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1 **Title:** An examination of long-term ecological studies of rotifers: comparability of methods and results, insights  
2 into drivers of change and future research challenges.

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16

17 **Abstract**

18 Long-term research (LTR) can provide insights into rotifer ecology that are not possible from short-term studies  
19 or experiments. However, such studies have become rarer in recent years due to budgetary constraints. This  
20 review examined 5023 published articles about rotifers to determine the number, location and types of LTR  
21 studies that had been undertaken. Forty-four articles reported the results of studies that spanned more than 10  
22 years. Of these, most focused on the impacts of climate change, acidification/liming, and  
23 eutrophication/recovery on waterbodies and soils. However, some investigated ecosystem function, especially in  
24 relation to the effects of invasive species or the development of cost effective and comparable sampling  
25 techniques. The types of sites examined in these LTR studies included lakes and reservoirs, rivers, lagoons, seas  
26 and estuaries, and soils, with the lengths of LTR records ranging from 10 to 82 years. Although their  
27 geographical locations ranged from North and South America to Asia, the Middle East and Europe, no studies  
28 were found from Africa, Australia or Antarctica. This review explores the role of LTR in quantifying the effects  
29 of environmental change and highlights gaps in existing knowledge.

30

31 **Keywords:** waterbodies, soils, climate, change, acidification, eutrophication

32

### 33 **Introduction**

34 According to Hobbie et al. (2003), long-term research can be defined by its primary goal: "... to understand  
35 long-term patterns and processes of ecological systems at multiple spatial scales". In addition to having 'time' as  
36 an essential feature, the outcomes of such efforts yield six important benefits. According to Hobbie and his  
37 colleagues these are: (1) attaining greater understanding of systems across wide spatial scales, (2) synthesising  
38 information and theory, (3) disseminating knowledge, (4) creating legacy experimental designs and archived  
39 samples, (5) training new professional and citizen scientists, and (6) delivery knowledge to stakeholders.

40 Although their review was presented within the context of ecological studies, the merits of studying any system  
41 (e.g. economic, medical, political, social) over a long time period has the same purpose and potential outcomes.

42  
43 Long-Term Research (LTR) in ecological systems, spanning years or even decades, is important because it  
44 provides insights into the effects of environmental change on complex systems that cannot be observed over  
45 shorter timescales or visualised by experimentation (Hampton 2013; Hampton et al. 2018; Hobbie et al. 2003;  
46 Lindenmayer & Likens 2009). For example, LTR on lakes in the English Lake District revealed a link between  
47 in-lake processes and large-scale climatic change associated with the North Atlantic Oscillation (Maberly &  
48 Elliott 2012). LTR studies also can provide important scientific evidence of responses to changing  
49 environmental pressures that can be used to inform management practices aimed at maintaining and/or restoring  
50 ecosystems (e.g. Carvalho et al. 2012; May & Spears 2012). Long-term studies, especially when working at  
51 international level, such asILTER and GLEON, "...provide a coordinated response to the need for scientific  
52 understanding of lake processes" (Hamilton et al. 2015; Maass et al. 2016; Rose et al. 2018).

53  
54 Regrettably, many LTR studies have failed to deliver useful results due to poor planning or the lack of tractable  
55 research questions that enable the work to be focused (Lindenmayer & Likens 2009). In its formative years, this  
56 lack of focus gave LTR a bad reputation (Lovett et al. 2007). In particular, Roberts (1991) criticised many LTR  
57 studies for using a 'collect now, think later' approach and Lindenmayer & Likens (2009) have suggested that  
58 LTR studies could be improved in future by adopting a more adaptive approach. This, they argue, would allow  
59 changes to emerging research challenges to be addressed more effectively, including the incorporation of better  
60 sampling methods and monitoring technologies as they become available. However, care should be taken to  
61 ensure data comparability, because changes to sampling procedures and analytical methods can make direct  
62 comparisons across time and space very difficult (Beard et al. 1999).

63

64 LTR studies could be seen as “unreplicated natural experiments” (Barley & Meeuwig 2017) and, as such, could  
65 attract criticism for not being replicable and, indeed, having no ‘control’ treatment (Hurlbert 1984). Thus, much  
66 of the work that we examined here presents “curiosity-driven monitoring ... [often] devoid of specific questions  
67 ... and [with] no underlying experimental design ...” (Likens & Lindenmayer 2018). Although there is no good  
68 way to replicate long-term studies, reviewing the results of past efforts is a practical way of glean  
69 information that can lead to the construction of testable hypotheses, and realization of some of the benefits  
70 suggested by Hobbie et al. (2003).

71

72 In spite of their limitations, LTRs have been key to improving our understanding of environmental pressures and  
73 their effects on freshwater ecosystems for many years. In the 1960s, they helped to highlight excessive use of  
74 phosphorus as being the main driver of eutrophication problems in lakes and rivers (Edmondson 1991; Smith &  
75 Schindler 2009). In the 1970s, they enabled us to identify acid rain as an important driver of water quality  
76 problems in lakes and rivers, especially across northern Europe (Folster et al. 2014). More recently, LTR data  
77 have provided insights into the ecological effects of increases in organic pollution and climate change effects  
78 (Folster et al. 2014).

79

80 Wherever there is sufficient liquid water to permit reproduction, the phylum Rotifera are ubiquitous. Besides  
81 lakes, ponds, and streams, their habitats include birdbaths and other anthropogenic objects, cryoconite holes, the  
82 water film on damp mosses, phytotelmata, puddles, rock pools, and soils (Walsh et al. 2014). Regardless of size  
83 of the system, rotifers are often critical to ecosystem functioning. By feeding on basal trophic levels and passing  
84 energy and nutrients to higher levels (invertebrate predators and fish), rotifers provide an important link within  
85 the classical, grazer driven food web, as well as being critical components within the microbial loop (Fermani et  
86 al. 2013; Onandia et al. 2015). Rotifers have practical use as bioindicators and sentinel species. Due to their  
87 rapid growth rates and sensitivity to variations in food, pH, temperature, and toxic agents, they are recognised  
88 widely as being useful in assessing the effects of changes in their habitat, both natural and experimental (e.g.  
89 Hampton 2005; Rico-Martínez et al. 2016; Snell & Marcial 2017). Thus, LTR studies that review the role of  
90 rotifers in a variety of ecosystems can provide insights into the effects of environmental change. It is within this  
91 context that we have reviewed published LTR studies from across the world to enhance our knowledge of the  
92 impacts of change on rotifer communities. In particular, we sought to address the following major questions: (1)

93 Do the existing LTR studies of rotifer habitats and communities represent all major habitat types? (2) Have  
94 these studies provided comparable information? (3) What are the effects of long-term environmental change on  
95 rotifer populations? (3) What can we glean from these LTR studies? (4) What are the main knowledge gaps that  
96 LTR needs to address? Addressing these questions enables us to distinguish between short-term trends and the  
97 long-term impacts of anthropogenically driven changes to the environment.

98

## 99 **Methods**

100

101 Potentially relevant literature was sought using Web of Science (<https://wok.mimas.ac.uk/>), an online  
102 subscription-based service that provides a comprehensive search facility for scientific publications. The initial  
103 search criterion used was ‘Rotifer\*’ in the abstract or title, where ‘\*’ indicates any value. So, in effect, the main  
104 search criteria were the words ‘rotifer’, ‘rotifers’, ‘rotifera’, etc. This returned 5023 references published  
105 between 1970 and 2018. All of these were downloaded into reference manager software (Endnote® version X8)  
106 and categorised according to additional criteria. The first was ‘season\*’ or ‘year\*’ in the title or abstract, which  
107 was taken to mean that the publication contained temporal information; this search returned 1016 references. Of  
108 these, references were then selected on the basis of being included in one of two habitat types: i.e. aquatic (476)  
109 or soils (2), with all other habitat types (540) being excluded. Separation into aquatic (ie lakes, reservoirs, rivers,  
110 lagoons, seas and estuaries) or soil habitats was undertaken because of the very different sampling regimes that  
111 are used in these environments. Studies that provided species lists but no quantitative data (i.e. no levels of  
112 abundance) were excluded from the study, as were studies of rotifers in ‘other habitat types’ such as sewage  
113 works, paddy fields, mesocosms or laboratory cultures.

