

2010

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

Z. M. Gilwicz

Wayne A. Wurtsbaugh  
*Utah State University*

E. Szymansk

Follow this and additional works at: [https://digitalcommons.usu.edu/wats\\_facpub](https://digitalcommons.usu.edu/wats_facpub)

 Part of the [Aquaculture and Fisheries Commons](#), [Environmental Sciences Commons](#), and the [Fresh Water Studies Commons](#)

## Recommended Citation

Gilwicz, Z.M., W.A. Wurtsbaugh (published as Wurtsbaugh), and E. Szymansk. 2010. Absence of predation eliminates coexistence: Experience from the fish-zooplankton interface. *Hydrobiologia*. 653:103–117. DOI 10.1007/s10750-010-0347-z

This Article is brought to you for free and open access by the Watershed Sciences at DigitalCommons@USU. It has been accepted for inclusion in Watershed Sciences Faculty Publications by an authorized administrator of DigitalCommons@USU. For more information, please contact [dylan.burns@usu.edu](mailto:dylan.burns@usu.edu).



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

4 **Z. Maciej Gliwicz · Wayne A. Wurtsbaugh · Errata Wurtsbaugh**  
5 **Ewa Szymanska**

6  
7 © Springer Science+Business Media B.V. 2010

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

A4 Z. M. Gliwicz (✉) · E. Szymanska  
A5 Department of Hydrobiology, University of Warsaw,  
A6 Banacha 2, 02-097 Warszawa, Poland  
A7 e-mail: gliwicz@hydro.biol.uw.edu.pl

A8 W. A. Wurtsbaugh  
A9 Department of Watershed Sciences, Utah State  
A10 University, Logan, UT 84322-5210, USA  
A11 e-mail: wayne.wurtsbaugh@usu.edu

**Keywords** Competitive exclusion · 49  
Diversity · Fish predation · Resource limitation · 50  
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.

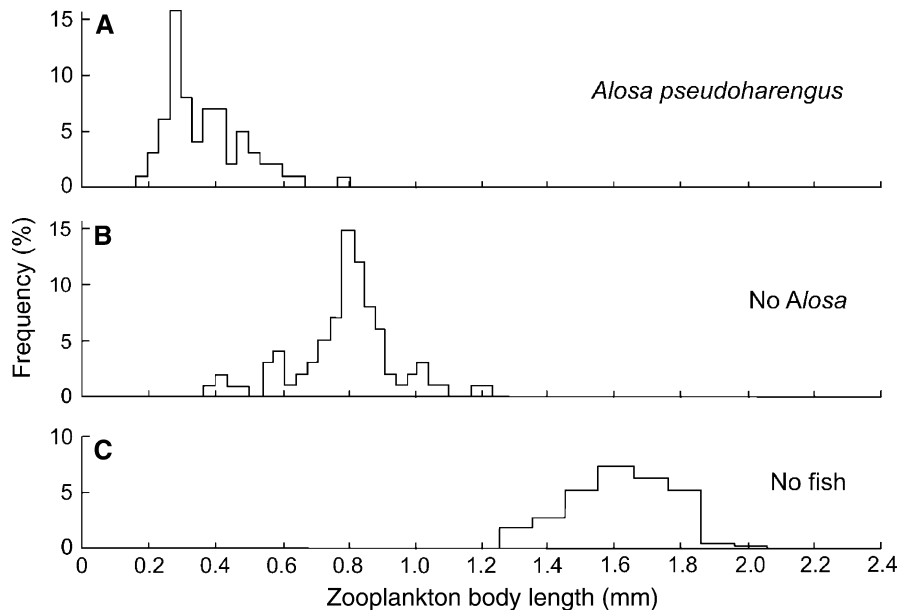
63 One of these inspirations was the 'Homage to Santa  
64 Rosalia or why are there so many kinds of animals' by  
65 Hutchinson (1959). This essay articulated most of the  
66 contemporary ideas of that time on the importance of  
67 food chain interactions and diversity of plants as both  
68 substrate 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

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

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



**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 & Schoener,  
 164 1998; Almany & Webster, 2004). Moreover, the  
 165 high diversity of zooplankton has often been attributed  
 166 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 km<sup>2</sup> 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 km<sup>2</sup> 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<sup>-1</sup>. 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 km<sup>2</sup> bay  
 289 receives considerable river inflow and thus has salin-  
 290 ities varying from <10–90 g l<sup>-1</sup>, 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- $\mu$ m mesh (no other rotifer species  
 301 were revealed from tube samples for phytoplankton  
 302 counts in the GSL and parallel hauls with 50- $\mu$ 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.

