Biodiversity of large branchiopods of Australian saline lakes

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Australia is a land of intermittent saline lakes, and there is a commensurate abundance of halophilic large branchiopods. These include two species of *Artemia*; a species swarm of *Parartemia*; a few *Branchinella* spp., including *B. simplex* to 62 ppt, *Eocyzicus parooensis* to 24 ppt, a variety of other spinicaudatans, and *Triops* sp. (near *australiensis*) to 93 ppt. Despite the low diversity of freshwater forms, halophilic species are higher in Australia, and upper limits equal or are higher than elsewhere in the world. Reasons for this are explored and osmotic mechanisms outlined.

Keywords: Australian saline lakes, diversity and salinity tolerance, endemic crustaceans, osmotic mechanisms.

Introduction

ATHALASSIC saline waters in Australia are dominated by endemic crustaceans, particularly by ostracods, copepods, cladocerans and anostracans[1–4]. Among the latter, *Parartemia zietziana* is ubiquitous in the numerous saline lakes of western Victoria and South Australia (SA)[5,6], *P. minuta* is common in the scattered saline lakes of the central and eastern inland[4,7], and in Western Australia (WA) there are numerous species of *Parartemia* in its various saline waters[2]. Some species of *Branchinella* (subgenus *Branchinella*) have also been reported from saline waters, mainly *B. australiensis*, *B. buchananensis*, *B. compacta* and *B. simplex*[8–11]. In essence this repeats the well-known presence of *Artemia* spp., *Phallocryptus spinosa*, and *Branchinectella media* in Eurasia and Africa[12,13], *Artemia* spp., *Phallocryptus wrightii*, *Dendrocephalus cervicornis* and *Thamnocephalus salinarum* in South America[14–16] and *Artemia* spp. and *Branchinecta campestris*, *B. lateralis* and *Phallocryptus sublettei* in North America[17–19], but apparently with greater diversity in Australia. Futhermore, a clam shrimp, *Eocyzicus parooensis* has been recently described from hyposaline lakes in the Paroo, Australia[20] and a species of *Triops* has been reported from hypersaline waters in Western Australia[11]. These records all point to a far greater diversity of large branchiopods in Australian saline waters than elsewhere in the world.

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The aim of this article is to collect scattered literature on halophilic large branchiopods in Australia and add to it my numerous unpublished records, in order to present a comprehensive review on the diversity and salinity tolerances of large branchiopods in Australian saline waters. I also review what is known about how large branchiopods manage to live in such hostile environments and to consider explanations for the greater diversity in Australia.

Methods

This article is both a review of the literature and a presentation of numerous records from field notebooks. The former source is frustrated by incomplete identifications and by an unfinished thesis by Alan Savage on *Parartemia*. My records have been accumulated over the last 20 years from numerous field trips to the Paroo (northwestern New South Wales (NSW) and southwestern Queensland), Eyre Peninsula in SA, and the goldfields and Esperance hinterland of WA. Some are in the process of being reported elsewhere, but not in this format (e.g. Eyre Peninsula records)[21] and many others have been extracted for the first time (e.g. see Figures 2 and 3). Most place names mentioned in the text are shown in Figure 1. Identifications have been made using Timms[10,22] for anostracans, Richter and Timms[20] for spinicaudatans, Longhurst[23] for notostracans and original descriptions in the case of some spinicaudatans. Field salinities were measured with a Hanna HI 8663 conductivity meter and converted to Total Dissolved Solids (TDS) in ppt using Williams's formula[24], or TDS was determined directly by gravimetry.

Results

Two species of *Artemia* occur in Australia, *A. francisciana* and *A. parthenogentica*, both introduced to salt works, though the latter also has a few natural populations in WA[25]. Published data on their field salinity ranges are scant, but *A. parthenogenetica* has been recorded within 61–330 ppt (Table 1).

