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Absence of predation eliminates coexistence: Experience from the fish-zooplankton interface

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2 **Absence of predation eliminates coexistence: experience**
3 **from the fish–zooplankton interface**

4 **Z. Maciej Gliwicz · Wayne A. Wurtsbaugh · Errata Wurtsbaugh**
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8 **Abstract** Examples from fishless aquatic habitats
9 show that competition among zooplankton for
10 resources instigates rapid exclusion of competitively
11 inferior species in the absence of fish predation, and
12 leads to resource monopolization by the superior
13 competitor. This may be a single species or a few
14 clones with large body size: a cladoceran such as
15 *Daphnia pulicaria*, or a branchiopod such as *Artemia*
16 *franciscana*, each building its population to a density
17 far higher than those found in habitats with fish. The
18 example of zooplankton from two different fish-free
19 habitats demonstrates the overpowering force of fish
20 predation by highlighting the consequences of its
21 absence. Released from the mortality caused by
22 predation, a population of a superior competitor

remains at a density equal to the carrying capacity 23
of its habitat, in a steady state with its food resources, 24
consisting of small green flagellate algae, which are 25
successful in compensating high loss rates due to 26
grazing, by fast growth. In such a situation, the high 27
filtering rate of *Daphnia* or *Artemia* reduces resources 28
to levels that are sufficient for assimilation to cover 29
the costs of respiration (threshold food concentra- 30
tion) in adults but not in juveniles. This implies 31
long periods of persistence of adults refraining from 32
producing live young, because production of instantly 33
hatching eggs would be maladaptive. Severe competi- 34
tion for limiting resources imposes a strong selective 35
pressure for postponing reproduction or for producing 36
resting eggs until food levels have increased. Off- 37
spring can only survive when born in a short time 38
window between such an increase in food levels and 39
its subsequent decline resulting from population 40
growth and intense grazing by juveniles. Such zoo- 41
planktons become not only a single-species commu- 42
nity, but also form a single cohort with a long-lifespan 43
population. The observations support the notion that 44
diversity may be sustained only where predation 45
keeps densities of coexisting species at levels much 46
below the carrying capacity, as suggested by Hutch- 47
inson 50 years ago. 48

A1 Guest editors: L. Naselli-Flores & G. Rossetti / Fifty years after
A2 the “Homage to Santa Rosalia”: Old and new paradigms on
A3 biodiversity in aquatic ecosystems

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Stabilizing selection · Zooplankton · 51
Competition · Predation · Saline 52

54 **Introduction**

55 The year 1959 was the centenary of the publication of
56 the first edition of Darwin's '*On the origin of species*
57 *by means of natural selection*' and the 150th anni-
58 versary of his birth. Perhaps there was something in
59 the air that year because this was also a time of
60 inspiration and excitement that accelerated our quest
61 to understand the reasons why biotic diversity is so
62 great in some habitats yet reduced in others.

63 One of these inspirations was the 'Homage to Santa
64 Rosalia or why are there so many kinds of animals' by
65 Hutchinson (1959). This essay articulated most of the
66 contemporary ideas of that time on the importance of
67 food chain interactions and diversity of plants as both
68 substrate and food resource as the key reasons for the
69 'extraordinary diversity of the terrestrial fauna'. This
70 was soon complemented by Hutchinson's original
71 notion of high diversity resulting from 'non-equilib-
72 rium conditions' outlined in another of his famous
73 papers on 'The paradox of the plankton' (Hutchinson,
74 1961). This concept of frequent environmental
75 changes altering the competitive abilities of coexist-
76 ing species opened the way to what was later known
77 as the 'intermediate disturbance hypothesis' (Connell,
78 1978). Both of Hutchinson papers supported the
79 notion of animal diversity reflecting the diversity of
80 their plant resources, allowing for fine niche parti-
81 tioning. These earlier papers focused on competition,
82 which at the time, was thought to be the primary factor
83 structuring ecological communities.

84 However, another source of inspiration that year
85 was an article on cichlids of Lake Nyasa/Malawi by
86 Fryer (1959a) which supported the completely differ-
87 ent concept that diversity within a food web may be
88 sustained by predation rather than from the bottom-up
89 processes of competition. Seeking reasons for the
90 stable coexistence of many cichlid species with
91 overlapping food niches in the same benthic habitat,
92 Fryer suggested that this may occur due to the activity
93 of predators by 'retarding the growth of populations of
94 non-predatory species', hence 'helping to prevent
95 competition between them for the available food'. In a
96 second article, he contemplated three particular rea-
97 sons why predation by piscivores may not only sustain
98 coexistence of different species, but could also assist
99 the speciation of non-predatory species (Fryer, 1959b).

100 Unaware of Fryer's hypothesis, Hutchinson (inspired
101 by a conversation with MacArthur) articulated the

102 same notion in his paper on 'The paradox of the
103 plankton' (Hutchinson, 1961). He asserted that 'if one
104 of the two species is limited by a predator, while the
105 other is either not so limited or is fed on by a different
106 predator, co-existence of the two species may in some
107 cases be possible'. This idea was later expanded
108 by Hutchinson's students and colleagues. Slobodkin
109 (1963) showed that the Lotka-Volterra model of inter-
110 specific competition would preclude the exclusion
111 of inferior species if supplemented with high preda-
112 tion-induced mortality in the population of each
113 competitor. This concept opened the way to the
114 mechanistic theory of competition of Tilman (1982),
115 with the outcome of competition strongly modified by
116 a population's ability to cope with high loss rates by
117 compensating for high mortality with equally high
118 reproduction. Rosenzweig & MacArthur (1963) sug-
119 gested that the risk of individual prey to predators is
120 reduced at low population density: that is, below a
121 level equal to the number of prey being able to find a
122 refuge. They argued that prey can persist at densities
123 below those where predators switch to alternate
124 resources or migrate in search of locations with more
125 abundant resources. Paine (1966) demonstrated that
126 experimental removal of a 'keystone species' (Paine,
127 1969), the starfish *Pisaster* sp., a top predator in
128 the intertidal zone, led to a community of reduced
129 diversity, because the resources became monopolized
130 by a superior competitor (a species of mussel). In a
131 more recent paper, Paine (2002) reached a similar
132 conclusion for plant diversity in the low intertidal
133 zone, which increased when the superior competitor,
134 annual kelp (*Alaria marginata*), was heavily grazed,
135 thereby permitting competitively inferior perennial
136 species to grow to high abundance. Additional early
137 work documented how the risk of predation can cause
138 herbivores to seek refuge and thus forage ineffectively
139 (Stein & Magnuson, 1976; Lima 1985, 1998). Con-
140 sequently, either direct predation or changes in prey
141 behavior may increase stocks of primary producers,
142 and reduce competitive exclusion of grazers.