114

115 Each of the 476 references pertaining to aquatic habitats was examined in detail to determine length of study,  
116 sampling method and frequency, and the research question(s) addressed. Studies where sites had been sampled  
117 at least monthly over the ice-free period were categorised according to length of study, with number of years  
118 being defined as the number of complete, but not necessarily consecutive, years of data. Of the 476 references,  
119 386 were found to be short-term (i.e. < 5 years), 46 medium-term (i.e. 5 to < 10 years) and 44 long-term (i.e. ≥  
120 10 years). Our definition of ‘long term’ followed that proposed by Lindenmayer & Likens (2010).

121

122 Within the context of our review, only studies identified as long-term were examined in more detail. The  
123 duration of these 44 studies ranged from 10 to 82 years, providing a substantial amount of information from  
124 which we could draw conclusions. However, it is unclear how many of these studies have continued to the  
125 present day. For the soil habitats, there were no long-term studies *per se*, so studies based on space for time  
126 sampling (i.e. a comparison of consistently undisturbed systems with those that had been disturbed up to 40  
127 years ago) have been included.

128

129 All of the LTR studies were reviewed in terms of the insights that they provide into the responses of rotifers to  
130 large scale and long-term environmental change, most of which would not have been evident from shorter  
131 studies.

132

### 133 **Results of literature survey**

134

#### 135 *Representativeness of existing studies*

136 The literature survey identified 44 LTR studies on aquatic environments and two on soils, located in a number  
137 of different countries (Table1). The lengths of study varied between 10 and 82 years, with one study starting as  
138 early as 1908 (Fig. 1; Table 2). The studies varied according to the types of habitat investigated, their  
139 geographical locations and the methods used to gather data.

140

#### 141 Types of habitat and geographical distribution

142 The LTR studies spanned a wide range of habitats, including soils, lagoons, estuaries, seas, rivers, and lakes.  
143 However, the number of studies per habitat type varied greatly, with lakes being by far the most common  
144 (Tables 1 & 2). In contrast, there were few studies on other types of habitat, and long-term studies of bdelloid  
145 rotifers were found to be especially rare.

146

147 There were insufficient data to categorise studies of soils, rivers, lagoons, estuaries, and seas beyond this very  
148 high-level habitat typology. However, as lake studies were more numerous, these were explored further to  
149 determine the types of lakes that were represented, based on their surface area, mean depth and volume (Fig. 2).  
150 These results are compared to summary data for the world population of lakes, below.

151

152 There are about 117 million lakes in the world, covering a total area of 5 million km<sup>2</sup> (Verpoorter et al. 2014).  
153 Of these, only 35 are included in long-term rotifer studies that have been published. Of the lakes studied, Crystal  
154 Lake (Minnesota, USA) is the smallest, covering an area of 0.38 km<sup>2</sup> (Rusak & Montz 2009), and Lake Baikal  
155 (Russia) is the largest, with a surface area of 31,722 km<sup>2</sup> (Hampton et al. 2014). More than half (22) were  
156 relatively small lakes, with surface areas of less than 100 km<sup>2</sup>; of these, 59% (13) had surface areas of less than  
157 10 km<sup>2</sup> (Fig. 2a). This is in contrast to the world population of lakes, which is believed to comprise about 3  
158 million lakes with a surface area of less than 100 km<sup>2</sup> and 3 million with a surface area of less than 10 km<sup>2</sup>  
159 (Downing et al. 2006). Clearly, the world's lakes are very under studied in terms of their rotifer communities.

160

161 There are few statistics available on the depths and volumes of the world's lakes. However, in terms of mean  
162 depth, the data that we compiled suggest that most long-term studies (58%) have focused on shallow lakes with  
163 mean depth of less than 10 m. The shallowest of these is Neusiedlersee (Austria), with a mean depth of only  
164 1.2 m (Dokulil & Herzig 2009). In contrast, only 4% of lakes with LTR data on rotifers had a mean depth of  
165 more than 200 m (Fig. 2a); the largest was Lake Baikal, with a mean depth of 744 m (Hampton et al. 2014). In  
166 terms of volume (calculated as mean depth x surface area, unless otherwise stated), most LTR studies of rotifers  
167 (50%) focused on relatively small lakes with volumes of less than 0.5 km<sup>3</sup>; only 4% had a volume of more than  
168 500 km<sup>3</sup> (Fig. 3c). Of these, the smallest lake was Lake Valkea-Kotinen (Finland), with a volume of 0.1 km<sup>3</sup>  
169 (Lehtovaara et al. 2014), whilst the largest was Lake Baikal, with a volume of 23,601 km<sup>3</sup> (Hampton et al.  
170 2014). Lake Baikal is the largest freshwater lake in the world in terms of depth and volume, but there are many  
171 other large lakes that have not been studied in terms of their rotifer populations.

172

173 The geographical distribution of lakes with long-term data on rotifers was divided into the following areas:  
174 Europe, North America, Asia, and South America (Fig. 3). Although distributed across the world, they are much  
175 more common on some continents than others. The majority of LTR sites (53; 75%) were found to be in Europe,  
176 where they span 15 different countries, while many more (11; 16%) were located in North America, where they  
177 are distributed across the USA and Canada. There were, however, few sites in other parts of the world, with only  
178 4 (6%) being in Asia (Siberia, China and Israel) and only 2 (3%) in South America (Brazil/Paraguay and  
179 Argentina) (Verpoorter et al. 2014). No LTR on rotifers was found in African lakes, highlighting a regrettable  
180 gap in our knowledge of some of the world's most iconic water bodies. There was also a notable lack of LTR  
181 sites in Australia and Antarctica.



182

183 Methods used and comparability of results

184 Beard et al. (1999) reviewed the value of using consistent methodologies for long-term environmental  
185 monitoring. The authors concluded that changes in procedures and analytical methods to improve data quality in  
186 the short-term could, in the longer term, make the results more difficult to compare – especially between one  
187 project and another. To gain insight into the comparability of results, the published information that we  
188 examined was assessed for consistency over time in terms of sampling frequency and collection methods. Most  
189 of the LTR studies examined had used the same sampling methods throughout. In only one case (Swan Lake,  
190 Canada) had a change of mesh size been reported: i.e. 77  $\mu\text{m}$  until 1977, then 35  $\mu\text{m}$  in subsequent years (Arnott  
191 et al. 2001). Although problems associated with using different mesh sizes are now better understood,  
192 Obertegger & Manca (2011) argue that the main benefit of using the same sampling method throughout a  
193 particular study is that it allows valid comparison of data across years. Caution must be exercised, however,  
194 when comparing data across time and space if different methods of collection have been used (Hampton et al.  
195 2014).

196

197 Mesh sizes of plankton nets

198 Most of the studies reviewed have used plankton nets to collect and concentrate rotifer samples for counting.  
199 Mesh sizes (where stated) ranged between 20  $\mu\text{m}$  and 130  $\mu\text{m}$ , with most studies using meshes of less than 100  
200  $\mu\text{m}$  (Fig. 4), although larger sizes (125  $\mu\text{m}$  and 130  $\mu\text{m}$ ) were used at two of the sites. It is well known that  
201 estimates of rotifer species composition and abundance are strongly affected by the size of mesh used to collect  
202 them or concentrate samples; for example, Bottrell et al. (1976) reported that using a 45  $\mu\text{m}$  mesh net to  
203 concentrate samples could result in underestimates of up to 80% compared to whole water sampling methods. In  
204 spite of this, only 29% of the long-term studies examined were found to have used mesh sizes  $\leq 45 \mu\text{m}$ .  
205 Although Bottrell et al. (1976) concluded that sedimentation was the best method of concentrating rotifers from  
206 whole water samples, only three of the LTR studies have used this technique; these were Loch Leven, UK (May  
207 et al. 2001), Donghu Lake, China (Shao et al. 2001; Yang et al. 2005), and Darß–Zingst Lagoon, Germany  
208 (Feike & Heerkloss 2008). The general preference for using nets to sample rotifers is probably caused by the  
209 practical constraints of collecting large volumes of water, especially in less productive waterbodies where  
210 population densities are low (Bottrell et al. 1976). However, where nets must be used to collect or concentrate  
211 rotifer samples, a mesh size of no greater than 20  $\mu\text{m}$  is recommended to keep underestimates of population

212 densities to a minimum (Chick et al. 2010). Of the LTR studies that gave details of their collection methods,  
213 only 19% were using nets within this size range.