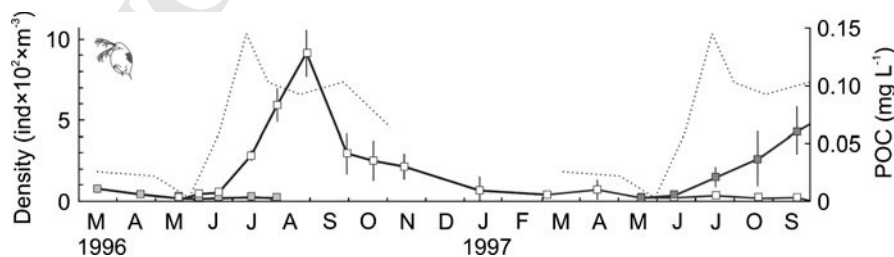
#### 316 Experimental test of the impact of food level 317 on reproductive performance

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<sup>-1</sup>: 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  $\mu$   
 g chlorophyll *a* l<sup>-1</sup> (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

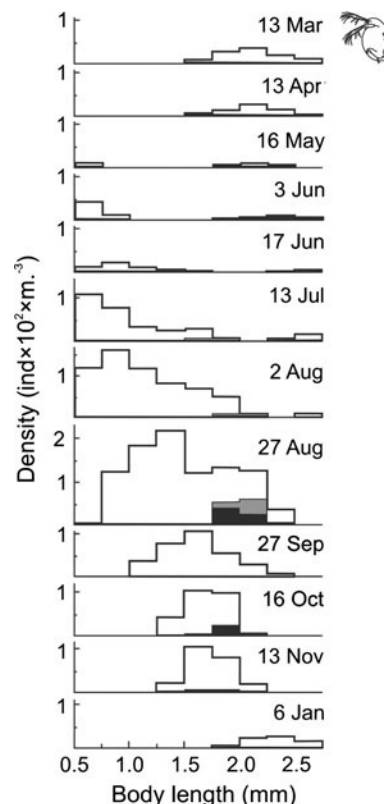
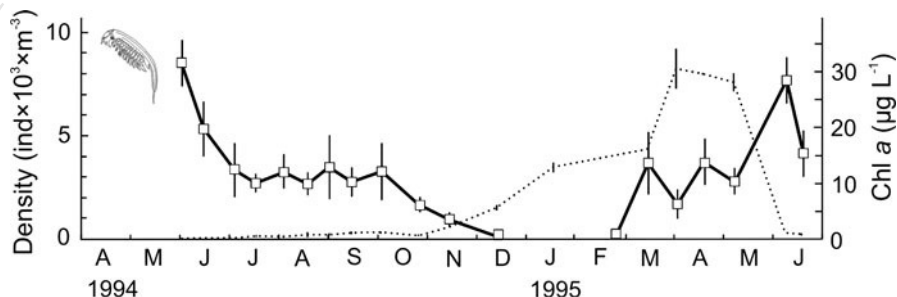
## 356 Results