143 Interestingly, the 'top-down' hypothesis has not
144 been successfully applied to explain the high diver-
145 sity of phytoplankton. Did Hutchinson have some
146 hint that high mortalities in algal populations result-
147 ing from strong grazing pressure by filter-feeding
148 zooplankton would lead to a single algal species
149 monopolizing resources rather than to the coexistence
150 of many taxa by preventing resource competition

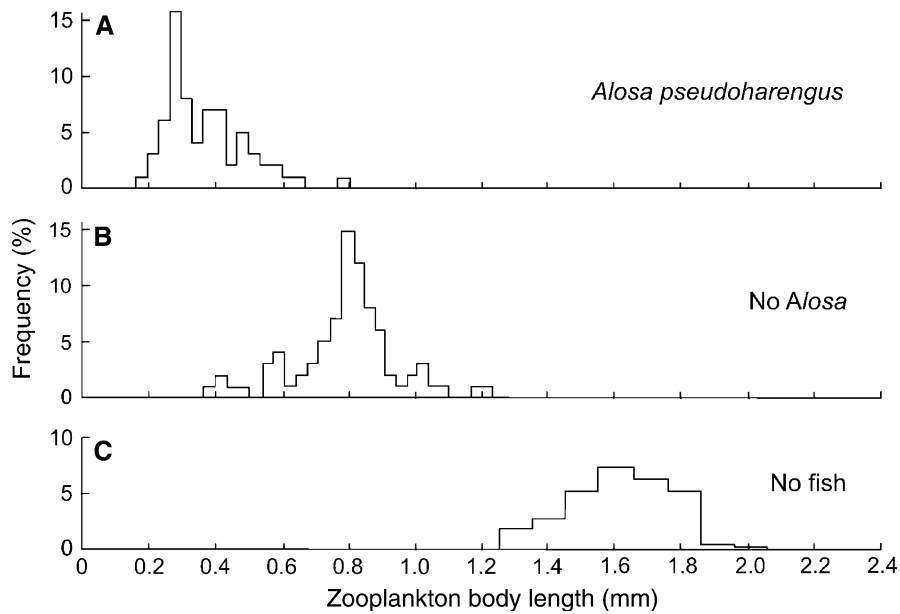


Fig. 1 Size distribution of a zooplankton community of diverse species composition in Crystal Lake (USA) sampled in 1964 (A) and 1942 (B). Large-bodied zooplankton, superior in competition for resources, were present in 1942 (B) but absent in 1964 (A) due to their inferiority in evading predation by a visually oriented planktivorous fish. The change in size distribution, which occurred between 1942 and 1964, followed

the establishment of a landlocked population of alewife (*Alosa pseudoharengus*) in the lake (A and B adapted from Fig. 4 in Brooks & Dodson, 1965). Judging from the size distribution of the zooplankton community of Lake Czarny (C)—a lake remaining fishless for millennia—the shift in body size would have been more severe in Crystal Lake if all species of fish had been absent in 1942

151 between them, as is the case in our lakes? Nor has the
 152 ‘top-down’ explanation been explored with regard to
 153 zooplankton diversity, even though the impact of fish
 154 predation on zooplankton size distribution has been
 155 known since it was first reported by Hrbáček et al.
 156 (1961, 1962), and was used as a cornerstone of the
 157 *size-efficiency hypothesis* of Brooks & Dodson (1965,
 158 Fig. 1A, B). On the contrary, the role of predation in
 159 sustaining the stable coexistence of closely related
 160 species has long been considered a hypothesis that is
 161 difficult to prove (Chesson, 2000; Chase et al., 2002),
 162 and frequently questioned by numerous examples of
 163 diversity reduced by predation (e.g. Spiller & Scho-
 164 ener, 1998; Almany & Webster, 2004). Moreover, the
 165 high diversity of zooplankton has often been attrib-
 166 uted to other reasons, such as resource partitioning,
 167 disturbance and density fluctuations (Weider, 1992;
 168 Huisman & Weissing, 1999; Chesson, 2000; Abrams
 169 & Holt, 2002; Nelson et al., 2005).

170 This ‘top-down’ explanation in relation to
 171 zooplankton diversity was eventually suggested
 172 by Gliwicz (2001) and supported by experimental

evidence showing that stable population density 173
 proportions of large- and small-bodied *Daphnia* 174
 species are fixed by size-selective and density- 175
 dependent predation by planktivorous fish (Gliwicz 176
 & Wrzosek, 2008). The population density level of 177
 each species is inversely related to its specific body 178
 size, hence the reaction distance from which it can be 179
 seen by a foraging fish and the threshold density level 180
 at which it is excluded from the fish’s diet. 181

This explanation also fits an earlier suggestion 182
 (Gliwicz, 2002) that only the rates of change of 183
 different parameters describing a zooplankton com- 184
 munity (the rate of individual body growth, rate of 185
 reproduction, population growth rate) are controlled 186
 from the bottom-up by resource limitation. In contrast, 187
 the state variables (biomass, individual body size, 188
 population density) are controlled from the top down, 189
 and fixed at a species-specific level by predation. The 190
 different nature of the bottom-up and the top-down 191
 impacts becomes more apparent when the zooplank- 192
 ton community and the population ecology of an 193
 individual are examined in habitats where top-down 194

195 impacts by planktivorous fish are precluded. These
 196 impacts of fish predation are often precluded in large
 197 eutrophic and mesotrophic lakes when fish are busy
 198 spawning for a limited time, producing a short-lived
 199 spring clear water phase by allowing a large-bodied
 200 *Daphnia* to increase in numbers with smaller cladoc-
 201 eran species competitively excluded (Lampert, 1988).
 202 Sarnelle (1993) showed that this type of competitive
 203 exclusion by large-bodied *Daphnia* may last for
 204 several weeks if the abundance of planktivorous fish
 205 is greatly reduced by a fish kill in the preceding
 206 winter. Spring clear water phases in large lakes are
 207 always terminated by summer when fish find their way
 208 to the sites with abundant *Daphnia* prey. Extensive
 209 periods of a clear water “phase” only occur in habitats
 210 that are free of fish. Such habitats are, however,
 211 always extreme because of one reason or another—the
 212 extremity often being the cause for the absence of fish.
 213 Here, we use two examples of fish-free lake ecosys-
 214 tems to show that in the absence of fish predation, the
 215 size distributions of zooplankton populations shift
 216 towards larger individuals (Fig. 1C) and the species
 217 diversity is reduced. The abiotic environmental con-
 218 ditions in these two ecosystems could also contribute
 219 to the low species diversity. Regardless of the cause of
 220 the low diversity, we show that one or a few large-
 221 bodied filter-feeding zooplankton species monopolize
 222 resources and hold them at extremely low levels that
 223 merely allow for slow growth of the most efficient
 224 individuals. In this situation, all efforts of an individ-
 225 ual become focused on competition for resources and
 226 the need to choose the right time for reproduction to
 227 allow for the survival of its offspring.

228 Materials and methods

229 To gain further insight into the most fundamental
 230 features of zooplankton from habitats free of fish,
 231 we reexamine our data from two fishless habitats that
 232 are distinctly different in their biological, chemical,
 233 and morphological characteristics: Lake Czarny in
 234 the Tatra mountains, Poland (Gliwicz, 1986; Gliwicz
 235 et al., 2001; Slusarczyk, 2009) and Great Salt Lake,
 236 Utah, USA (Wurtsbaugh & Gliwicz, 2001; Gliwicz,
 237 2003). We also present unpublished results of exper-
 238 iments designed to explain some peculiarities of
 239 reproduction in zooplankton from fish-free habitats.

