig. 5. Population abundance and vertical distribution of the medium abundant rotifer species

850 in Lake Gjerstadvann during 1980/1981. a) *Kellicottia longispina*; b) *Keratella hiemalis*; c)

851 *Keratella cochlearis*; d) *Collotheca libera* and *C. liepetterseni*; e) *Ascomorpha ecaudis*; f)

852 *Lecane* species (see text for the different *Lecane* spp.).

853

854 Fig. 6. Population abundance of the less abundant species: *Asplanchna priodonta, Synchaeta*

855 gr. *tremula-oblonga*, *Keratella serrulata* and *Keratella ticinensis* in Lake Gjerstadvann during

856 1980/1981.

857

858 Fig. 7. Total rotifer abundance and their relationship to mean values (0 – 10 m depth) of

859 temperature and potential food as algae ($mm^3 m^{-3}$) and organic matter calculated as TOC (mg

860 L^{-1}) in Lake Gjerstadvann 1980/1981. See text for further details.

861

862 Fig. 8. NMDS ordination diagram based on Bray-Curtis dissimilarity of fourth root-

863 transformed rotifer abundances, showing species loadings using the abbreviations below and

864 with fitted environmental gradients and biotic interactions indicated by grey arrows. Sample

scores are colour coded by month and indicated by thin lines from individual score points to
the monthly centroid. The potential predators shown as *C. flavicans* (larvae) and Cyclopoids
(see Methods), and finally the two potential competitors *E. gracilis* and *B. longispina*. Key to