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*

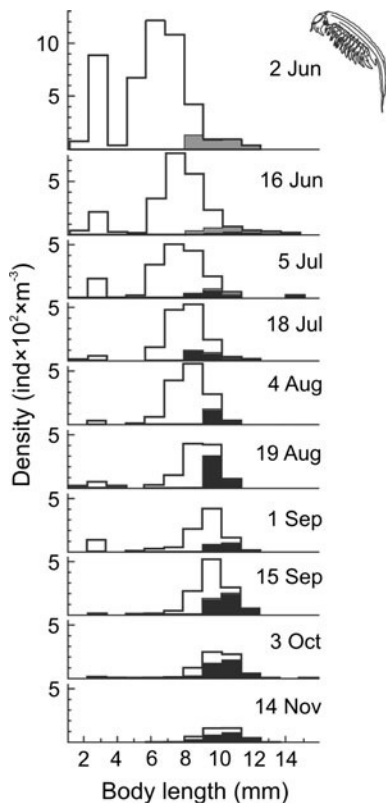
380 One-year of data on LC zooplankton (Gliwicz et al.,  
 381 2001) revealed that the large-bodied *Daphnia*, the  
 382 sole filter-feeding herbivore monopolizing resources  
 383 in the absence of fish, co-exist with cyclopoid  
 384 copepods, *Cyclops abyssorum taticus*, and, sporadically,  
 385 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

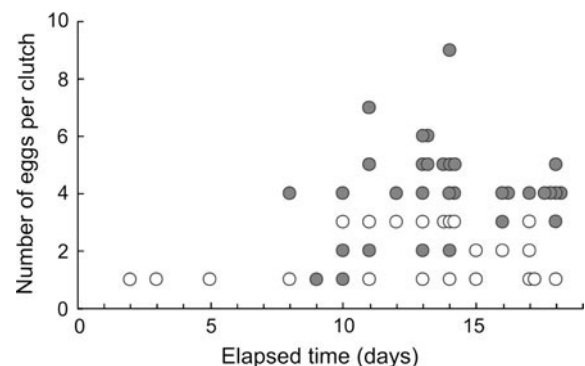


**Fig. 5** Seasonal changes in the size distribution and fecundity of GSL *Artemia* shown as the density of each discrete size class on each of the 10 sampling dates, from 2 June to 14 November 1994. The proportions of egg-bearing females (light shaded) and females with cysts in their egg sacks (dark 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 Slusarczyk  
 (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  $\text{mg POC l}^{-1}$ , 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*

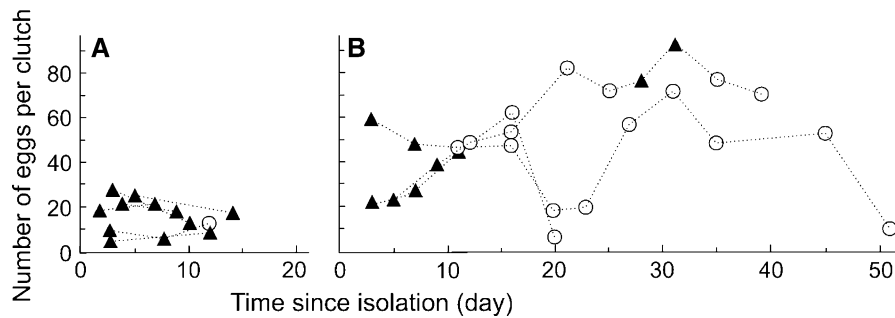
457 In the GSL *Artemia* was the sole zooplankton found  
458 across the entire GSL southern basin (Gilbert Bay)  
459 from March to December (Fig. 3). After *Artemia*  
460 disappeared in December, chlorophyll increased from  
461 ca.  $1\text{--}25 \mu\text{g l}^{-1}$ , and an elongate ciliate (measuring  
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  $240 \text{ ml d}^{-1}$  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).