The lakes

240
 241 Lake Czarny (LC, Czarny Staw pod Rysami, 49° 11'
 242 18" N, 20° 4' 34" E) is located just above the
 243 timberline at an elevation of 1581 m above sea level
 244 in one of the largest valleys in the Tatra ridge. It is a
 245 classic example of a glacial cirque lake or tarn with
 246 a regular circular shape, an area of 21 ha and a
 247 maximum depth of 76 m. It is ultraoligotrophic, with
 248 Secchi disc transparency ranging from 10–24 m, and
 249 supports low densities of phytoplankton composed of
 250 small flagellate Chlorophyta, representing extremely
 251 low levels of food for filter-feeding zooplankton.
 252 Unlike the neighboring downstream Lake Morskie
 253 Oko (at an elevation 1395 m), fish are absent from
 254 Lake Czarny [the two lakes are compared in Gliwicz
 255 et al. (2001) and Gliwicz (2003)]. The outflow that
 256 cascades over a moraine edge down to Morskie Oko
 257 is impenetrable to the salmonid fish that have been
 258 present in the neighboring lake for millennia. In
 259 contrast to the diverse zooplankton community of
 260 Morskie Oko, that of Lake Czarny is very simple,
 261 being comprised of *Daphnia*, a single predacious
 262 copepod *Cyclops abyssorum taticus* (Kozminski),
 263 and low densities of the rotifer *Asplanchna priodonta*
 264 Gosse, which appears for a short period in summer.
 265 Great Salt Lake (GSL, 112° 30'W, 42° N), located at
 266 an elevation of 1280 m, is another rare example of an
 267 aquatic habitat that lacks fish. It is a eutrophic terminal
 268 lake, a remnant of the former freshwater Lake Bonne-
 269 ville which covered 49,000 km² of the Great Basin of
 270 western North America 15,000 years ago. The lake's
 271 southern basin (Gilbert Bay), separated from an even
 272 more saline northern basin (Gunnison Bay) by a
 273 railway causeway, covered an area of 2626 km² during
 274 the study, and had respective mean and maximum
 275 depths of 4.9 and 9.5 m and varying salinity within the
 276 range of 130–160 g l⁻¹. High salinity levels ensure
 277 that this portion of the lake is completely free of fish.
 278 This lake has a very simple food web with a plankton
 279 community consisting primarily of the flagellated
 280 green phytoplankter *Dunaliella viridis* (Teodoresco),
 281 that usually constitutes over 95% of the phytoplankton
 282 at any one time, although over 50 phytoplankton taxa
 283 have been identified (G. Belovsky, personal commu-
 284 nication). *D. viridis* is the mayor food source for the
 285 single zooplankter, *Artemia franciscana* Kellog, a
 286 brine shrimp (Montague et al., 1982; Wurtsbaugh,
 287 1995). We also analyzed plankton in Farmington Bay

288 of the Great Salt Lake. This shallow 260 km² bay
 289 receives considerable river inflow and thus has salin-
 290 ities varying from <10–90 g l⁻¹, and consequently it
 291 has a more diverse plankton assemblage including
 292 invertebrate predators. It also receives excessive
 293 nutrient loading and is hypereutrophic.

294 Field data

295 The zooplankton communities of the two lakes were
 296 sampled in 1996–1998 (LC, at one station) and 1994–
 297 1995 (GSL, at 12 stations), respectively, by vertical
 298 hauls from depths of 45 and 3–9 m to the surface
 299 using 44- and 30-cm diameter conical plankton nets
 300 with 200- and 153- μ m mesh (no other rotifer species
 301 were revealed from tube samples for phytoplankton
 302 counts in the GSL and parallel hauls with 50- μ m
 303 mesh nets in LC). The samples were preserved in 4%
 304 sugar-formaldehyde which prevented the loss of eggs
 305 from *Daphnia* brood cavities in LC. Phytoplankton
 306 and microzooplankton samples were collected from
 307 each lake using a tube sampler and preserved with
 308 either Lugol's iodine solution (LC) or sugar-formalin
 309 (GSL). These samples indicated moderate abun-
 310 dances of ciliated protozoans, but no rotifers. The
 311 vertical profiles of temperature in the lakes were
 312 assessed with thermistors. The dry weight of GSL
 313 *Artemia* was measured by weighing individual spec-
 314 imens that had been killed in formalin, rinsed in
 315 distilled water and dried overnight at 60°C.

316 Experimental test of the impact of food level 317 on reproductive performance

318 Live *Daphnia* and *Artemia* from each lake were
 319 transferred to the laboratory in natural lake water held

at a temperature close to that of the lake and placed in
 the experimental systems subsequently used to assess
 patterns of reproduction at different food levels.

Daphnia collected from LC in May, from under the
 ice cover, were grown at a temperature of 6°C (2°C
 higher than in LC) in a flow-through system (Stich &
 Lampert, 1984), to minimize food level fluctuations,
 for 18 days until 70% of the animals growing at the
 highest food level had laid eggs into their brood
 cavities. Food was provided by a constant flow of
 filtered lake water carrying suspensions of the green
 algae *Scenedesmus obliquus*. Each 250 ml chamber
 contained 20 animals and there were three replicate
 chambers for each of three food levels of 0.015, 0.05,
 and 0.15 mg POC (particulate organic carbon) l⁻¹: the
 lowest level corresponding to that observed in the lake
 throughout the winter until May (Fig. 2). During daily
 inspections, egg-bearing females were removed from
 the system and the number of eggs per clutch counted.

Artemia were grown at 20°C (0–5°C lower than
 GSL in June–September) for 50 days as batch cultures
 in 36 glass beakers filled with 100 ml filtered lake
 water supplemented with the green algae *D. viridis* as
 food. Each beaker contained one female and one male
 in coupled pair. Two food levels were employed,
 fluctuating within the ranges of 0.1–1.0 and 10–20 μ
 g chlorophyll *a* l⁻¹ (18 and 18 beakers with each), with
 the lower level corresponding to the natural lake
 situation throughout the summer and fall. Every day,
 each *Artemia* pair was transferred to a new beaker
 containing fresh medium, while the offspring—both
 the naupli from the ovoviviparous eggs and cysts—
 were counted to assess the clutch size. Each of the 36
 couples produced at least a single clutch of eggs, but
 in the low food level many females died on the day
 that they produced their first clutch.

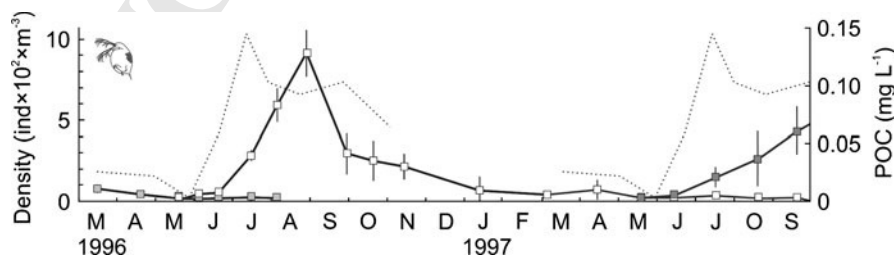


Fig. 2 Seasonal changes in the mean water column density of three subsequent cohorts of LC *Daphnia* (thick lines showing means and SE from three vertical hauls) and POC (dotted line) in Lake Czarny [according to Gliwicz et al. (2001) and Slusarczyk

(2009)]. The two coexisting *Daphnia* morphs are not discriminated here, but their densities can be found in Slusarczyk, (2009). The POC measurements used for 1996–97 were assumed to be the same as those of the following year, 1997–1998

356 Results

357 The datasets from both the Lake Czarny (LC) and
 358 Great Salt Lake (GSL) experiments revealed that in
 359 the absence of fish, a single species of large-bodied
 360 filter-feeding entomostracan monopolized resources
 361 (Figs. 2, 3). Food resources in each of the lakes
 362 persisted at an extremely low level throughout the
 363 summer in spite of the dramatic difference in fertility.
 364 Chlorophyll *a* was undetectable ($<1 \mu\text{g l}^{-1}$) in LC
 365 even during the June peak of POC following the
 366 spring overturn (Fig. 2). Chlorophyll was not much
 367 higher in GSL (Fig. 3), although the low level in this
 368 lake resulted almost entirely from the high feeding
 369 rate of *Artemia*, which are capable of filtering the
 370 entire lake volume more than once a day. The severe
 371 food limitation persisting in the two habitats (an
 372 obvious reason for the population density at the
 373 carrying capacity level) resulted in the dominance of
 374 a single-cohort generation in both LC *Daphnia* and
 375 GSL *Artemia* throughout the summer, with younger
 376 individuals being gradually eliminated by starvation,
 377 and the majority of older individuals refraining from
 378 producing immediately hatching eggs (Figs. 4, 5).