214

#### 215 Sampling effort

216 Estimates of abundance are also affected by sampling effort. Rusak & Montz (2009) compared results obtained  
217 from four north temperate lakes to determine the amount of sampling effort required to quantify rotifer species  
218 and communities. The data had been collected from lakes sampled at fortnightly intervals during the ice-free  
219 period and at 6-weekly intervals during the winter, and each dataset comprised 10 full years of data spanning a  
220 26-year period. The authors found that, to estimate mean annual abundance of individual rotifer species with a  
221 precision of about 20%, 34–86 samples were needed per year. However, if the aim of a study was simply to  
222 determine patterns of change in abundance and community structure, comparable results could be obtained from  
223 as few as five samples per year. Rusak & Montz (2009) concluded that, although acceptable boundaries of  
224 sampling precision depended upon the aims of any particular study, for most zooplankton species, collecting and  
225 enumerating just 5–10 samples per year could provide enough detail for long-term trends in populations and  
226 communities to be evaluated. The authors noted, however, that aggregated rotifers were the only taxon for  
227 which patterns shown by fortnightly and monthly data were not more or less synchronous. So, they urged  
228 caution in using this approach to interpret patterns within individual species and among aggregated taxa that  
229 have high intra-annual variability. Voutilainen & Arvola (2017) explored 21 years of data from Valkea-Kotinen  
230 (Sweden) to determine factors associated with sampling frequency that were likely to affect the conclusions  
231 derived from LTR studies. They found that the number of missing values needed to be minimised because  
232 incomplete data could cause bias; they also concluded that replacing missing values by mean values could lead  
233 to misleading results. Voutilainen & Arvola (2017) also highlighted the importance of taking samples during  
234 winter for the detection of long-term trends, because differences between winter and summer tend to be larger  
235 than differences between consecutive years.

236

237 Most of the LTR studies examined in the current study were found to meet the above criteria for tracking long-  
238 term trends in rotifer (i.e., 5–10 samples per year), but few collected enough samples (i.e. 34–38 samples per  
239 year) for annual mean abundances to be estimated accurately. However, it should be noted that, by  
240 deconstructing data collected at 3-day intervals to explore the impact of longer interval sampling and different  
241 start dates, Berner-Fankhauser (1987) was able to demonstrate that even 34–38 samples per year (a sampling

242 interval of about 10 days) would not be able to pick up the rapid changes in abundance that rotifers undergo  
243 over short time intervals, especially during the summer.

244

#### 245 *Insights into the effects of environmental change on rotifer populations*

246 Three important environmental changes have provided much insight into rotifer population dynamics. These  
247 are: water temperature, water quality and invasive species. While the ultimate cause of each of these changes is  
248 fundamentally anthropogenic, the speed at which they occur and their immediate consequences vary widely. In  
249 most cases, their long-term impacts are cumulative rather than sudden, and are often caused by complex  
250 ecosystems re-equilibrating under constantly changing conditions. These overarching trends in drivers and  
251 responses would not be visible from short term monitoring or experimental data, which are often dominated by  
252 short term (and especially within year) temporal variation.

253

254 There are few LTR studies of rotifers in rivers, and those that do exist provide little information on changes in  
255 species composition or abundance in response to environmental change. One of the exceptions to this is that of  
256 Bonecker et al. (2013), who examined the temporal diversity of rotifers in the Upper Parana River (Brazil)  
257 between 2000 and 2009. Their study showed that, over time, the gamma and alpha diversities of the rotifer  
258 communities decreased, while their beta diversity increased. Another exception is a study of the zooplankton of  
259 the middle Parana River (Argentina) between 1971 and 2007, which found that rotifer numbers declined  
260 significantly after 1999 and that there was growing evidence that levels of competition between rotifers and  
261 cladocerans were increasing (de Paggi et al. 2014). One final example is that of Deksne (2011), who analysed  
262 data collected between 1962 and 1968, and between 2005 and 2009, from the Duagava River, which lies  
263 between Belarus and Latvia. Again, the dominant group of zooplankton in the river was rotifers, and it was  
264 noted that there was a tendency for the species diversity of zooplankton in this river to decrease over time.

265

266 Studies of rotifers in soils are much rarer than studies in aquatic systems, and those aimed at investigating  
267 changes over time are not based on LTR data, as such. Instead, they are based on space-for-time comparisons of  
268 rotifers in soils of different ages. An example is the study of Devetter & Frouz (2011), who compared rotifers  
269 from a range of un-reclaimed, clay, post mining, soils of various ages (i.e. 2, 11, 14, 20, 43 years). In total, 34  
270 rotifer taxa were found, with the number of species increasing with age of plot. The most important variables  
271 affecting the rotifer community were found to be wood cover, sodium concentration, and age of plot. While

272 some species, such as *Macrotrachela quadricornifera* Milne, 1886, were found to be present throughout the  
273 chronosequence, others were found in plots of a certain age, only. The pioneer species in the newer plots  
274 included *Encentrum incisum* Wulfert, 1936, *Habrotrocha rosa* Donner, 1949, and *Macrotrachela papillosa*  
275 Thompson, 1892, while *Adineta vaga* (Davis, 1873), *Encentrum arvicola* Wulfert, 1936, *Habrotrocha filum*  
276 Donner, 1949, and *Macrotrachela nana* (Bryce, 1912) were more common in 14–20 year old plots. In contrast,  
277 the oldest plots were dominated by *Adineta steineri* Bartoš, 1951 and *Encentrum mucronatum* Wulfert, 1936. In  
278 a similar study, Hanel (2001) explored the rotifer communities of soils in pine plantations situated on coal  
279 mining sands near Cottbus (Germany). By comparing a 30-year time series of data from this site with a 40 year-  
280 old semi-natural pine forest on natural sandy soil, the author concluded that rotifer population densities  
281 increased with age of stand, and that there was rapid colonisation of the coal-mining sands by rotifers. More  
282 specifically, the rotifer populations increased from undetectable levels in the spring of 1997 to  $50 \times 10^3$   
283 individuals  $m^{-2}$  by the autumn of 1998.

284

#### 285 Changes in water temperature

286 In terms of climate change, the main physical impacts on lakes are increases in water temperature and changes  
287 in the frequency and intensity of mixing events. Many studies have reported that some rotifer species show  
288 temperature preferences that result in seasonal changes in community structure and abundance. This is  
289 especially true of planktonic species (e.g. Berzins & Pejler 1989; May 1983; May 1987). For example, in an 11-  
290 year study of Loch Leven, UK (1977–1982 and 1994–1998), May et al. (2001) found that the seasonal  
291 occurrence of *Trichocerca pusilla* (Jennings, 1903) was limited to periods when the water temperature was  
292 above 10° C. In a similar study, Andrew & Andrew (2005), using data from Lough Neagh, Northern Ireland,  
293 that had been collected between 1968 and 1982, showed that water temperature was one of the main drivers of  
294 change in the lake's rotifer populations. The results of Halvorsen et al. (2004) also support these findings; while  
295 analysing data from Lake Atnsjøen (Norway), collected during ice-free periods between 1985 and 1997, these  
296 authors observed that the lake was usually dominated by low numbers of cold-stenotherms and by eurytherms  
297 that are typical of cold oligotrophic lakes. However, in 1995, they found that the rotifer populations in Lake  
298 Atnsjøen were much more abundant than in previous or subsequent years. As this is a subalpine lake that is  
299 almost completely unaffected by anthropogenic disturbance, the authors concluded that this change had been  
300 caused by increases in water temperature associated with unusually warm and dry weather in 1995.