rotifer species: C.unic (*Conochilus unicornis*), Poly.spp (*Polyarthra* spp.), K.longi
(*Kellicottia longispina*), K.hiem (*Keratella hiemalis*), K.cochl (*Keratella cochlearis*), K.serrul
(*Keratella serrulata*), Coll.liep (*Collotheca liepetterseni*), Coll.lib (*Collotheca libera*),
Asmo.eca (*Ascomorpha ecaudis*), Lec.spp (*Lecane* spp.), Synch.spp (*Synchaeta* gr. *tremula-oblonga*).
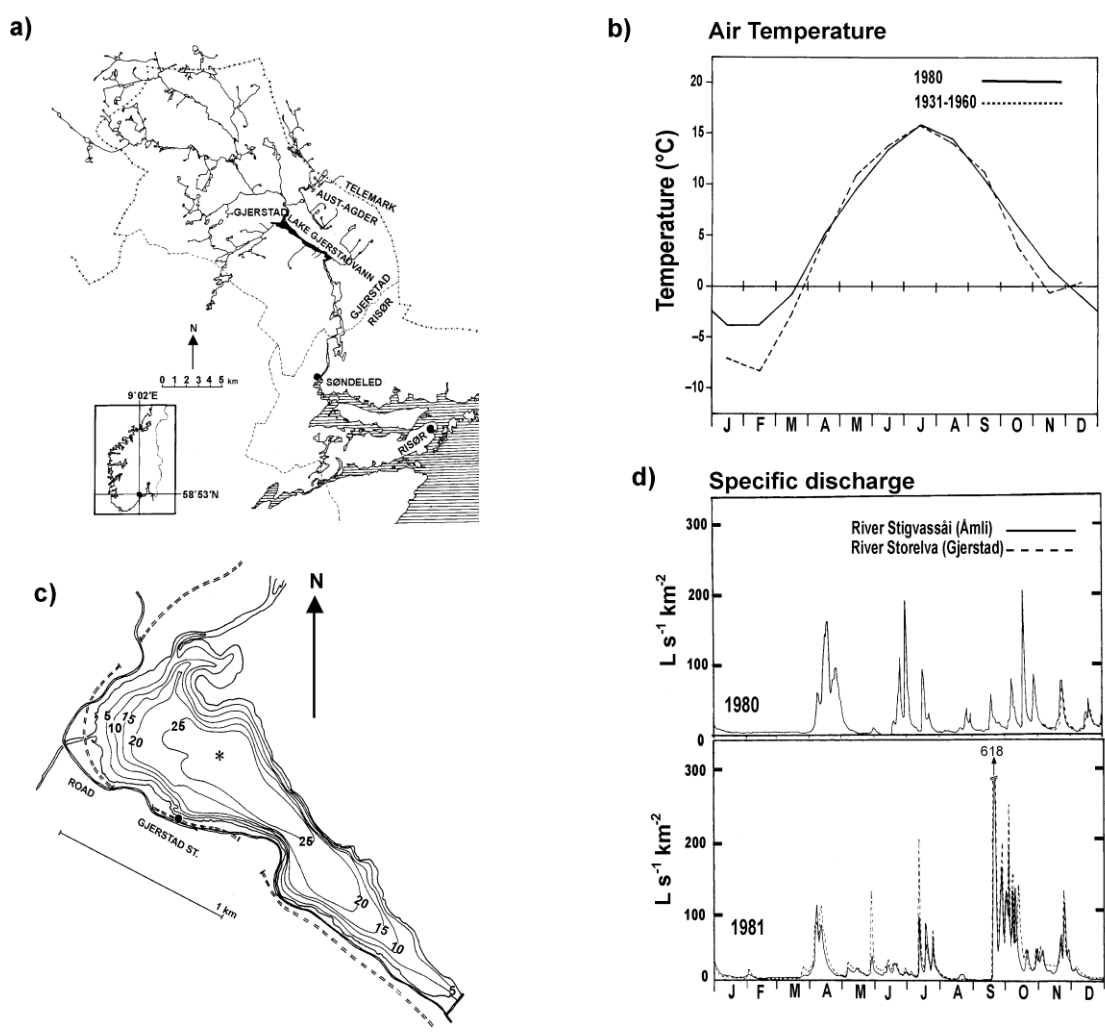
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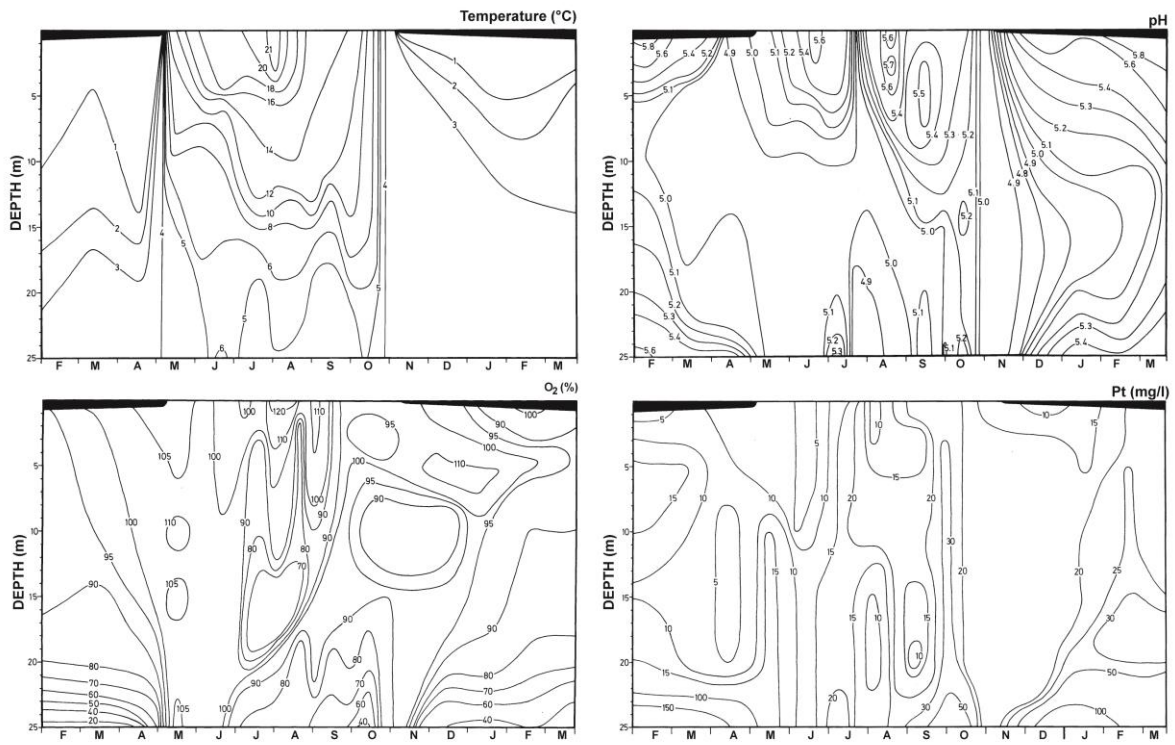
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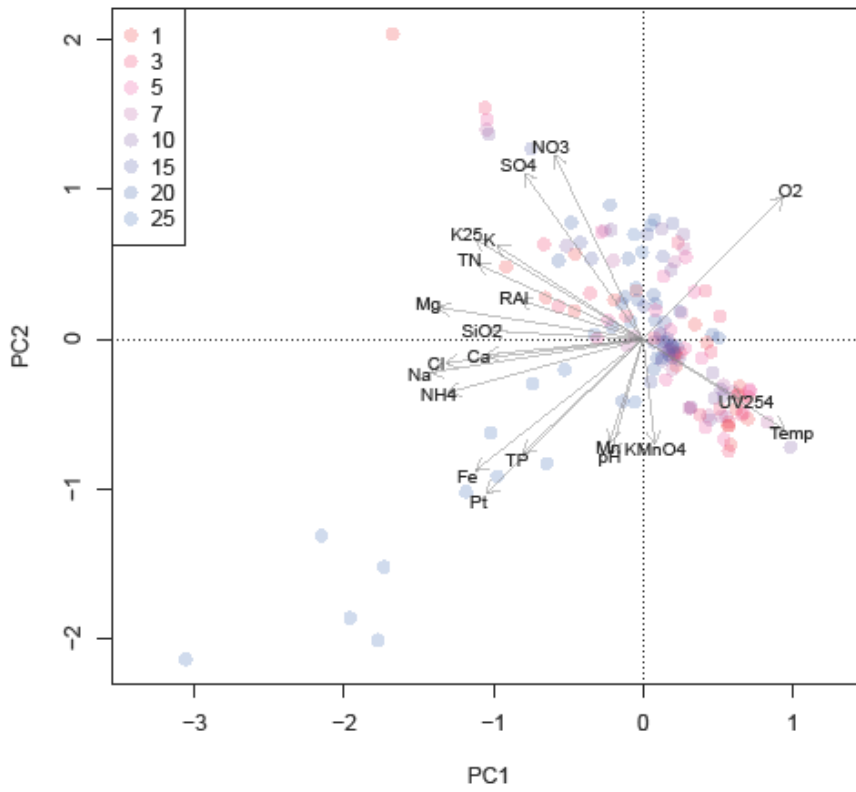
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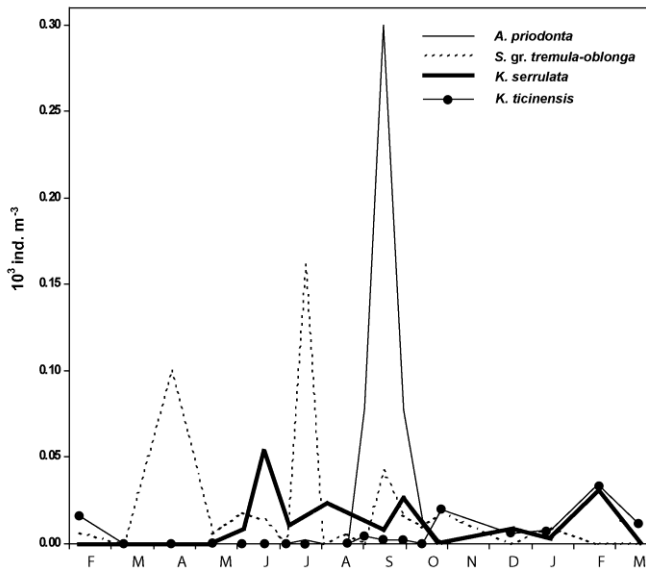