379 The Lake Czarny *Daphnia*

380 One-year of data on LC zooplankton (Gliwicz et al.,
 381 2001) revealed that the large-bodied *Daphnia*, the
 382 sole filter-feeding herbivore monopolizing resources
 383 in the absence of fish, co-exist with cyclopoid
 384 copepods, *Cyclops abyssorum taticus*, and, sporadically,
 385 with the uncommon predatory rotifer *Asplanchna priodonta*.
 386 In contrast to the scarce small-bodied *Daphnia*, which
 387 reproduce year-round in the fish-containing downstream
 388 lake, the LC *Daphnia* persisted as a single cohort of
 389 individuals born or hatched from ephippia during a short
 390 summer period when food was most abundant (Fig. 2).
 391 The LC

Fig. 3 Seasonal changes in the mean water column density of *A. franciscana* (thick lines showing means and SE from 5–12 stations) and epilimnetic chlorophyll *a* levels (dotted line) in the Great Salt Lake [according to Wurtsbaugh & Gliwicz (2001)]

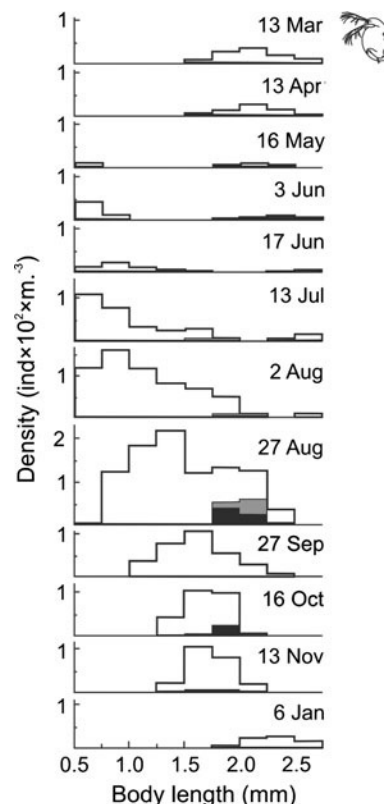
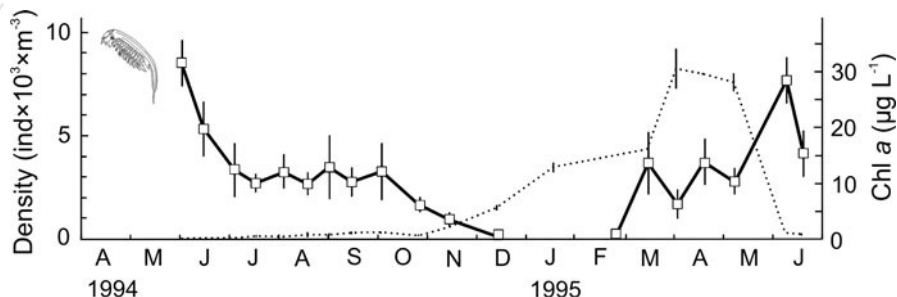


Fig. 4 Seasonal change in the body size distribution and fecundity of LC *Daphnia* shown as the density of each discrete size class on each of the 12 sampling dates, from 13 March 1996 to 6 January 1997. The proportions of egg-bearing (light shaded) and ephippia-bearing (dark shaded) females are indicated. The two coexisting morphs are not discriminated here, but their size distributions can be found in Slusarczyk (2009). Two discrete cohorts clearly coexisted in the lake from 16 May to 16 October 1996. The earlier generation of adults survived from the summer of 1995, and the new 1996 generation hatched from ephippia (starting a new population of the 'transparent' morph) or from instantly developing eggs [starting the new cohort of the 'orange' morph, from Gliwicz (2003)]

Daphnia born in summer were able to over-winter, 392
 either as ephippia or in the form of active adults that 393
 refrained from reproduction until the following year, 394

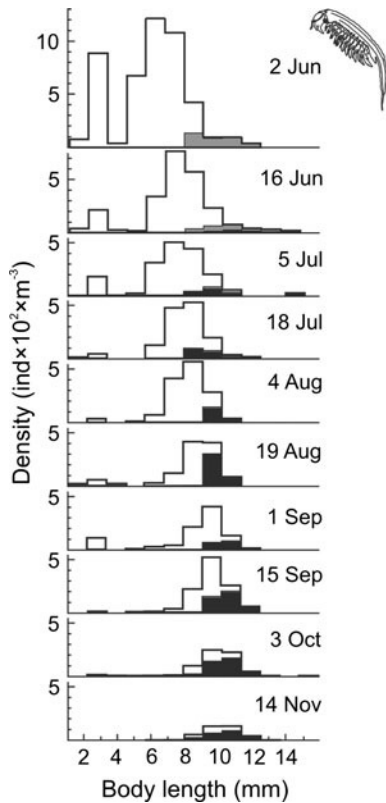


Fig. 5 Seasonal changes in the size distribution and fecundity of GSL *Artemia* shown as the density of each discrete size class on each of the 10 sampling dates, from 2 June to 14 November 1994. The proportions of egg-bearing females (light shaded) and females with cysts in their egg sacks (dark shaded) are indicated [from Gliwicz (2003)]

395 when they produced eggs at an age of almost 1-year-
 396 old (Fig. 4). The new-year generation was initiated
 397 from both ephippial eggs and eggs released by the
 398 over-wintering adults. Only a small fraction of the
 399 adult population was recruited from the second new-
 400 year generation arising from eggs released by a few
 401 new generation females. In each of the two genera-
 402 tions, reproductive effort was restricted to a short
 403 time window when food levels were sufficiently high
 404 (Fig. 2) to allow juvenile growth and predation by
 405 *Cyclops* was low enough to permit adequate survival
 406 of eggs and neonates. No immediately hatching eggs
 407 were produced outside this reproductive period
 408 despite the fact that the body lipid levels of the adult
 409 *Daphnia* were as high as at the time of summer
 410 reproduction (Gliwicz et al., 2001; Slusarczyk, 2009),
 411 suggesting a deliberate halt to reproduction and its
 412 postponement until the following summer.

The two LC *Daphnia* color morphs that were
 considered to be *D. pulicaria* Forbes in our earlier
 study (Gliwicz et al., 2001), were recently shown to
 represent distinct lineages, with the 'orange' morph
 related to an eastern Nearctic clade of *D. pulicaria*,
 and the 'transparent' morph related to a European
 clade of the *tenebrosa* group (Slusarczyk, 2009).
 Thus, the previous notion of a single *Daphnia* species
 monopolizing resources had to be replaced by a new
 notion of the two large-bodied *Daphnia* sub-species
 coexisting partitioning the scarce resources by adopt-
 ing dramatically different life histories. Slusarczyk
 (2009) has shown that while the 'transparent' morph
 was found to complete its life cycle within a single
 season by investing its resources into diapausing eggs
 that would hatch the following summer, the 'orange'
 morph remained active throughout the winter, post-
 poning its reproduction until the next-year peak in
 food abundance, when the newborn had the best
 chance of surviving and growing to maturity. The
 gradual shift in size distribution and size-specific
 fecundity depicted in Fig. 4 has been separately
 demonstrated for each of the two morphs by Slus-
 zarczyk (2009), revealing similarity between the
 'transparent' LC *Daphnia* morph and the GSL *Artemia*
 (see below).

The 'orange' LC *Daphnia* morph, brought to the
 laboratory in May and grown in the flow-through
 system at three different food levels, exhibited the
 ability to break the pause in reproduction that
 normally extended to 10 months in the lake (Fig. 6).