301

302 In addition to responding to seasonal changes in water temperature, rotifers also react to longer-term changes in  
303 water temperature over larger scales, such as those caused by climate change. For example, studying the North  
304 Baltic Sea, Finland, between 1979 and 2008, Suikkanen et al. (2013) found a rotifer community comprising  
305 mainly *Keratella* spp. and *Synchaeta* spp. However, as the surface water warmed steadily between 1979 and  
306 2008, they found that the planktonic food web shifted towards larger numbers of smaller organisms that  
307 supported increasing numbers of rotifers. Similarly, Haberman & Haldna (2017), studying Lake Võrtsjärv  
308 (Estonia) between 1965 and 2014, found that the main driver of change in rotifer occurrence was water  
309 temperature. By focusing their analyses on spring and autumn data, when rotifers comprised 92% and 70% of  
310 the zooplankton, respectively, the authors found that shifts from cold- to warm-water species in spring and back  
311 again in autumn tended to occur when the lake water reached about 10° C. By the end of the 50-year monitoring  
312 period, the date on which this threshold occurred was 7 days earlier in spring and 6 days later in autumn than it  
313 had been at the beginning of their study. Winder & Schindler (2004), analysing long-term data from Lake  
314 Washington, USA (1975 to 1995), also found evidence of changes in water temperature affecting the timing of  
315 ecological events within the rotifer communities. In particular, the authors reported that spring peaks of  
316 *Keratella* were occurring about 15 days earlier in 1995 than they had been in the earlier years. In a novel study  
317 focusing on data collected during only the winter months, Dokulil & Herzig (2009) explored a 40-year record  
318 from Neusiedlersee (Austria). They showed that high zooplankton concentrations in winter were caused, mainly,  
319 by high densities of the rotifer *Rhinoglena fertoensis* (Varga, 1929). The level of abundance of this rotifer was  
320 closely related to winter weather conditions, especially ice cover.

321

322 Several authors have used LTR data to demonstrate the impacts of climate change on rotifers, as mediated  
323 through its effects on the thermal structure of lakes. These include Hampton et al. (2014), who analysed data  
324 from Lake Baikal (Siberia) and found that the density weighted average depth of rotifers in the lake had shifted  
325 upwards rapidly (by 0.57–0.75 m y<sup>-1</sup>) between 1955 and 2000. This seemed to be related the fact that an  
326 increase in surface water temperatures had strengthened the thermal gradient within the top 50 m of the water  
327 column. Similarly, in Lake Constance (Germany), using data collected between 1984 and 1996 (excluding 1985  
328 and 1986), Tirok & Gaedke (2006) found that rotifer densities were correlated with changes in wind induced  
329 mixing, with less mixing enhancing rotifer abundances. In addition, Wagner & Adrian (2011), exploring data  
330 from Müggelsee (Germany) collected between 1982 and 2007, found that the number of stratification events in  
331 the lake had increased over that period. When the lake was stratified, the surface water became warmer and

332 rotifers became more abundant; this is in contrast to the responses of cyanobacteria and cladocerans to these  
333 conditions.

334

#### 335 Changes in water quality and quantity

336 There are few LTR studies that provide any insight into the effect of changes in salinity on rotifers in brackish  
337 or marine environments. For example, while Johansson et al. (1993) looked at temporal variation in rotifers in  
338 the North Baltic Sea (Sweden) between 1976 and 1988 and found marked seasonal cycles in abundance, they  
339 did not explore the reason for this. Instead, they simply noted that rotifers comprised about 33% of the  
340 zooplankton. Viitasalo et al. (1995), who investigated the zooplankton of the Baltic Sea (Finland) in relation to  
341 weather and hydrology between 1967 and 1984, also provided little information about the rotifers that they  
342 found; instead, they simply noted that the optimal conditions for rotifers were a warm and stable environment.  
343 In a more detailed study, Feike & Heerkloss (2008) examined a brackish lagoon in the south Baltic Sea,  
344 collecting samples at weekly or three-weekly intervals between 1983 and 2004. However, as this lagoon showed  
345 high temporal stability in terms of its salinity, it provided little information on the effects of change on its rotifer  
346 populations. The authors did, however, conclude that composition and abundance of the zooplankton  
347 community was strongly affected by a range of other environmental factors, including the suppression of rotifers  
348 by the copepod *Eurytemora affinis* (Poppe, 1880) in spring. In contrast, Delpy et al. (2011) published one of the  
349 few long-term studies that did explore the relationship between rotifers and salinity. By monitoring the impacts  
350 of a new freshwater (diluting) discharge on the saline Berre Lagoon between 1966 and 2000, they were able to  
351 show that rotifer abundance was affected by the discharge itself and, later, by its regulatory control. While  
352 rotifers had previously been abundant in the lagoon, the strong modification of its salinity resulting from  
353 changes in the level of freshwater discharged into it caused the rotifer population to disappear almost  
354 completely.

355

356 In contrast to the lack of knowledge on the effects of changes in salinity, there are several long-term studies that  
357 indicate that rotifers respond quickly to changes in pH associated with the acidification and liming of  
358 waterbodies. For example, Arnott et al. (2001) found that the species richness and relative abundance of rotifers  
359 in Swan Lake (Canada) changed markedly between 1977 and 1990, when emissions from a local smelting works  
360 were reduced. Significant shifts in the rotifer community were especially evident between 1977 and 1984. These  
361 included a decline in the acidophilic species *Keratella tauracephala* Myers 1938, alongside an increase in the

362 abundance of more acid sensitive species such as *Trichocerca similis* (Wierzejski, 1893), *Conochilus natans*  
363 (Seligo, 1900), *Gastropus stylifer* Imhof, 1891, *Keratella crassa* Ahlstrom, 1943, and *Ploesoma truncatum*  
364 (Levander, 1894). By 1987, the species composition (richness) of the rotifer community was similar to that of  
365 nearby reference lakes that had not been affected by the smelting works. However, when drought-induced, re-  
366 acidification of the lake occurred in 1988, the authors found that the recovery process was quickly reversed,  
367 with the species composition and relative abundance of rotifers in the lake returning to the same levels as had  
368 been recorded in 1977. Stenson & Svensson (1995) reported similar results in relation to the effects of liming on  
369 rotifers in a study of two Swedish lakes between 1979 and 1991. The study compared an acidified reference lake  
370 (Norra Häskevatten) with a manipulated lake (Gårdsjön). Although both lakes were acidified, originally,  
371 Gårdsjön was treated with lime for 3 years after which brown and rainbow trout were introduced. The authors  
372 reported that liming had had a positive effect on rotifer diversity and abundance in the manipulated lake  
373 compared to the reference lake, and they concluded that liming could be used to restore the zooplankton  
374 communities of acidified lakes. However, they also noted that the overall structure of any re-established  
375 zooplankton community would probably depend on site-specific predation and competitive interactions within  
376 any treated lake. Research by both Lehtovaara et al. (2014) and Voutilainen & Arvola (2017), supported this  
377 view. They reported results from a 20-year (open water period; 1990–2010) study on Lake Valkea-Kotinen, a  
378 shallow lake in Finland. These authors found that, since the end of 1980s, the lake and its catchment had been  
379 recovering slowly from acidification as a result of a dramatic decline in sulphur deposition in the area.  
380 Lehtovaara et al. (2014) reported that rotifer abundances had fallen over the recovery period, suggesting that this  
381 may have been due to an inverse relationship between rotifers and cladocerans within the lake. However, in  
382 contrast, Voutilainen & Arvola (2017) revisited the data and concluded that the observed variations in rotifer  
383 numbers may have been driven by changes in water temperature. In contrast to these results, a study of Lake  
384 Flosek (Poland) undertaken by Weglenska et al. (1997), 1966–1974 and 1990–1993, showed a stable  
385 zooplankton community that had changed little over the 20 years since the lake had been limed in 1970. They  
386 attributed this lack of change to complicated feedback relationships. The broad range of responses to changes in  
387 pH outlined above seem to suggest that the very complex interactions that occur within ecosystem can strongly  
388 affect the way that a water body responds to, and recovers from, acidification.