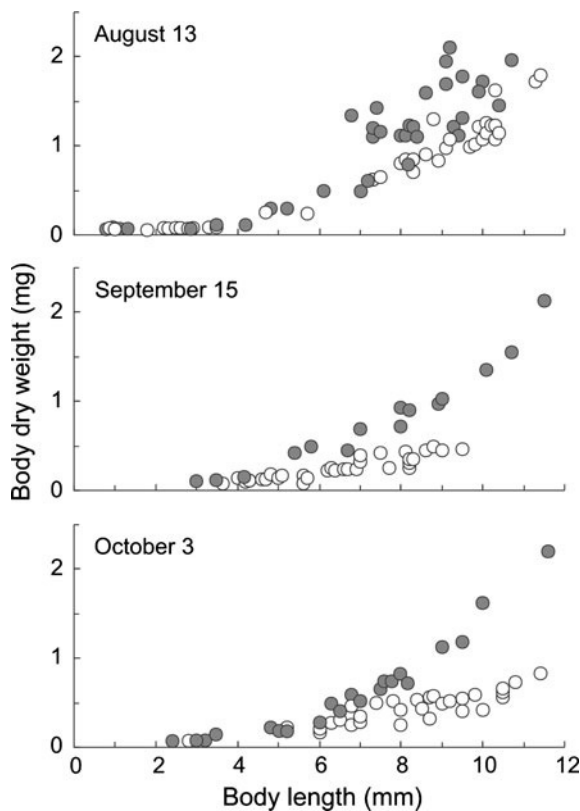
The low phytoplankton availability in the GSL  
512 during the summer is the probable reason why: (i) the  
513 lipid index of individual *Artemia* was found to  
514 gradually decline from June to November (Wurts-  
515 baugh & Gliwicz, 2001), (ii) the survival of juvenile  
516 *Artemia* was much lower 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



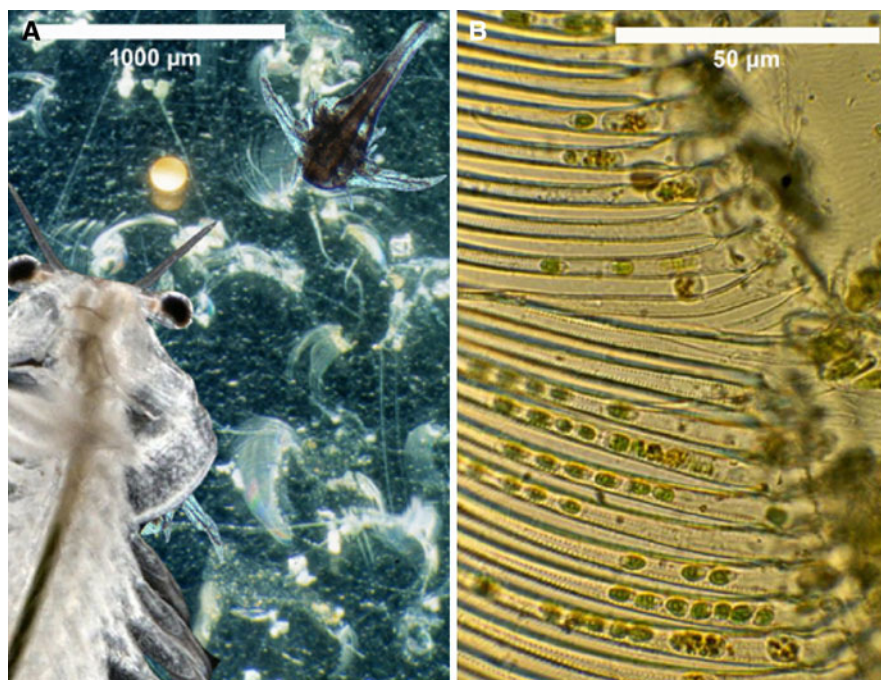
**Fig. 8** Length-weight relationships of GSL *Artemia* from two different habitats: the southern basin offshore station with low food level ( $<0.5 \mu\text{g chlorophyll l}^{-1}$ , empty circles) and the Farmington Bay with high food level ( $20\text{--}30 \mu\text{g chlorophyll l}^{-1}$ , filled circles). 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  $1 \text{ mm}$  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  $25^\circ\text{C}$ , 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- $\mu\text{m}$  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 ( $\pm 12$ ) 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  $\mu g$  chl *a*  $l^{-1}$  on 10 May to  $<1$   $\mu g$  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<sup>-1</sup>. 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.