There are eight described species of *Parartemia* in Australia[26,27] and at least ten undescribed species, most of which are known by an epithet of species a, b, . . . , etc.[22] (A. Savage, pers. commun., and P. Hudson, pers. com-

Table 1. Salinity ranges for populations of *Artemia parthenogenetica* in Australia

Population	Records (no.)	Salinity range (g/l)	Reference
Dry Creek Saltworks, SA	63	186–330	56
Rottnest Is, WA	6	69–173	57
L. Hayward, WA	Many	70–220	58, 59
Esperance hinterland	4	120–146	Unpublished data
Lake Boonderro, Nullarbor	Few	61–192	A. Clarke, pers. commun.

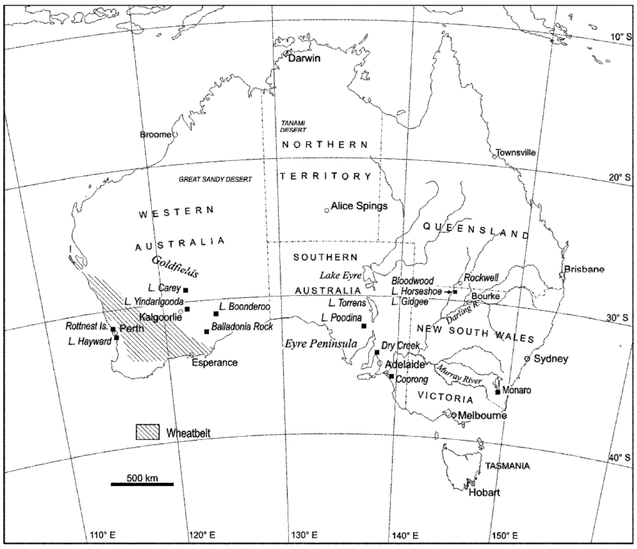

Figure 1. Map of Australia showing most places listed in the text and tables.

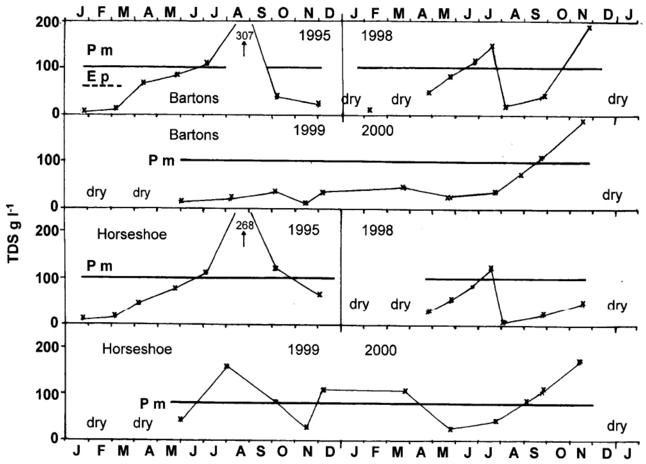

Figure 3. Presence of two large branchiopods (Ep, *Eocyzicus parooensis* (evenly dashed line); and Pm, *Parartemia minuta* (solid line) in Bartons Pool and Horseshoe Lake on Bloodwood Station, Paroo, during 1995 and 1998–2000 and corresponding lake salinities as TDS in ppt.

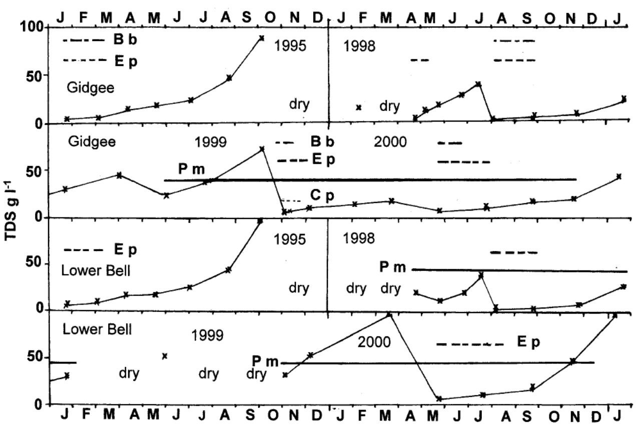

Figure 2. Presence of four large branchiopods (Bb, *Branchinella buchananensis* (unevenly dashed line); Ep, *Eocyzicus parooensis* (evenly dashed line); Pm, *Parartemia minuta* (solid line) and Cp, *Caenestheriella packardi* (dotted line)) in Gidgee Lake and Lower Bell Lake on Bloodwood Station, Paroo, during 1995 and 1998–2000 and corresponding lake salinities as TDS in ppt.