389

390 Relatively speaking, rotifers have been used widely to examine processes of eutrophication and recovery in  
391 degraded lakes. For example, Arndt et al. (1993) used data from 1908–1935 and 1976–1990 to examine the

392 effects of eutrophication on the zooplankton of Muggelsee (Germany). They found that, although food resources  
393 increased as much as 10-fold over the eutrophication period, only rotifers and the ciliate *Epistylus rotans* Svec,  
394 1897, increased their abundance to a similar extent. Crustaceans, in contrast, only doubled in number over the  
395 same period. The authors attributed differences in the magnitude of response to trophic relationships within the  
396 zooplankton, especially between rotifers and crustaceans. However, it was noted that these relationships varied  
397 from year to year, highlighting the complexity of the response and the fact that focusing on a single year's data  
398 could lead to misleading conclusions. In a study of Loosdrecht Lake (Netherlands) between 1981 and 1991,  
399 Gulati et al. (1992) demonstrated that rotifers respond much more rapidly to change than crustaceans. Prior to  
400 1984, Loosdrecht Lake had become highly eutrophic due to inputs of phosphorus (P) laden effluent from the  
401 River Vecht. From 1984 onwards, this input was replaced by dephosphorised water from the Amsterdam-Rhine  
402 canal, which reduced the P input to the lake by 97%. Comparing their results with the historical data of Geelen  
403 (1955), the authors concluded that eutrophication had resulted in 13-fold and 5-fold increases in crustacean and  
404 rotifer densities, respectively, between 1955 and 1985, and that this was likely to have been associated with a  
405 400% increase in seston particles. However, the rotifer or crustacean abundances changed little between 1984  
406 and 1991, suggesting that the reduction in P loading had been insufficient to enable the lake to recover rapidly.  
407 In contrast, when Blank et al. (2017) used data collected between 2003 and 2012 to compare the rotifers in  
408 Lakes Peipsi and Pihkva (Estonia) over a period when P loading had reduced by about 19%, they found that  
409 rotifer abundance was showing a subtle shift towards recovery. Both studies demonstrate the importance of LTR  
410 in assessing rates and extents of recovery from eutrophication once management interventions have been put in  
411 place. Using a more experimental approach to assessing eutrophication and recovery, Rublee & Bettez (2001)  
412 compared the rotifers in an artificially divided lake between 1982 and 1990. One half of the lake had been  
413 fertilised at five times the natural loading over this period (treated), while the other had not (control). Neither  
414 side of the lake was fertilised between 1991 and 1999. The authors compared rotifers on each side of the lake  
415 during the eutrophication and recovery phases. They found that abundances increased as a result of fertilisation  
416 in the treated side of the lake but returned to pre-fertilisation levels relatively quickly (< 2 years) once  
417 fertilisation stopped. This rapid timescale for recovery is in contrast to the results obtained by Gulati et al.  
418 (1992) and Blank et al. (2017), and may reflect the fact that internal recycling of nutrients within this  
419 experimental lake was insufficient to delay recovery to the same extent as had been observed in the other two  
420 lakes. The authors suggested that this might have been due to the experimental lake having much lower water  
421 temperatures than the Dutch and Estonian lakes due to its proximity to the arctic.



422

423 In addition to pollution causing an increase in rotifer abundances, other authors have found that pollution can  
424 cause a decrease in abundances. For example, Bowen & Currie (2017) examined the zooplankton of Hamilton  
425 Harbour, Lake Ontario, between 2002 and 2014, which had long been under increasing pressure from cultural  
426 eutrophication, urbanisation, and invasive species. These authors found that, although most zooplankton species  
427 had remained relatively stable, rotifers had declined markedly (from 40% to 4% of total zooplankton biomass)  
428 over the previous 40 years although the reason was unclear. In a study that demonstrated a different response of  
429 rotifers to pollution, Dekšne (2011) investigated the influence of wastewater on zooplankton of the Duogava  
430 River (Balrus/Latvia) by comparing data collected between 1962 and 1968 with that collected between 2005 and  
431 2009 (i.e. before and after a new wastewater treatment plant had been installed). Over both periods, the data  
432 collected from up- and down- stream of the wastewater treatment works showed that the dominant group of  
433 zooplankton in the river was rotifers, and that their species composition had changed between 1962/63 and  
434 2008/09. The authors also showed that wastewater pollution influenced rotifers in the river only when water  
435 level and rates of discharge were low. This highlights an important difference in the way that pollution affects  
436 rotifers in rivers compared to lakes. Under high flow conditions, effluents discharged to rivers are diluted  
437 resulting in lower pollutant concentrations and less impact on ecology (Bowes et al. 2008).

438

#### 439 Species invasions and introductions

440 Species invasions or introductions can change the structure and function of complex ecological systems very  
441 quickly, but it may take years for impacted systems to adjust to these types of events. So, LTR studies are key to  
442 improving our understanding of both the short-term responses of the system and the longer-term processes that  
443 underpin its re-equilibration. Several such studies exist. For example, Koksvik et al. (2009) examined the  
444 zooplankton communities of Lake Jonvatn (Norway) over the ice-free period between 1980 and 2006 to  
445 investigate the impact of introducing *Mysis relicta* Lovén, 1862, into the system. In the outlet basin, the authors  
446 found that the cladoceran population fell by 95–99% over the seven years after mysids were introduced, and  
447 remained at this lower level for the next decade. Eventually, *Daphnia galeata* Sars, 1864, was replaced by  
448 *Daphnia longispina* O.F. Müller, 1776, which seemed to be able to maintain a relatively high population density  
449 despite presence of high numbers of mysids. In the main basin, however, there were no detectable effects of  
450 mysids on the zooplankton community for about 15 years after the introduction, in spite of high numbers of  
451 mysids developing within the first eight years. The authors suggested that differences between the two basins

452 may partially be explained by differences in temperature, stratification, light transmission and depth, but this  
453 was not confirmed. However, results of this study highlight the complexity of system responses to change. In  
454 another study, Winder & Jassby (2011) investigated the upper San Francisco Estuary (California) between 1997  
455 and 2008, and reported on changes within the zooplankton community due to invasions by a non-native bivalve  
456 and the cyclopoid copepod *Limnithoina tetraspina*. In the upper estuary, these invasions resulted in a long-term  
457 decline in rotifer biomass, a response that would not have been evident in a short-term study.

458

459 Invasions or introductions of fish can also have a marked effect on ecosystem structure and function. For  
460 example, Yang et al. (2005) showed that changes in the overall zooplankton community of Lake Donghu,  
461 (China) between 1962 and 1996, were closely related to a 10-fold increase in fish abundance in the lake (from  
462 95 kg ha<sup>-1</sup> in 1962 to 945 kg ha<sup>-1</sup>). However, although the biomass of crustaceans decreased due higher levels of  
463 fish predation, the authors could find no consistent pattern of change in rotifer biomass. Shao et al. (2001)  
464 analysed an even longer dataset, collected from Lake Donghu between 1956 and 1998, and found similar results.  
465 Wissel & Benndorf (1998) also explored the impact of fish on rotifers, using data collected from two  
466 experimental lakes in Germany between 1979 and 1995. All planktivorous fish had been removed from one of  
467 the lakes in 1979, while the other had been left unmanipulated. The authors found that, after 12 years, large  
468 *Chaoborus* had replaced smaller individuals within the manipulated system and that, by 1995, the size and  
469 volume of the zooplankton community (including the rotifers) had decreased dramatically due to heavier  
470 predation losses. In contrast, within the reference lake, fish had eliminated most crustaceans, but high numbers  
471 of rotifers remained. A similar situation was reported from Lake Kinneret (Israel) by Gophen (2005) who  
472 analysed data collected between 1969 and 2002 and found that rotifer populations were not controlled by food  
473 supply alone, but also by broader food web interactions. In particular, fish predation seemed to play an  
474 important role in regulating rotifer abundance, especially during spring/summer and in autumn.

475

#### 476 Bottom-up and top-down controls

477 LTR studies have also provided an opportunity for the relative importance of bottom-up and top-down control  
478 on rotifer communities in lakes to be investigated. In one such study, Horn & Horn (2008) investigated control  
479 of autotrophic picoplankton (APP) in the Saldenbach Reservoir (Germany) between 1996 and 2006. They found  
480 that the mean annual biovolume of rotifers in the reservoir was high in 1996, but fell the following year and  
481 remained relatively stable after that. The data revealed a strong impact of large grazers on APP, especially in

482 relation to daphnids. In contrast, the grazing influence of rotifers on APP was much less pronounced, although  
483 still evident from the inverse relationships between rotifers and APP. Overall, the authors found no evidence of  
484 bottom-up control within this long data series. In a similar study, Low et al. (2010) explored the potential for  
485 zooplankton to control phytoplankton abundance using a 15-year dataset from 12 reservoirs in Singapore. Their  
486 analyses suggested that calanoid, cyclopoid, and rotifer abundances, but not cladoceran abundances, had an  
487 important influence on the structure of phytoplankton communities. They also found that some phytoplankton  
488 taxa (e.g. *Ankistrodesmus*, *Cosmarium*, *Peridinium*) decreased in abundance as calanoid, cyclopoid and rotifer  
489 numbers increased, while others (e.g. *Melosira*, *Synedra*, *Planktothrix*, *Scenedesmus*) were inversely correlated  
490 with the abundance of calanoid copepods, alone. The authors concluded that zooplankton exert top-down  
491 control on certain algal communities within these tropical lentic systems, although they conceded that the use of  
492 broad taxonomic groups could have masked species-specific information on how zooplankton exert this  
493 pressure. In contrast, Zuykova et al. (2009) compared data from 1989–2005 with those from 1928–1931 for  
494 Lake Teletskoye, a deep oligotrophic waterbody situated in the northeastern part of the Altai Mountains (Russia)  
495 at 436 m above the sea level. They found that rotifers remained at the same level of biomass and abundance  
496 throughout the study except in 1992, when there was a sudden increase in the rotifer *Conochilus unicornis*  
497 Rousselet, 1892. The authors concluded that, in these types of waterbodies, changes in the rotifer community are  
498 most strongly affected by the harsh environmental conditions rather than the balance of ecological interactions  
499 within the plankton.