927 **Acknowledgments** We are grateful to Piotr Maszczyk and  
928 Alan Ward for their assistance in the field and laboratory work,  
929 Mirek Slusarczyk and John R. Gittins for their instructive  
930 comments on the earlier drafts of this manuscript, and the two  
931 anonymous reviewers for their very constructive and helpful  
932 suggestions. This research was supported by Quinney Visiting  
933 Scholarship, Utah State University to Z.M.G., by grant from  
934 the Utah Division of Wildlife Resources to W.A.W., and by  
935 grants 6P04F01921 and 2P04G01430 from the State  
936 Committee for Scientific Research, Poland, to Z.M.G.

## 937 References

- 938 Abrams, P. A. & R. D. Holt, 2002. The impact of consumer  
939 resource cycles on the coexistence of competing con-  
940 sumers. *Theoretical Population Biology* 62: 281–295.  
941 Alcock, J., 1994. Postinsemination associations between males  
942 and females in insects: the mate-guarding hypothesis.  
943 *Annual Review of Entomology* 39: 1–21.  
944 Almany, G. R. & M. S. Webster, 2004. Odd species out as  
945 predators reduce diversity of coral-reef fishes. *Ecology*  
946 65: 2933–2937.  
947 Brooks, J. L. & S. I. Dodson, 1965. Predation, body size and  
948 composition of plankton. *Science* 150: 28–35.

- Cammarano, P. & M. Manca, 1997. Studies on zooplankton  
949 in two acidified high mountain lakes in the Alps. *Hydro-  
950 biologia* 356: 97–109. 951  
Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson,  
952 R. D. Holt, S. A. Richards, R. M. Nisbet & T. J. Case,  
953 2002. The interactions between predation and com-  
954 petition: a review and synthesis. *Ecology Letters* 5: 302–  
955 315. 956  
Chesson, P., 2000. Mechanisms of maintenance of species  
957 diversity. *Annual Review of Ecology and Systematics* 31:  
958 343–366. 959  
Connell, J. H., 1978. Diversity in tropical rain forests and coral  
960 reefs. *Science* 199: 1302–1310. 961  
Fott, J., V. Korinek, M. Prazakova, B. Vondrus & K. Forejt,  
962 1974. Seasonal development of phytoplankton in fish  
963 ponds. *Internationale Revue der gesamten Hydrobiologie*  
964 59: 629–641. 965  
Fott, J., B. Desortova & J. Hrbacek, 1980. A comparison of the  
966 growth of flagellates under heavy grazing stress with a  
967 continuous culture. In *Continuous cultivation of micro-  
968 organisms*. Proceedings of the 7th Symposium, Prague:  
969 395–401. 970  
Fryer, G., 1959a. The trophic interrelationships and ecology of  
971 some littoral communities of Lake Nyasa and a discussion  
972 on the evolution of a group of rock-frequenting Cichlidae.  
973 Proceedings of the Zoological Society of London 132:  
974 153–281. 975  
Fryer, G., 1959b. Some aspects of evolution in Lake Nyasa.  
976 *Evolution* 13: 440–451. 977  
Gliwicz, Z. M., 1986. Predation and the evolution of vertical  
978 migration in zooplankton. *Nature* 320: 746–748. 979  
Gliwicz, Z. M., 1990. Food thresholds and body size in  
980 cladocerans. *Nature* 343: 638–640. 981  
Gliwicz, Z. M., 2001. Species-specific population-density  
982 thresholds in cladocerans? *Hydrobiologia* 442: 291–300. 983  
Gliwicz, Z. M., 2002. On the different nature of top-down and  
984 bottom-up effects. *Freshwater Biology* 47: 2296–2312. 985  
Gliwicz, Z. M., 2003. Between hazards of starvation and risk of  
986 predation: the ecology of offshore animals. *International  
987 Ecology Institute, Oldendorf/Luhe*: 379 pp. 988  
Gliwicz, Z. M. & D. Wrzosek, 2008. Predation-mediated  
989 coexistence of large- and small-bodied *Daphnia* at dif-  
990 ferent food levels. *The American Naturalist* 172: 358–374. 991  
Gliwicz, Z. M., W. A. Wurtsbaugh & A. Ward, 1995. Brine  
992 shrimp ecology in the Great Salt Lake, Utah. June 1994–  
993 May 1995 performance report to the Utah Division of  
994 Wildlife Resources, Salt Lake City, Utah: 83 pp. 995  
Gliwicz, Z. M., M. Slusarczyk & A. Slusarczyk, 2001. Life-  
996 history synchronization in a long-lifespan single-cohort  
997 *Daphnia* population of an alpine lake free of fish. *Oeco-  
998 logia* 128: 368–378. 999  
Hrbáček, J., 1962. Species composition and the amount of  
1000 zooplankton in relation to the fish stock. *Rozprawy  
1001 ceskosloveske Akademie Véd Rada Matematicko-  
1002 Prirodovedecka* 72: 1–114. 1003  
Hrbáček, J., M. Dvorakova, V. Korinek & L. Prochazkova,  
1004 1961. Demonstration of the effect of the fish stock on the  
1005 species composition of zooplankton and intensity of  
1006 metabolism of whole plankton association. *Verhandlun-  
1007 gen der Internationalen Vereinigung für Theoretische und  
1008 Angewandte Limnologie* 14: 192–195. 1009