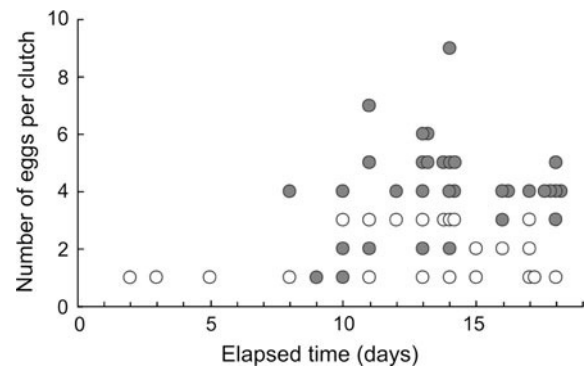


Fig. 6 Clutch size and the time required to produce the first clutch of eggs in 'orange' morph LC *Daphnia* brought into the laboratory in May 2004 and grown in a flow-through system at three different food levels: 0.015 mg POC L⁻¹ (no eggs produced), 0.050 mg POC L⁻¹ (empty circles) and 0.150 mg POC L⁻¹ (filled circles)

444 This restarting of reproduction was due to the
 445 presence of higher food levels. In the lowest food
 446 level of $0.015 \text{ mg POC l}^{-1}$ (similar to the lake
 447 throughout the winter), no eggs were produced.
 448 However, at the intermediate food level of 0.05
 449 mg POC l^{-1} , the first *Daphnia* produced an egg in
 450 just 2 days, and the group of 60 attained a mean clutch
 451 size of $1.8 \pm 0.9 \text{ SD}$, with 22 of the females releasing
 452 eggs. At the highest food level of $0.15 \text{ mg POC l}^{-1}$
 453 the eggs were not produced until the 8th day, but the
 454 42 producing females in this group of 60 attained a
 455 mean clutch size of $3.7 \pm 1.8 \text{ SD}$.

456 The Great Salt Lake *Artemia*

457 In the GSL *Artemia* was the sole zooplankton found
 458 across the entire GSL southern basin (Gilbert Bay)
 459 from March to December (Fig. 3). After *Artemia*
 460 disappeared in December, chlorophyll increased from
 461 ca. $1\text{--}25 \mu\text{g l}^{-1}$, and an elongate ciliate (measuring
 462 $80 \times 19 \mu\text{m}$) became abundant and persisted through-
 463 out the winter (details in Wurtsbaugh & Gliwicz,
 464 2001). Interestingly, whenever grazing by *Artemia*
 465 was prevented in GSL water samples, chlorophyll *a*
 466 levels rose to high levels. When lake water with
 467 chlorophyll levels below $0.5 \mu\text{g Chl l}^{-1}$ was brought
 468 into the laboratory and *Artemia* removed, chlorophyll
 469 *a* increased to $25 \mu\text{g chl l}^{-1}$ in 10 days. In these
 470 experiments *Dunaliella* was the dominant or even the
 471 exclusive component of the phytoplankton (details in
 472 Gliwicz, 2003).

473 In the lake, however, the density of *Dunaliella* was
 474 extremely low and its biovolume was sometimes less
 475 than that of other taxa. An earlier study (Wurtsbaugh,
 476 1992) also demonstrated that low phytoplank-
 477 ton density was the result of high grazing pressure
 478 by *Artemia*. According to Reeve (1963), a single
 479 *Artemia* filters 240 ml d^{-1} and therefore, at the
 480 average population density of four sub-adult and
 481 adult individuals per liter, this branchiopod is capable
 482 of filtering the entire lake volume once a day. Thus,
 483 the *Dunaliella* population density remains extremely
 484 low, as do the densities of other green algae, diatoms
 485 and cyanobacteria that are able to reproduce fast
 486 enough to compensate for grazing losses. In contrast
 487 to *D. viridis*, which is a typical euplanktonic species,
 488 many other taxa are not suspended in the lake water,
 489 but live in refuges where grazing losses are lower,
 490 among them large singular diatoms such as *Nitzschia*

epithemides and *Amphora coffeiformis*. These refuges
 491 are provided by the interiors of the long tubular setae
 492 of the *Artemia* exoskeleton, which form the combs on
 493 the filtration appendages. The exoskeleton is shed at
 494 each of the 13 or 14 molts necessary for *Artemia* to
 495 attain maturity and large quantities float in the water.
 496 The appendages are more resistant to bacterial deg-
 497 radation than other parts of the exoskeleton because
 498 of their thick chitinous walls which provide the
 499 necessary flexibility to these locomotory and filtration
 500 structures. Each has dozens of long tubes with an
 501 extensive exterior and interior surface area colonized
 502 by different species of algae and cyanobacteria that
 503 grow and multiply fast due to the high nutrient levels
 504 and light intensity in the GSL (details in Gliwicz,
 505 2003). This diverse algal–cyanobacteria community
 506 was found to represent up to 20% of the available
 507 food for adult *Artemia* throughout the summer and
 508 fall, when the preferred free-swimming *Dunaliella*
 509 was held at an extremely low density in the entire
 510 GSL southern basin (Fig. 3).

The low phytoplankton availability in the GSL
 512 during the summer is the probable reason why: (i) the
 513 lipid index of individual *Artemia* was found to
 514 gradually decline from June to November (Wurts-
 515 baugh & Gliwicz, 2001), (ii) the survival of juvenile
 516 *Artemia* was much lower than that of full grown
 517 adults (Fig. 5), (iii) *Artemia* switched their mode of
 518 reproduction from cyst production to instantly hatch-
 519 ing eggs at low food levels in the lake (Fig. 7), and
 520 (iv) *Artemia* body weight was considerably smaller
 521 than in the Farmington Bay of the GSL (Fig. 8),
 522 where chlorophyll was much higher and *Artemia* less
 523 abundant due to lower salinity that allowed inverte-
 524 brate predators to become abundant and control
 525 *Artemia* abundance. A similar phenomenon has been
 526 reported for the entire southern basin where a
 527 temporary decline in its salinity allowed the preda-
 528 ceous insect *Trichocorixa verticalis* to invade the
 529 pelagic region of the lake and change the ecosystem
 530 from the overwhelming domination of *Artemia* to a
 531 multi-species zooplankton community (Wurtsbaugh
 532 & Berry, 1990; Wurtsbaugh, 1992).

The algae colonizing discarded exoskeletons are
 534 not readily accessible to *Artemia* juveniles and
 535 unavailable to naupli—the exoskeletons are simply
 536 too large to be ingested by small naupli (Fig. 9). This
 537 may be why *Artemia* survival was found to be higher
 538 in older than younger instars, which is evident from
 539

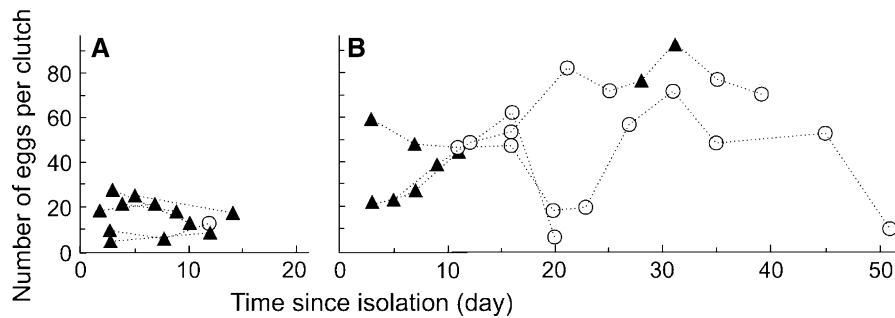


Fig. 7 Clutch size and its distribution in time in GSL *Artemia* brought into the laboratory in July 1994 and grown in a batch culture at two different food levels: $0.5 \mu\text{g chlorophyll l}^{-1}$ (low food) imitating the level in the southern bay (A), and $30 \mu\text{g chlorophyll l}^{-1}$ (high food) similar to that in the