500

501 The marked, and often rapid, responses of rotifer communities to environmental change in lakes suggest that  
502 they have good potential for use as indicators of change in water quality monitoring programmes. For example,  
503 Haberman & Laugaste (2003) examined LTR data from Lakes Peipsi (1965–2001) and Vorsjarv (1966–2000) to  
504 determine how small differences in levels of trophic were reflected in the ratio of zooplankton to phytoplankton  
505 biomass, and in the mean body weight of zooplankton. Their results indicated that these parameters could be  
506 used to evaluate the trophic of a waterbody and the health of its ecosystem, especially in relation to developing  
507 methods for the permanent monitoring of changes in ecological quality.

508

509 Changes in rotifer population levels are not confined to single drivers. Over a 33-year period (1962–1994) on  
510 Lake Washington, Hampton (2005) followed changes in the abundances of two colonial congeneric rotifer  
511 species, *Conochilus hippocrepis* (Schrank, 1803) and *Conochilus unicornis* Rousselet, 1892. Summer

512 population peaks were consistently <40 individuals l<sup>-1</sup>, except in 1977 and 1978 when *C. hippocrepis* peaked at  
513 or above 40 individuals l<sup>-1</sup>. Abundances of both species began to fluctuate in 1988, peaking at ~200 individuals  
514 l<sup>-1</sup> for *C. hippocrepis* in 1992 and at >120 individuals l<sup>-1</sup> for *C. unicornis* in 1989. Moreover, a pronounced shift  
515 in the population peaks was observed during the summer months. *Conochilus hippocrepis* shifted to August-  
516 September and *C. unicornis* to late spring. Using Dynamic Linear Modelling to analyse the data, Hampton  
517 suggested that these phenological changes were driven by a combination of drivers including (1) longer and  
518 warmer growing season, with concomitant greater abundance of their food, and (2) a depression of small  
519 Unicells (<10 µm) by a competitor (*Daphnia*).

520

521 Although temperature and pollution effects are clear among LTR studies, rotifers form part of a complex  
522 ecosystem structure where the impacts of one species or community on another are also part of the ecosystem's  
523 response to change. For example, although May et al. (2001) showed that the occurrence of *T. pusilla* was  
524 limited to periods when the water temperature was above 10° C, they also showed that the abundance of this  
525 species at these temperatures was determined by availability of the filamentous diatom *Aulacoseira* sp., which  
526 provided a source of food and a relatively secure place for it to deposit its eggs. The availability of *Aulacoseira*,  
527 in turn, was determined by the concentration of dissolved silica in the water column. Long-term rotifer studies  
528 have also shed light on other species interactions within freshwater ecosystems. For example, Ozkan et al.  
529 (2014) provided evidence of a strong relationship between rotifers and phytoplankton in their analysis of data  
530 collected from 17 Danish Lakes between 1989 and 2009. This study showed that rotifers were one of the most  
531 diverse groups within the plankton and that phytoplankton composition appeared to be more closely, and more  
532 strongly, correlated with rotifer species composition and abundance than with cladocerans or copepods.

533

#### 534 *Inferences gleaned from LTR studies*

535 In spite of the limits of LTR, our review shows that such efforts provide considerable insight into drivers of  
536 change and ecosystem responses (Herzig 1987). Firstly, such efforts are key to developing hypotheses that  
537 separate annual variations from long-term trends in relation to habitat change. Secondly, they permit tracking of  
538 degradation and recovery processes in waterbodies, supporting the decision-making that underpins restoration  
539 and remediation. Thirdly, they can help us understand cause and effect in complex systems, especially in  
540 relation to ecosystem stability. Fourthly, they can provide us with the information required to develop  
541 representative sampling techniques, especially in relation to consistency of measurement and comparability of

542 data. Finally, they highlight the importance of using appropriate protocols for sampling and analyses. As  
543 Wagner & Adrian (2011) concluded, the impact of long-term environmental change on ecosystem processes  
544 could have been missed if studies had been restricted to seasonal or annual observations.

545

#### 546 Do existing studies represent all major habitat types?

547 Although the results of several LTR studies on rotifers have been published for lakes, there are few for rivers or  
548 saline environments, and even less for soils. Even where lakes have been monitored, they do not provide a  
549 representative sample of all lake types, as most studies have been focused on small and shallow systems. In  
550 addition, most studies have been confined to Europe and North America, with relatively few studies in South  
551 America and Asia, and a complete lack of studies from African, Australian and Antarctica. So, the geographical  
552 distribution of monitoring sites is very patchy, and non-existent in some areas.

553

#### 554 Have studies provided comparable data?

555 In some cases, data from the LTR studies have been used to develop cost effective sampling techniques.  
556 However, in general, data collection has been too infrequent for detailed analyses of the causes and effects of  
557 change in rotifer communities to be studied in detail. That said, the long-term nature of the studies, even with  
558 infrequent data collection, do provide information on long-term trends in rotifer communities as a result of long-  
559 term environmental change such as acidification, eutrophication, species invasions and climate change. A  
560 concern, however, is consistency across sites of the data collected, especially in relation to the widespread use of  
561 nets that vary from site to site and have mesh sizes that are too large ( $> 20 \mu\text{m}$ ) to collect smaller species  
562 effectively.

563

#### 564 What are the effects of long term environmental change on rotifers?

565 Data collected during LTR studies are often used, mainly, to investigate the impacts of climate change,  
566 acidification/liming, and eutrophication/recovery on waterbodies and soils. However, in some cases, they have  
567 been used to investigate changes in ecosystem function, especially in relation to the impacts of invasive or  
568 introduced species. This review has shown that the drivers of change are different in lakes and rivers, and in  
569 freshwater compared to saline environments, and that rotifers respond differently in each type of habitat. It was  
570 found that ecosystem recovery rates vary, depending on the magnitude and type of pressure, and the structure of

571 the ecosystem. The published data strongly suggest that rotifers are good indicators of change because they  
572 respond more rapidly to different types of change than other components of the ecosystem.

573

574 What are the main knowledge gaps?

575 Over 30 years ago, Herzig (1987) offered a plea for LTR studies, suggesting that one of the benefits of this type  
576 of research was the ability to use its outcomes to formulate meaningful and testable hypotheses for future  
577 research. Fontaneto et al. (2012) repeated this entreaty and emphasised the importance of LTR in understudied  
578 regions such as northern Asia, southern Africa, and central northern America. Regardless of the need for more  
579 studies, our review of over 40 LTR studies of rotifers leads us to identify five important research gaps that need  
580 be filled. These are as follows:

- 581 1) Few studies have examined the long-term effects of environmental change on rotifers in rivers.  
582 Particular knowledge gaps include the effects of pollutant dilution and changes in salinity.
- 583 2) Our knowledge of the dynamics of soil rotifers is incomplete. Given that climate models have predicted  
584 dramatic changes in rainfall and drought patterns, long-term experiments that imitate weather extremes  
585 could improve understanding of the dynamics of soil meiofauna.
- 586 3) Although ecosystem responses to change are complex, and include changes in species interactions,  
587 more LTR studies are needed to support whole system approaches that investigate pressures and  
588 impacts that develop over long periods.
- 589 4) LTR studies of bdelloids are rare in natural habitats. Most information has been collected from  
590 experiments and other short-term studies, so the impact of long-term environmental change on their  
591 population dynamics is unknown.
- 592 5) The geographical distribution of LTR studies is restricted, mostly, to Europe and North America; no  
593 studies were found from Africa, Australia, or Antarctica, indicating a significant gap in our  
594 understanding of rotifers in these areas.