- 1010 Huisman, J. & F. J. Weissing, 1999. Biodiversity of plankton  
1011 by species oscillations and chaos. *Nature* 402: 407–410.
- 1012 Hutchinson, G. E., 1937. Limnological studies in Indian Tibet.  
1013 *Internationale Revue der gesamten Hydrobiologie* 35:  
1014 124–177.
- 1015 Hutchinson, G. E., 1959. Homage to Santa Rosalia or why are  
1016 there so many kinds of animals? *The American Naturalist*  
1017 93: 145–159.
- 1018 Hutchinson, G. E., 1961. The paradox of the plankton. *The*  
1019 *American Naturalist* 95: 137–146.
- 1020 Kreutzer, C. & W. Lampert, 1999. Exploitative competition in  
1021 differently sized *Daphnia* species: a mechanistic expla-  
1022 nation. *Ecology* 80: 2348–2357.
- 1023 Lampert, W., 1988. The relationship between zooplankton  
1024 biomass and grazing. A review. *Limnologica* 19: 11–20.
- 1025 Larsson, P. & I. Wathne, 2006. Swim or rest during winter—  
1026 what is best for an alpine daphnid? *Archiv für Hydrobi-  
1027 ologie* 167: 265–280.
- 1028 Lima, S. L., 1985. Maximizing feeding efficiency and mini-  
1029 mizing time exposed to predators: a trade-off in black-  
1030 capped chickadee. *Oecologia* 66: 60–67.
- 1031 Lima, S. L., 1998. Stress and decision making under the risk of  
1032 predation: developments from behavioral, reproductive,  
1033 and ecological perspectives. In Møller, A. P., M. Milinski  
1034 & P. J. B. Slater (eds), *Stress and Behavior. Advances in*  
1035 *the Study of Behavior*, Vol. 27. Academic Press, San  
1036 Diego: 215–290.
- 1037 Löffler, H., 1968. Die Crustaceenfauna der Binnengewässer  
1038 ostafrikanischer Hochberge. *Hochgebirgsforschung* 1(8):  
1039 107–170.
- 1040 Manca, M., P. Cammarano & T. Spagnulo, 1994. Notes on  
1041 Cladocera and Copepoda from high altitude lakes in the  
1042 Mount Everest Region (Nepal). *Hydrobiologia* 287: 225–  
1043 231.
- 1044 Montague, C. L., W. R. Fey & D. M. Gillespie, 1982. A causal  
1045 hypothesis explaining predator-prey dynamics in Great  
1046 Salt Lake, Utah. *Ecological Modeling* 17: 243–270.
- 1047 Nelson, W. A., E. McCauley & F. J. Wrona, 2005. Stage-  
1048 structured cycles promote genetic diversity in a predator-  
1049 prey system of *Daphnia* and algae. *Nature* 433: 413–417.
- 1050 Paine, R. T., 1966. Food web complexity and species diversity.  
1051 *The American Naturalist* 100: 65–75.
- 1052 Paine, R. T., 1969. A note on trophic complexity and com-  
1053 munity stability. *The American Naturalist* 103: 91–93.
- 1054 Paine, R. T., 2002. Trophic control of production in a rocky  
1055 intertidal community. *Science* 296: 736–739.
- 1056 Reeve, M. R., 1963. The filter-feeding in *Artemia*. I. In pure  
1057 cultures of plant cells. *Journal of Experimental Biology*  
1058 40: 195–205.
- 1059 Rosenzweig, M. L. & R. H. MacArthur, 1963. Graphical rep-  