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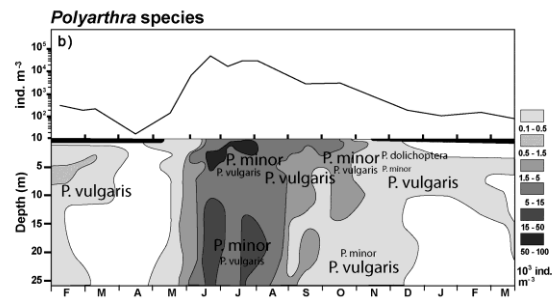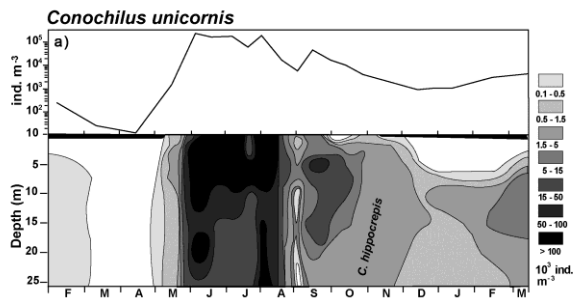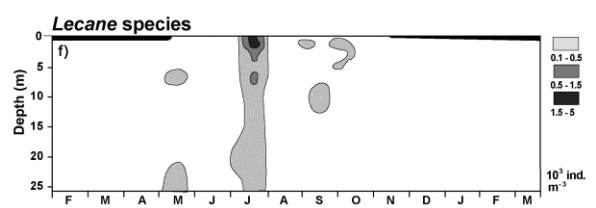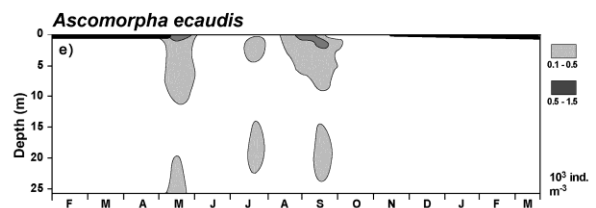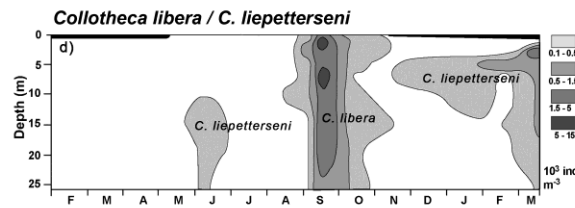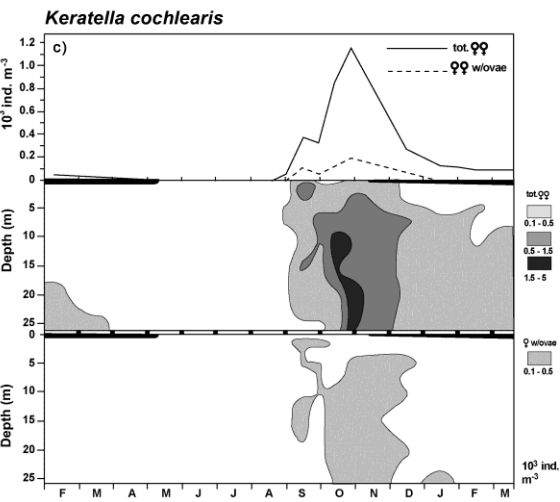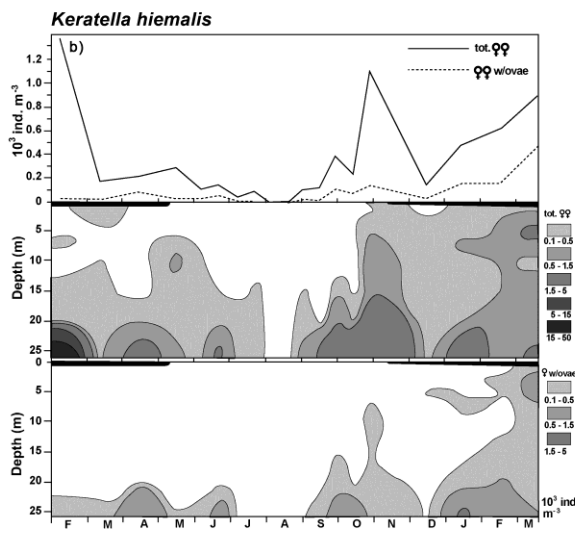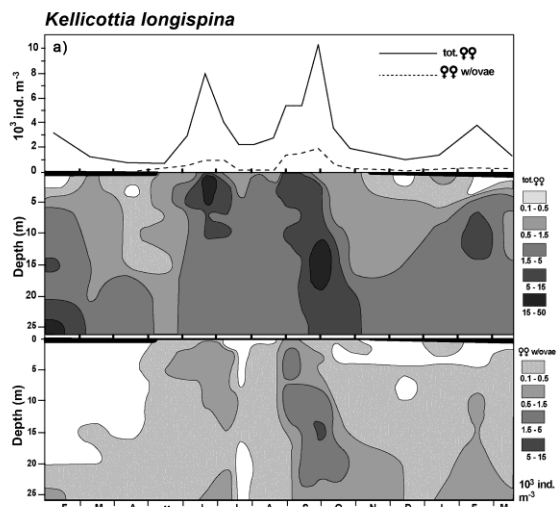
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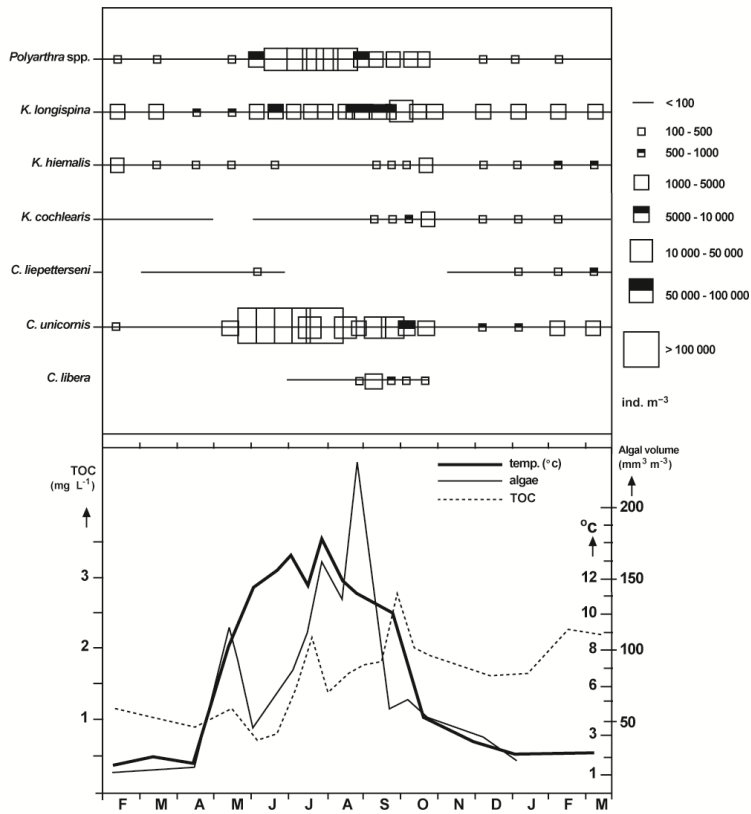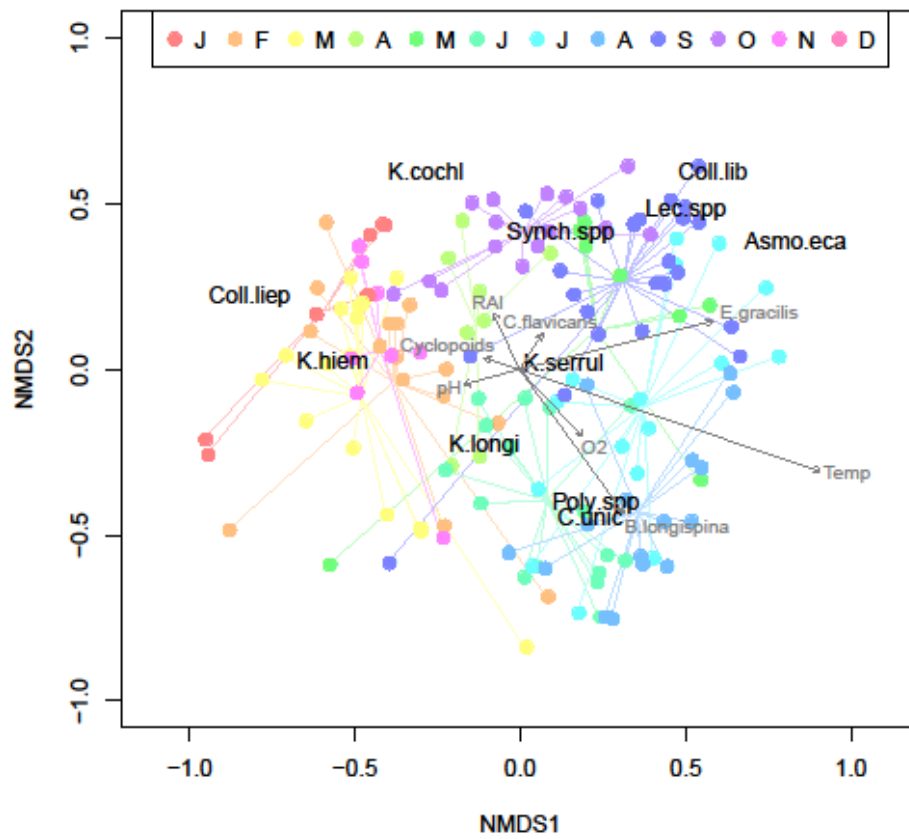
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887   Fig. 6

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890   Fig. 7 Updated Nov 2017

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Fig. 8 Updated Nov 2017

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Rebuttal letter

Dear Diego Fontaneto
CNR Institute of Ecosystem Study

The above revised version of the manuscript have taken into consideration most of the comments from the reviewers and Editor.

The structure of the manuscript is made more clear, we have moved some parts from the results into the methods. We have tried to sort out all the inferences.

The abstract is made more clear by starting with a hypothesis equivalent with the abstract conclusions.

The methods is revised to improve the clarity, and species identification is updated in accordense with suggested nomenclature.

The English language is now corrected again throughout the whole paper.

Due to species identification updating, three Figs. (5, 7 and 8) are updated since they were

influenced by e.g. the change to *C. liepetterseni* species name. Fig. 8 is updated in accordense

with the paper text to give species names in Italics.

Kind regards,
Svein Birger Wærvågen
Associate Professor,