595

#### 596 **Conclusions: a prospectus for the future**

597 In addition to the above, there are also some very important research questions that have not been addressed by  
598 the LTR publications that we have reviewed. Some examples of these are outlined below.

599

600 Short term (within year) studies have shown that rotifer populations can crash catastrophically when they  
601 become infected with parasites (Miracle 1977; Ruttner-Kolisko 1977) and studies on *Daphnia* have shown that  
602 such infestations can affect the genetic diversity of a population (Duffy et al. 2008). However, the long-term  
603 effects of such infestations, and the potential impact of environmental (especially climate) change on rates of  
604 infection, are generally unknown. Caceres et al. (2014) considered the impacts of global change on parasite  
605 infestations in *Daphnia* and concluded that the effects of a new infestation on zooplankton dynamics could  
606 “play out over several years”. This is also likely to be the case for rotifers. Examining the likely impact of such  
607 infestations on rotifer populations requires LTR data.

608

609 Climate change is likely to affect all types of ecosystems in the longer term, including those with rotifer  
610 communities. Although some of these effects have been discussed above, others have received little or no  
611 attention - especially in relation to the combined impacts of multiple stressors. It is unclear, for example, how  
612 climate change will interact with other pressures, such as changes in habitat or species invasions, to affect rotifer  
613 communities; however, variations in response traits could affect this process (Hébert et al. 2017). It is also  
614 unclear how inter- and intra-specific interactions within complex ecosystems will moderate these effects,  
615 although these are probably the main explanation for different ecosystems responses in different locations  
616 (Smith et al. 2009). For example, climate change could affect cryptic speciation, life history traits, or the  
617 environmental conditions that trigger mixis and resting egg production in rotifers, all of which would affect  
618 community composition and behaviour. In general, such effects are only likely to become evident in LTR  
619 studies due to the complexity of the interactions involved and the time taken for ecosystems to re-equilibrate to  
620 their new conditions (Wagner & Adrian 2011).

621

622 Some authors have predicted that increasing temperatures may lead to a mismatch between grazers/predators  
623 and their food supply in aquatic systems (Thackeray 2012; Winder & Schindler 2004). However, Ricci &  
624 Perletti (2006) showed that some rotifers can adapt quickly to unfavourable conditions, so it is unclear whether  
625 such ‘mismatch’ problems occur in rotifers. More importantly, it is also unclear whether rotifers have the  
626 adaptive capacity to fill the gap created by the trophic mismatch of other zooplankton species, thus allowing  
627 species from higher trophic levels to survive. LTR data are essential for investigating this phenomenon.

628

629 Ultimately, LTR will allow us to evaluate the role of rotifers in ecosystem development, and in their resistance  
630 and resilience to both subtle and major perturbations. For example, with the loss of continental ice, new habitats  
631 are being produced, but few studies have documented their progression (Sommaruga 2015). LTR can also  
632 document how quickly rotifers adapt to changes in the seasonal thermal regime of water bodies in high latitude  
633 and altitude habitats. For example, how will earlier and longer periods of higher temperatures affect rotifer  
634 community structure? Or, will northern temperate lakes follow a complex pattern of hysteresis or a simpler  
635 symmetrical reversal in disassembling (in autumn) and reassembling (in spring) their rotifer community structure?  
636 In addition, we do not have a good understanding of how propagule resting egg banks will impact on these  
637 communities. Will the resident propagules dominate (De Meester et al. 2002; De Meester et al. 2016; Orsini et  
638 al. 2013) or will distant source pools be important (Rivas et al. 2018; Rivas et al. 2019). Without continued  
639 investment in LTR studies, these questions will remain unanswerable.

640

641 Since the beginning of the global initiative of long-term ecological research in the early 1990s, the ILTER has  
642 developed into a large and important collaborative network (Mirtl's et al. 2018; Vanderbilt & Gaiser 2017).  
643 Indeed, this enterprise is vast, encompassing some 200 institutions, with 1000s of scientists working in multiple  
644 disciplines, both aquatic and terrestrial. The research agendas of these studies are strong and incorporate cutting-  
645 edge technologies. The data legacy that has been developed spans >100 years and is continually being enriched  
646 by thousands of peer-reviewed published works. The future of this global cooperation is likely to include greater  
647 coordination and linkage among research sites (Haase et al. 2018) and possibly with other initiatives focused on  
648 conservation policy (e.g. Darwall et al. 2018). But what of rotifers — how can research on these tiny animals fit  
649 into the vast global scale of LTR networks? We suggest that the best practice for researchers focusing on rotifers  
650 is to develop hypotheses aligned to the research gaps that we have articulated here, making sure that they  
651 employ appropriate methodologies and that the data collected are recorded in such a way that it can be deposited  
652 easily in a variety of database platforms.

653

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657

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926 Figure captions

927

928 **Fig. 1** Number of long-term rotifer studies initiated per decade.

929 **Fig. 2** Percentage of rotifer long-term research sites in Asia, North and South America, and Europe.

930 **Fig. 3** Percentage of long-term research lakes in each size category in terms of (a) mean depth, (a) surface area  
931 and (c) volume.

932 **Fig. 4** Number of studies using different mesh sizes to collect rotifers from aquatic environments.

933

934 Table captions

935

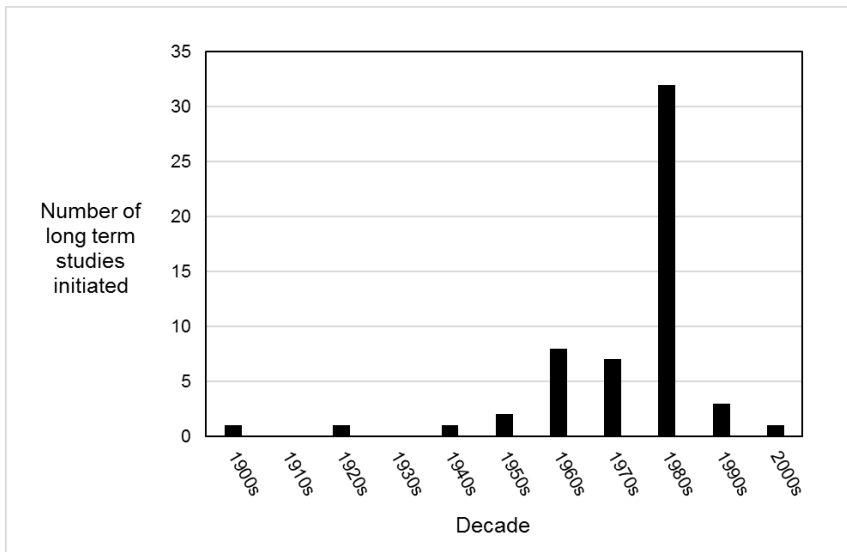
936 **Table 1** Number of rotifer studies associated with each of the main habitat types, showing geographical extent  
937 expressed as number of countries represented.

938

939 **Table 2** Long term monitoring studies grouped by start date.

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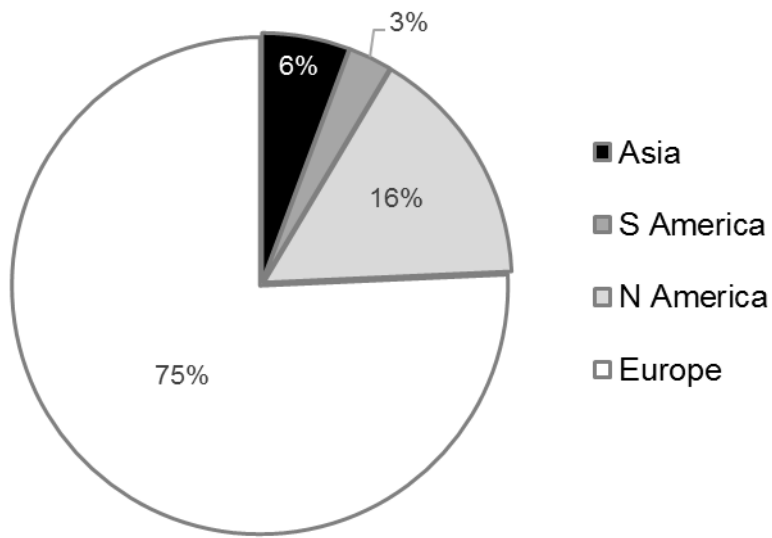
941 Figure 1