mun.). All live in saline waters, but data on most are fragmentary and uneven (Table 2). It is clear that *P. zietziana* has the widest and greatest salinity tolerance, equal to that of *Artemia* spp.[28]. Other species with wide and high field salinity ranges include *P. informis*, *P. longicaudata*, *P. minuta*, *P. serventyi*, *Parartemia* sp. a, *Parartemia* sp. d and *Parartemia* sp. f. On the other hand, *P. cylindrifera* occurs at lower salinities, especially compared with other species in the same area, in the Coorong, SA[6], on the Eyre Peninsula, SA[21,29], and in the wheatbelt, goldfields and Esperance hinterland of WA (unpublished data; Table 2). In the laboratory *P. zietziana* adults[30] have an upper LD_{50} of 267 ppt, *P. zietziana* nauplii an upper $LD_{50} > 225$ ppt and *P. contracta* nauplii[1,31] an upper $LD_{50} < 100$ ppt.

While many species have been recorded from various districts, it is extremely rare for two species to coexist (A. Savage, pers. commun.). For example, in the Esperance hinterland area (unpublished data), although *Parartemia* species a and f have similar wide salinity ranges, *Parartemia* sp. a occurs in alkaline saline lakes and *Parartemia* sp. f in acid lakes. Furthermore, *P. cylindrifera* lives in lakes that normally are less saline, and *P. longicaudata* and *P. serventyi* live in lakes normally more saline. Factors separating the latter two are not clear, but could include relative permanence, for *P. longicaudata* in the Esperance hinterland area lives in lakes which fill more regularly and for longer than lakes with *P. serventyi*.

Seven species of *Branchinella* have been recorded at salinities >3 ppt (Table 3). Two (*B. affinis* and *B. fron-*

Table 2. Field salinity ranges for species of *Parartemia* in Australia

Area	Species	Salinity range (ppt)	Records (no.)	Reference
Western Victoria	*P. zietziana*	41.4–298	Many	8
Dry Creek, SA	*P. zietziana*	112–258	100	56
Coorong, SA	*P. cylindrifera*	6–123	58	6
Coorong, SA	*P. zietziana*	74–353	21	6
Eyre Peninsula, SA	*P. cylindrifera*	31–37	2	29
Eyre Peninsula, SA	*P. zietziana*	27–195	4	29
Eyre Peninsula, SA	*P. cylindrifera*	5.8–123	47	21
Eyre Peninsula, SA	*P. zietziana*	22–298	23	21
Parro, NSW, 1987	*P. minuta*	8.4–255	34	60
Parro, NSW, 1995	*P. minuta*	2–181	109	Unpublished data, 61
WA	*P. contracta*	106.6	1	62
WA	*P. cylindrifera*	3–20	2	62
WA	*P. extracta*	27.4	1	62
WA	*P. informis*	29.9–186.2	7	62
WA	*P. longicaudata*	59.9–192.6	6	62
WA	*P. serventri*	34.4	1	62
WA, wheatbelt	*P. contracta*	84–240	3	A. Pinder, pers. commun., 2
WA, wheatbelt	*P. cylindrifera*	20–49	2	A. Pinder, pers. commun., 2
WA, wheatbelt	*P. informis*	52–88	2	A. Pinder, pers. commun., 2
WA, wheatbelt	*P. longicaudata*	41–226	4	A. Pinder, pers. commun., 2
WA, wheatbelt	*P. serventyi*	60–74	3	A. Pinder, pers. commun., 2
WA, wheatbelt	*Parartemia* sp. a	49	1	A. Pinder, pers. commun., 2
WA, wheatbelt	*Parartemia* sp. b	33	1	A. Pinder, pers. commun., 2
WA, wheatbelt	*Parartemia* sp. c	50–120	2	A. Pinder, pers. commun., 2
WA	*Parartemia* sp. g	8–51	5	11
Lake Cary catchment	*Parartemia* sp. x	22–105	15	11
WA	*P. cylindrifera*	12–240	16	Unpublished data
Esperance hinterland	*P. longicaudata*	87–240	10	Unpublished data
Esperance hinterland	*P. serventri*	119–258	4	Unpublished data
Esperance hinterland	*Parartemia* sp. a	20–235	41	Unpublished data
Esperance hinterland	*Parartemia* sp. f	35–210	42	Unpublished data
WA	*P. cylindrifera*	35–73	4	Unpublished data
Goldfields	*P. informis*	34–162	4	Unpublished data
Wheatbelt	*P. longicaudata*	78–184	9	Unpublished data
Wheatbelt	*P. serventyi*	15–262	13	Unpublished data
Wheatbelt	*Parartemia* sp. d	74–123	6	Unpublished data
Wheatbelt	*Parartemia* sp. g	78–141	5	Unpublished data
Lake Yindarlgooda (via Kalgoorlie)	*Parartemia* sp. d	50–140	Many	V. Campagna, pers. commun.