Farmington Bay (B). Note that in *Artemia* transferred to high food level (B), the production of ovoviviparous eggs (circles) becomes replaced by cysts (triangles) production but only after 10 days of evident adjustment

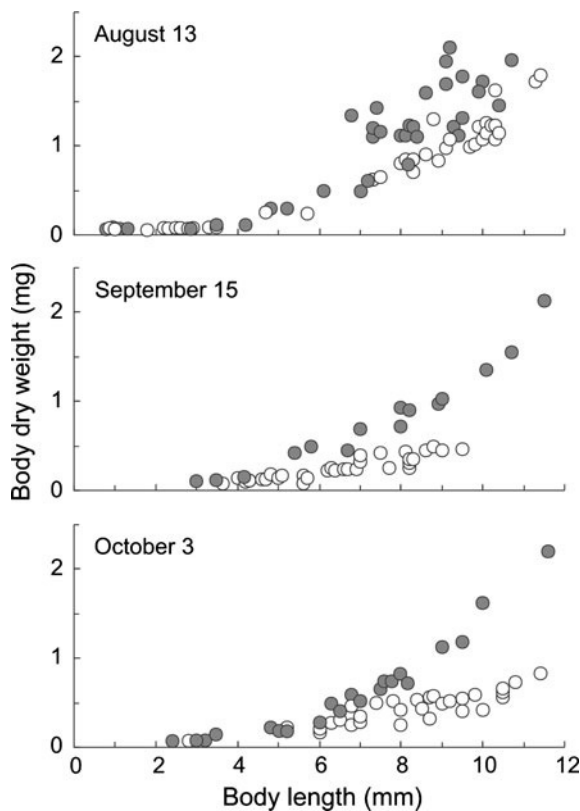


Fig. 8 Length-weight relationships of GSL *Artemia* from two different habitats: the southern basin offshore station with low food level ($<0.5 \mu\text{g chlorophyll l}^{-1}$, empty circles) and the Farmington Bay with high food level ($20\text{--}30 \mu\text{g chlorophyll l}^{-1}$, filled circles). The difference between the slopes and the elevations is significant on each of the three datasets at $P < 0.0476$ for the slopes on 14 August, and $P < 0.0001$ for the slopes on 15 September and 3 October, and the elevations on all three dates

the seasonal change in size distribution shown by the densities of discrete size classes (Fig. 5).

From June onwards the larger juveniles ($>5 \text{ mm}$ body length) grew slowly by about 1 mm per month (Fig. 5). The increase in body length in the main cohort of *Artemia* juveniles stopped altogether in August, when the majority of animals attained maturity and their reproduction became mainly oviparous, with 96–98% producing clutches of cysts. Small numbers of naupli continued to be produced in mid-summer and up until September, but survival of these was apparently minimal and few grew beyond sizes of 2–3 mm (Fig. 5). Thus, there was no measurable recruitment into the early juvenile stages (3–5 mm) until the last adults died in December.

It is possible that recruitment of nauplii was decreased during the low food period due to a phenomenon that females can withhold eggs in the egg sacks and not release them into the lake water. This phenomenon was observed in the laboratory experiments (Gliwicz et al., 1995). The eggs were retained in the brood sacs as long as two conditions remained unfulfilled:

- (1) A new clutch of eggs has to be produced in the ovaries. Below a threshold food concentration, *Artemia* females are prevented from allocating sufficient resources to reproduction, which results in a long inter-brood interval as the clutches of eggs are withheld in the brood sacs. Even at the raised temperature of 25°C , many ovigerous females failed to release eggs from their brood sacs until they eventually died after 10 to 16 days.

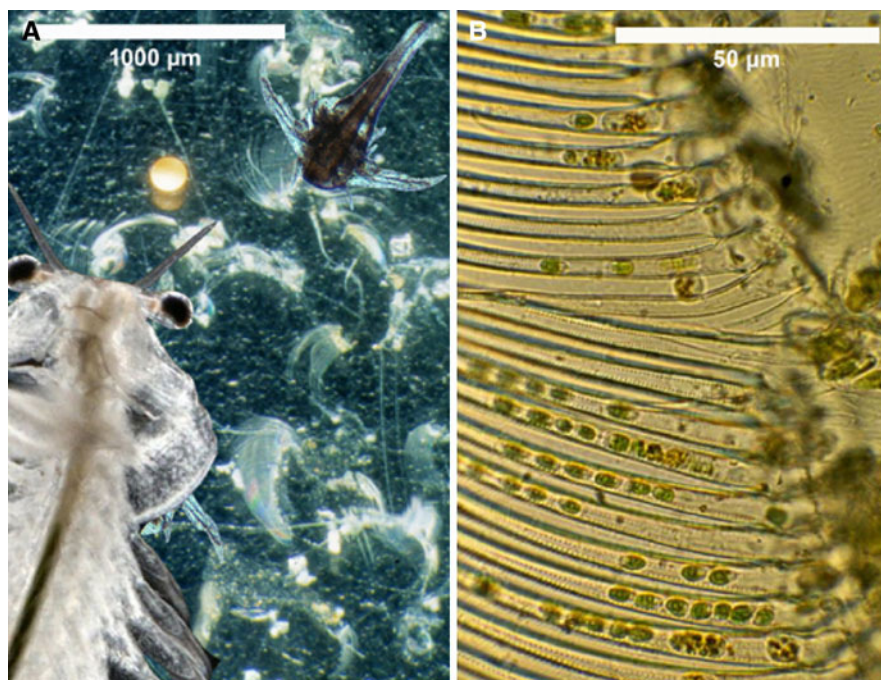


Fig. 9 **A** The residue viewed under a dissecting microscope of a typical plankton sample with a 153- μm mesh net from the Great Salt Lake with two *Artemia* cysts, a day old nauplius (top-right corner), and a grown adult male (bottom-left corner). In the background are multiple shed exoskeletons of *Artemia* filtering limbs, each with green algae (mainly *Dunaliella*) colonizing the interior and exterior surface of each seta that can

be seen under higher magnification of an inverted microscope (**B**). The size proportions show that algae colonizing discarded exoskeletons are not accessible to *Artemia* naupli and not easy to ingest by *Artemia* adults, yet many adults sampled from the lake had their intestines filled with densely packed exoskeletons with most algae digested, but some surviving the gut passage alive

572 (2) A male has to be available to fertilize the next
573 clutch of eggs. This was found to be the case
574 with both ovoviviparous and oviparous eggs. On
575 several occasions, in experiments to assess
576 inter-brood intervals, two females were acci-
577 dentally kept without a male. In this situation,
578 both individuals retained the eggs in their brood
579 sacs for up to 14 days, until the mistake was
580 recognized.