1060 resentation and stability conditions of predator-prey  
1061 interactions. *The American Naturalist* 47: 209–223.
- Rühe, F. E., 1915. Die Süßwassercrustaceen der deutschen  
Südpolarexpedition 1901–1903 mit Ausschluss der  
Ostracoden. *Deutsche Südpolar-Expedition 1901–1903.*  
*Zoologie* 16(8).
- Rylov, M., 1930. Cladocera et Copepoda in Abhandlungen der  
Pamir. Expedition 1928. II. *Zoologie*: 105–133.
- Sarnelle, O., 1993. Herbivore effects on phytoplankton suc-  
cession in a eutrophic lake. *Ecological Monographs* 63:  
129–149.
- Schoener, T. W., 1973. Population growth regulated by intra-  
specific competition for energy or time: some simple  
representations. *Theoretical Population Biology* 4: 56–84.
- Slobodkin, L. B., 1963. *Growth and regulation of animal*  
populations. Holt, Rinehart & Winston, New York.
- Slusarczyk, M., 2009. Extended lifespan traded for diapause in  
*Daphnia*. *Freshwater Biology* 54: 2252–2262.
- Spiller, D. A. & T. W. Schoener, 1998. Lizards reduce spider  
species richness by excluding rare species. *Ecology* 79:  
503–516.
- Stein, R. A. & J. J. Magnuson, 1976. Behavioral response of  
crayfish to a fish predator. *Ecology* 57: 751–761.
- Stich, H. B. & W. Lampert, 1984. Growth and reproduction in  
migrating and non-migrating *Daphnia* species under  
simulated food and temperature conditions of diurnal  
vertical migrations. *Oecologia* 61: 192–196.
- Tilman, D., 1982. *Resource competition and community*  
structure. Princeton University Press, Princeton.
- Wear, R. G. & S. J. Haslett, 1987. Studies on the biology and  
ecology of *Artemia* from Lake Grassmere, New Zealand.  
In Sorgeloos, P., et al. (eds), *Artemia* research and its  
applications. Vol. 3. Ecology, culturing and use in aqua-  
culture. Universa Press, Wetteren, Belgium: 101–133.
- Weider, L. J., 1992. Disturbance, competition and the main-  
tenance of clonal diversity of *Daphnia pulex*. *Journal of*  
*Evolutionary Biology* 5: 505–522.
- Williams, W. D., A. J. Boulton & R. G. Taaffe, 1990. Salinity  
as a determinant of salt lake fauna: a question of scale.  
*Hydrobiologia* 197: 257–266.
- Wurtsbaugh, W. A., 1992. Food-web modification by an  
invertebrate predator in the Great Salt Lake (USA).  
*Oecologia* 89: 168–175.
- Wurtsbaugh, W. A., 1995. Brine shrimp ecology in the Great  
Salt Lake, Utah. 1995 performance report to the Utah  
Division of Wildlife Resources, Salt Lake City, Utah.
- Wurtsbaugh, W. A. & T. S. Berry, 1990. Cascading effects of  
decreased salinity on the plankton, chemistry, and physics  
of the Great Salt Lake (Utah). *Canadian Journal of Fish-  
eries and Aquatic Sciences* 47: 100–109.
- Wurtsbaugh, W. A. & Z. M. Gliwicz, 2001. Limnological  
control of brine shrimp population dynamics and cysts  
production in the Great Salt Lake, Utah. *Hydrobiologia*  
466: 119–132.