dosa) reach salinities of almost 7 ppt. Three (*B. compacta*, *B. nana* and *B. papillata*) have upper limits near 16 ppt. *B. buchananensis* can penetrate mesosaline waters and *B. simplex* can even live in hypersaline waters. A few more species can withstand salinities almost >3 ppt. This list includes *B. arborea*, *B. hattahensis*, *B. lyrifera* and *B. proboscida* (unpublished data). Most saline lake areas have one or two halophilic species of *Branchinella*, but the Paroo has three and WA has six. SA has *B. buchananensis* in Lake Poodina (P. Hudson, pers. commun.) and an unknown *Branchinella* has been recorded in Lake Torrens[32]. It is not known for halophilic species of *Branchinella* to co-occur, but often they share the habitat with a species of *Parartemia*, especially as salinities increase, e.g. as in Lake Carey[11].

The other two genera of anostracans in freshwater in Australia (*Streptocephalus* and *Australobranchipus*) have never been recorded from saline waters.

Four clam shrimps have been found in Australian saline waters (Table 4). The most widespread and best known is *Eocyzicus parooensis*. It lives in waterbodies up to 23.9 ppt, with occurrences from 3 to 15 ppt common (Figure 2, Table 4). Typically it occurs in the first few weeks of filling of mesosaline or hypersaline lakes, when the waters are hyposaline. Examples are known from the Paroo in northwestern NSW and southwestern Queensland, the Tanami desert in the Northern Territory (W. Lewis, pers. commun.) and WA (Table 4). *Caenestheria dictyon* is not well known, but it is known to live in hyposaline samphire pans in the Carey catchment, WA[11]. The widespread *Caenestheriella packardi* can live in subsaline waters as part of its wide adaptabily to various environmental factors[33]. A species of *Limandia*, close to *L. cygnorum*, sometimes occurs in hyposaline lakes, as well as in freshwater lakes, in the Esperance hinterland area (unpublished data). Four of the occurrences in Table 4

Table 3. Field salinity ranges for various species of *Branchinella* in Australia

Area	Species	Salinity range (ppt)	Records	Source
Western Victoria	*B. australiensis*	0.15–1.2	?	55
Western Victoria	*B. compacta*	1.53–15.9	?	55
WA	*B. simplex*	21	1	9
Queensland	*B. buchananensis*	15.7–42.6	2	9
Paroo, Northwest NSW	*B. australiensis*	0.3–11.2	10	60
Paroo, Northwest NSW	*B. buchananensis*	1.9–11.2	10	60
Paroo, 1996–2004	*B. affinis*	0.8–6.7	5	Unpublished data
Paroo, 1996–2004	*B. australiensis*	1.2–8.6	7	Unpublished data
Paroo, 1996–2004	*B. buchananensis*	2.1–15.2	12	Unpublished data
WA	*B. affinis*	0.02–1.15	14	11
Carey catchment	*B. australiensis*	0.02–4.2	9	11
Carey catchment	*B. frondosa*	0.02–4.2	7	11
Carey catchment	*B. simplex*	12.8–62	6	11
WA	*B. affinis*	0.01–4.2	4	Unpublished data
Goldfields and Esperance	*B. nana*	2–13	2	Unpublished data
Goldfields and Esperance	*B. papillata*	13–14	2	Unpublished data
Monaro, Southeast NSW	*B. australiensis*	0.2–1.8	5	Unpublished data
Monaro, Southeast NSW	*B. compacta*	0.6–4.7	5	Unpublished data