581 A switch in reproduction from cysts to instantly
582 developing eggs was observed in the GSL *Artemia*
583 when transferred from low to high food level. A
584 dramatic difference in selecting the mode of repro-
585 duction was also apparent between mating couples
586 grown at the different food levels: the low food level
587 ($0.5 \mu\text{g}$ chlorophyll $a \text{ l}^{-1}$) imitated the situation in the
588 southern bay, while the high food level ($30 \mu\text{g}$
589 chlorophyll $a \text{ l}^{-1}$) was similar to that found in the
590 Farmington Bay (Fig. 7). At the low food levels, only
591 1 of the 13 broods produced was ovoviviparous, with

the bulk of the reproduction going into cysts, and 592
brood size were relatively small—15.6 (mean \pm 7.3 593
1SD) eggs female $^{-1}$ day $^{-1}$. In contrast, after the 10th 594
day in the high food level treatment, 85% of the 595
broods were ovoviviparous, and mean brood size was 596
53.6 (mean, \pm 24.8 1 SD) eggs female $^{-1}$ day $^{-1}$. Note, 597
however, that there were frequent shifts between 598
ovoviviparity and cyst production even within single 599
mating pairs (Fig. 7). 600

Discussion 601

Habitats free of fish—a single lesson from two 602
different lakes 603

The analysis of two very different systems lacking 604
fish predators, and few invertebrate predators shows 605
how a dominant herbivore can monopolize food 606
resources and minimize the growth of other 607

608 plankton—even their own offspring. In the Great
609 Salt Lake, the dominance of *Artemia* and the low
610 zooplankton diversity is largely driven by the fact
611 that few invertebrates have evolved to tolerate
612 salinities above 10% (Williams et al., 1990). Never-
613 theless, the importance of predation in structuring the
614 Great Salt Lake community was demonstrated during
615 extreme wet years when the salinity was reduced to
616 <6%, and the invertebrate predator, *T. verticalis*,
617 invaded the open waters of the lake and greatly
618 reduced the abundance of *Artemia*. Without the
619 dominant herbivore, phytoplankton levels rose mark-
620 edly, and the community became more diverse with
621 large populations of rotifers, two copepods and some
622 *Artemia* (Wurtsbaugh, 1992).

623 The phenomenon of withholding eggs in the
624 ovaries or in brood sacs by *Artemia* females may
625 also be associated with the ability of females to assess
626 whether food levels are above a threshold concentra-
627 tion sufficient to allow naupli and neonates to survive
628 and grow. This *Artemia* reproductive behavior would
629 thus resemble that of LC ‘orange’ *Daphnia* which
630 refrain from reproducing until the next-year time
631 window where the food level has increased to meet
632 the demands of the offspring. Although such a
633 possibility cannot be excluded, this phenomenon
634 would most probably play a different role in *Artemia*.
635 Our experimental *Artemia* females shifted between
636 producing ovoviviparous eggs and cysts every sec-
637 ond, third or fourth clutch. Even at very low food
638 levels, there was never a complete switch to cyst
639 production. Instead, the inter-brood interval was
640 extended or females refrained from releasing eggs
641 altogether (Gliwicz et al., 1995). In the very low
642 summer food levels in the GSL, the fate of most
643 ovoviviparous eggs was death, but cysts fared better.
644 Despite the fact that massive numbers of cysts are
645 harvested for the aquaculture industry from the lake
646 surface (1,800 tons dry weight annual average in
647 1990–1996; Wurtsbaugh & Gliwicz, 2001), many
648 would be left intact until the high spring temperatures
649 and high food levels allow them to hatch and initiate
650 the new generation.

651 GSL *Artemia* naupli can survive, grow in length
652 and even molt to produce the second or third instars
653 on maternal reserves only. However, at food levels
654 below the threshold concentration required for assim-
655 ilation to equal respiration, they cannot increase body
656 mass. The threshold food concentration for *Artemia*

juveniles is presumably higher than that for adults, as
is the case in other filter-feeding herbivores such as
Daphnia (Gliwicz, 1990; Kreutzer & Lampert, 1999).
Food limitation is also likely to be more severe for
juveniles because the diverse algal–cyanobacteria
community colonizing *Artemia* exoskeletons is not
accessible to them. This inability of naupli and
juveniles to survive competition with adults was
confirmed in our laboratory and in in situ experiments
(Gliwicz et al., 1995); the naupli lost weight and died
as 15-day-old juveniles at the length that they had
hatched at. The only reasonable explanation for the
production of some clutches of ovoviviparous eggs in
their natural habitat is that the lake’s spatio-temporal
complexity (with shallow bays and estuaries of small
rivers in which food levels may periodically be
higher than offshore) affords latecomers some chance
of survival.

The LC *Daphnia* juveniles are probably unable to
survive the long periods of low food during the
winter. The experiments with the ‘orange’ morph of
LC *Daphnia* brought into the laboratory in May
showed that females are able to assess the chance of
juvenile survival in the lake and do not reproduce
until they receive strong and persistent information
indicating higher food levels. Furthermore, most
appeared to wait for another couple of days to make
sure that any food increase was not a short-term
phenomenon (Fig. 6). Otherwise, they seem willing
to postpone reproduction until the time window in
July when both higher food levels (Fig. 2) and a
lowered risk of falling prey to *Cyclops* (Gliwicz et al.,
2001) increase the chances of survival and growth of
their offspring. Both factors may work in tandem,
complementing and reinforcing one another, with
individual fitness stemming from a trade-off in terms
of selecting the right time for reproduction.

The July time window for the reproduction of the
‘orange’ LC *Daphnia* morph also represents a high
food window for the ‘transparent’ LC *Daphnia*
morph to hatch from ephippia. At present, we do
not know whether this morph could be induced to
switch its mode of reproduction from producing
resting eggs to oviparity if they were taken from the
lake in October, when the last females produce their
final eggs of the year (Fig. 4). Throughout the time
the two morphs coexist in the lake, the ‘transparent’
LC *Daphnia* has remained significantly smaller than
the ‘orange’ LC *Daphnia* morph (Slusarczyk, 2009).

This smaller size may be the reason for its competitive inferiority and the slightly higher food threshold concentration needed for growth and reproduction, as predicted by the size-efficiency hypothesis (Brooks & Dodson, 1965; Gliwicz, 1990). Thus, it may also explain why the 'transparent' LC *Daphnia* does not remain active in wait for the June peak in food abundance. Instead, in competition with the superior 'orange' morph for scarce food resources, it produces diapausing eggs to successfully survive the long, cold and hungry winter.

Even without the synchrony of reproduction observed in the 'transparent' LC *Daphnia*, the pattern of the growth and survival for an *Artemia* cohort is nearly the same (Figs. 4, 5). However, in *Artemia*, the outcome is not exclusively the product of inter-clonal and intraspecific competition for resources, but also reflects a more complex mode of obligatory sexual reproduction. A male *Artemia* grasps the female using its powerful claws, renewing its permanent grip after the molt to stay with the same sexual partner for the next stage duration. This avoids competition with co-occurring males that might otherwise inseminate a clutch of eggs ready to be released to the egg sac ('post-insemination mate association'). This behavior, where time is invested to prevent the partner from re-mating, is common in insects and mites (Alcock, 1994); an increased chance of paternity is preferred to the possibility of fertilizing another female that lacks a mate.

The time window for reproductive success is clearly different in GSL *Artemia* and LC *Daphnia*. In GSL, early spring, when the primary producers have recovered from the previous year's grazing pressure, is the only time of high food levels and appropriate temperatures for growth. Therefore, this is the time of mass hatching from diapausing cysts and of intense reproduction in *Artemia* (Wurtsbaugh & Gliwicz, 2001). In 1995, most of the first-cohort *Artemia* were already adult by 5 May, with 90% of the females bearing large clutches of ovoviviparous eggs: 170 (± 12) eggs per clutch (mean \pm SE) or 77 eggs l^{-1} . However, at the next sampling (5 June), the density of juveniles was only 7 ind. l^{-1} , or a tenth of the expected value based on egg production. Therefore, 90% of the second generation hatching from ovoviviparous eggs had died, evidently because food levels had declined from 25 μg chl *a* l^{-1} on 10 May to <1 μg chl *a* l^{-1} . Most of the survivors may have been

juveniles that had hatched early enough to enjoy high food levels, so that the population mainly consisted of the offspring of the first members of the new generation arising from cysts that had over-wintered at locations where spring began earlier. Other reproductive patterns have been noted in the GSL in different years, with nauplii production and growth into juvenile stages occurring in the summer of some years (G. Belovsky, personal communication).