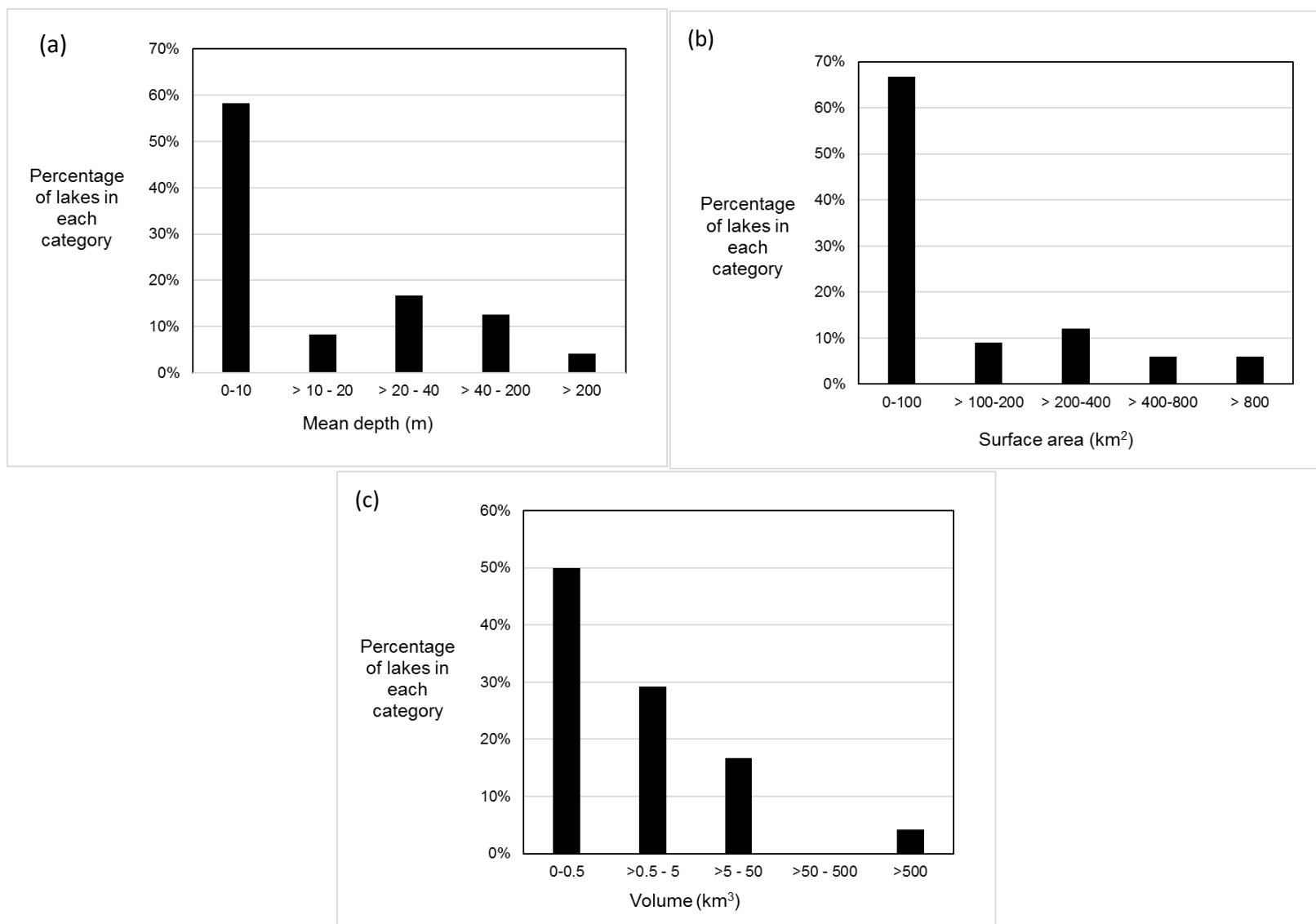
942

943 Figure 2

944

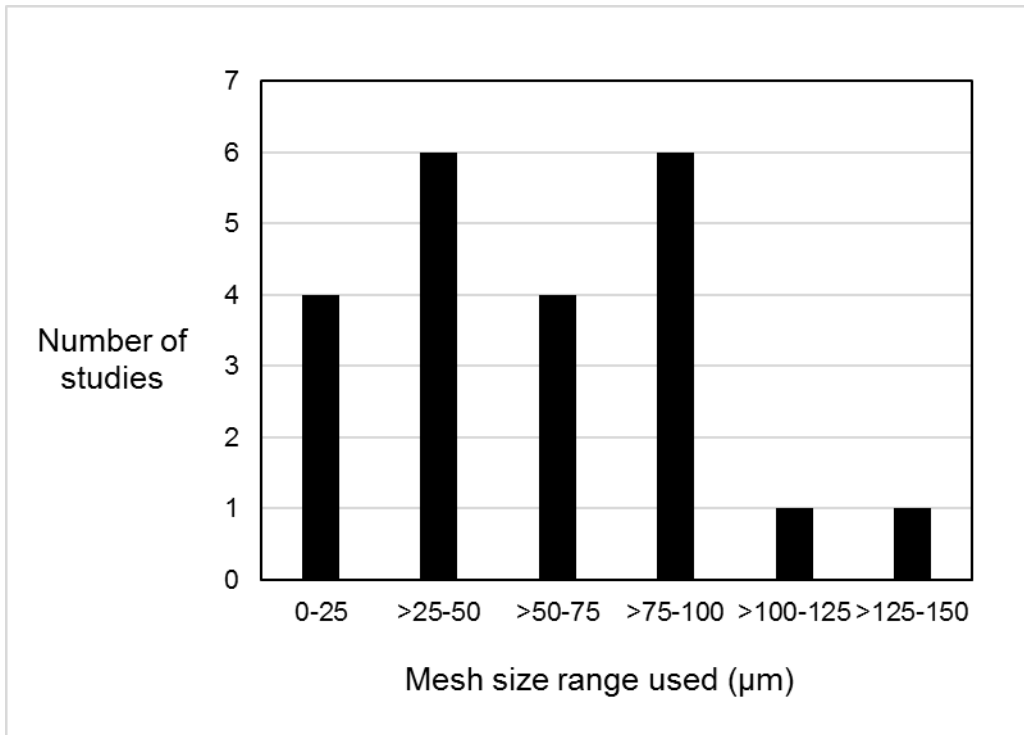


1 Figure 3



1 Figure 4

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6 Table 1

7

<b>Habitat type</b>	<b>Number of study sites</b>	<b>Geographical extent (number of countries)</b>
Soils	2	2
Rivers	3	3
Lagoons, estuaries and seas	6	5
Lakes	35	17

8

9



10 Table 2

11

<b>Start date</b>	<b>Habitat type</b>	<b>References</b>
1900s	Lakes/reservoirs	Arndt et al. (1993)
1940s	Lake/reservoir	Obertegger & Manca (2011)
1950s	Lakes/reservoirs	Hampton et al. (2014); Shoa et al. (2001)
1960s	Lakes/reservoirs	Andrew & Andrew (2005); Dokulil & Herzig (2009); Gophen (2005); Haberman & Haldna (2017); Haberman & Laugaste (2003); Weglenska et al. (1997); Yang et al. (2005)
	Rivers	Deksne (2011)
1970s	Lakes/reservoirs	Arnott et al. (2001); May et al. (2001); Stenson & Svensson (1995); Winder & Schindler (2004); Wissel & Benndorf (1998)
	Rivers	de Paggi et al. (2014)
	Lagoons, estuaries and seas	Johansson et al. (1993); Suikkanen et al. (2013)
1980s	Lakes/reservoirs	Gulati et al. (1992); Halvorsen et al. (2004); Koksvik et al. (2009); Ozkan et al. (2014); Rublee and Bettez (2001); Rusak & Montz (2009); Tirok & Gaedke (2006); Vasseur & Gaedke (2007); Voutilainen et al. (2012); Wagner & Adrian (2011); Zuykova et al. (2009)
	Lagoons, estuaries and seas	Delpy(2011); Feike & Heerkloss (2008); Viitasalo et al. (1995);
1990s	Lakes/reservoirs	Horn & Horn (2008); Lehtovaara et al. (2014); Voutilainen & Arvola (2017)
	Lagoons, estuaries and seas	Winder & Jassby (2011)
2000s	Lakes/reservoirs	Blank et al. (2017); Bowen (2017)
	Rivers	Bonecker et al. (2013)

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