The results of hatching experiments with both *Daphnia* and *Artemia* showed that the adult females are physiologically ready and, in spite of food shortages, have accumulated sufficient maternal resources to reproduce. These experiments also showed that the temporary abstention from reproduction of immediately hatching eggs is an important life-history decision in both species when the chance of survival has been reduced due to the sub-threshold food levels available to the newborn. With the perspective that food resources would be held at this low level by adults until they die or until the spring overturn makes food more abundant, the females either have to wait, or to produce resting stages (ephippia or cysts). The former strategy is employed by the 'orange' LC *Daphnia* lineage, while the latter by the 'transparent' LC *Daphnia* and the GSL *Artemia*.

In contrast to the 'orange' LC *Daphnia* that over-winter in temperatures close to 4°C, the GSL *Artemia* cannot survive winter temperatures that can fall to $-1^{\circ}C$ throughout this lake. As a result, the population ceases to exist in December, and restarts again the following spring with the hatching of cysts. The newborn juveniles enjoy high food levels which allow high rates of growth and reproduction and at this point, the GSL *Artemia* represent a perfect example of a typical time-limited population (Schoener, 1973). For a time-limited population at high food levels, a slightly higher temperature is more important than the absolute food level. With increases in temperature and growth of individuals, the population soon becomes resource limited again, when its density and biomass return to the carrying capacity level. *A. franciscana* transported to warmer climates can over-winter as adults (e.g., Wear & Haslett, 1987), thus following a similar strategy to that used by the 'orange' LC *Daphnia*.

In comparison to the 'orange' LC *Daphnia*, the 'transparent' LC *Daphnia* is likely to be more

804 demanding with regard to food levels. Although the
805 individual threshold food concentration of adults of
806 the two lineages has not been estimated, the 'trans-
807 parent' *Daphnia* were found to be persistently smaller
808 than the 'orange' ones when their sizes were com-
809 pared throughout the entire time of their coexistence
810 in the lake (see Fig. 3b in Slusarczyk, 2009).

811 In conclusion, from the study of both the LC
812 *Daphnia* and the GSL *Artemia* it is apparent that in
813 the absence of fish predation, the zooplankton
814 community is substituted by a single herbivore that
815 monopolizes resources. Interspecific competition is
816 replaced by even harsher intraspecific competition,
817 which leads to synchronous life histories, resulting in
818 the competitive superiority of adults over juveniles.
819 In addition, the *Artemia* example shows that the same
820 population may be time-limited in spring, but
821 resource-limited in summer.

822 Habitats free of fish—highlighting the importance 823 of fish predation

824 Each of the two lakes of our study represents an
825 extreme habitat. The Lake Czarny is a typical alpine
826 lake, cold and infertile. The Great Salt Lake is highly
827 fertile but hypersaline. However, less extreme habitats
828 are seldom free of fish because humans stock nearly
829 every available water hole, and no less extreme
830 habitats could be located to be used as examples of
831 lakes free of fish. There are other examples, but they
832 are either equally extreme, and just as remote, or they
833 are examples of small, temporary or manipulated
834 systems, many of them reviewed by Gliwicz (2003).
835 There are examples of a single large-bodied *Daphnia*
836 in isolated arctic or high-elevation ultraoligotrophic
837 lakes of Europe, Equatorial Africa and Asia, in ponds
838 of Norwegian highlands (*Daphnia umbra* of Larsson
839 & Wathne, 2006) and Italian Alps (*D. longispina* of
840 Cammarano & Manca, 1997), tarns of Mount Elgon
841 and Mount Kenya at 3475 to 4330 m ASL (*Daphnia*
842 *dolichocephala* Sars of Löffler, 1968), in the Pamir
843 (Rylov, 1930), Hindukush (Rühe, 1915) and Tibetan
844 Himalaya (*Daphnia tibetana* of Hutchinson, 1937 and
845 Manca et al., 1994). There is also an example of a
846 highly eutrophic Bohemian fishpond that, by mistake,
847 was left unstocked for the entire season. Its otherwise
848 diverse zooplankton was rapidly replaced by a single-
849 species, a large-bodied *Daphnia pulicaria*, that were
850 surviving on low food levels of flagellated green algae

851 which were suppressed by heavy grazing from 60–80
852 *Daphnia* l⁻¹. The *Daphnia* were unable to reproduce
853 for 100 days, until the mistake was detected and the
854 pond was stocked with carp again (details in Fott
855 et al., 1974, 1980; Gliwicz, 2003).

856 The importance of fish predation in shaping the
857 structure of zooplankton communities has been clear
858 since it was first reported by Hrbáček et al. (1961,
859 1962), and subsequently used as a keystone of the
860 *size-efficiency hypothesis* of Brooks & Dodson
861 (1965). It is evident that the increased impact of fish
862 predation causes zooplankton size distribution to shift
863 considerably towards small-bodied species (Fig. 1). It
864 might also be anticipated that increased fish predation
865 should keep different zooplankton species at densities
866 well below the carrying capacity level to allow stable
867 coexistence, as was the case with different cichlid
868 species in Lake Malawi (Fryer, 1959a, 1959b) and
869 sedentary invertebrates on the rocky shore of Wash-
870 ington's Pacific coast (Paine, 1966).

871 However, the outcome when fish are completely
872 absent, thus allowing competition that is not
873 restricted by mortality induced by predation, is often
874 ignored or unknown. Only by consideration of the
875 zooplankton communities in habitats free of fish,
876 such as Lake Czarny or Great Salt Lake, is it possible
877 to grasp the real role of fish predation in shaping
878 zooplankton community composition and the age
879 structure of each component species. Only then can
880 some comprehension be gained of the real world
881 where fish predation fosters the coexistence of many
882 zooplankton species in spite of the high overlap in
883 their diets and hence niche dimensions. Furthermore,
884 only then does it become clear why (i) the densities of
885 coexisting zooplankton species are similar from one
886 lake to another, with small-bodied species always
887 more abundant than large-bodied ones, and (ii) the
888 proportions of large and small-bodied species are
889 similar across habitats comprising a wide productiv-
890 ity spectrum, with each species at a density fixed by
891 fish predation at the species-specific level where it
892 becomes included in a fish's diet (Gliwicz &
893 Wrzosek, 2008).

894 This simple world of fish-free habitats is unknown
895 to most limnologists and absent from contemporary
896 textbooks. Current knowledge of aquatic systems and
897 our understanding of diversity offshore are based on
898 observations of habitats that have contained fish for
899 millennia. Aquatic habitats that are free of fish are rare

900 and marginal. Although they may provide important
901 forage for birds, they are considered a waste by fishery
902 people. They may also seem uninteresting to limnol-
903 ogists as well, for they lack complex food webs and
904 the multitude of intriguing interactions that occur
905 between the many coexisting species in a typical
906 marine or freshwater habitat. They also lack the
907 challenging magic of the Hutchinson's 'paradox of
908 the plankton'. There is, however, one aspect of the
909 limnology of fish-free habitats that makes understand-
910 ing them more important. This does not relate to the
911 habitats themselves, but rather lies in the chance they
912 offer to grasp the overpowering force of fish preda-
913 tion by illustrating the consequences of its absence.
914 Besides this powerful lesson, the example of zoo-
915 plankton from two different fish-free habitats dis-
916 cussed here also strengthens the argument that
917 diversity may be sustained only where predation
918 keeps densities of coexisting species at levels below
919 the carrying capacity, as was pondered by Hutchinson
920 50 years ago. It shows that different species coexist
921 because each is maintained at a low species-specific
922 density level, which is inversely related to body size
923 and irrespective of food level, because greater
924 recruitment at higher food is instantly compensated
925 for by raised mortality resulting from the response of
926 fish to increased prey abundance.

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