Table 4. Salinity ranges for Spinicaudata and Notostraca in Australia

Species	Area and time	Records (no.)	Salinity range (ppt)	Reference
Eocyzicus parooensis	Greater Paroo, northwest NSW, 1987–92	19	0.2–11.2	60
Eocyzicus parooensis	Paroo, Bloodwood and Rockwell stations only, 1995–2004	36	0.5–23.9	Unpublished data
Eocyzicus parooensis	Lake Carey catchment, WA, 2003–04	14	0.08–18	11
Eocyzicus parooensis	WA Goldfields and Esperance hinterland, 2007	6	0.1–15.2	Unpublished data
Caenestheria dictyon	Lake Carey catchment, WA, 2003–04	9	0.06–18.1	11
Caenestheriella packardi	Paroo, Bloodwood and Rockewell stations only, 1995–2004	11	1.5–3.8*	Unpublished data
Limnadia nr cygnorum	Esperance hinterland, 2007	11	0.08–15.5	Unpublished data
Triops nr australiensis	Lake Carey catchment, WA, 2003–04	10	12.8–93	11
Triops nr australiensis	WA Goldfields and Esperance hinterland, 2007	5	16–73.5	Unpublished data

*Numerous records <1.4 ppt.

refer to two such lakes on two occasions each. Its maximum field salinity is 15 ppt.

A shield shrimp close to *Triops australiensis* occurs in waters as high as 93 ppt. This taxon occurs only in WA (Table 4)[11,34] (unpublished data). Its upper salinity tolerance may be affected by temperature, as in January 2007, it was observed dying in two sites in southern WA (east of Norseman and near Salmon Gums, via Kalgoorlie) when water temperatures were 38–40°C and salinities only 31–34 ppt (unpublished data).

Colonization events of large branchiopods in the Bloodwood saline lakes, 130 km northwest of Bourke, NSW, over many years are instructive in how four halophilic species respond to local conditions (Figures 2 and 3). Three species have univoltine life cycles and appear only after salinity is lowered to <5 ppt and as long as lake salinity remains below about 15 ppt (Figures 2 and 3). Of these, *E. parooensis* is the most reliable, occurring in Lake Gidgee and Lower Bell lakes everytime they fill from dryness or their salinity is reduced to <5 ppt. It is completely excluded from Lake Horseshoe because this lake never drops to low salinities, and was found only once in Barton's pool, which leads into Horseshoe Lake, when salinity was 2.5 ppt. *B. buchananensis* behaves similarly, but less reliably in Lake Gidgee and has never been seen in the other three sites (Figures 2 and 3). A *C. packardi* population was found only once, probably fortuitously, in Lake Gidgee after a major inflow and salinity reduction. It did not persist for long (Figure 2). *P. minuta* inhabited all four sites over a wide range of salinities, but rarely occurred when a site filled from dryness and was <5 ppt (e.g. in Gidgee Lake, throughout 1995 and 1998). It is multivoltine and so can maintain populations for long periods (years) should salinities be within its tolerance levels (e.g. in Gidgee Lake, mid-1999 to late 2000). Thus *B. buchananensis* and *P. minuta* rarely co-occur, and if they do, competition should be minimal considering their size differences[33]. *E. parooensis* and *B. buchananensis* often co-occur, but they live different lifestyles, the former largely feeding on the bottom in the littoral, and *B. buchananensis* filtering phytoplankton in open water.

Discussion

There are many reports of anostracans in world saline lakes, but few of spinicuadatans and notostracans, and none of laevicaudatans. Hypersaline lakes and salt works throughout the world contain various species of *Artemia*, about eight in all, but usually only one in any geographical area[13]. *A. parthenogenetica* occurs naturally in WA and lives within its known salinity-tolerance limits[25], and both this species and *A. franciscIana* have been introduced to many salt works[35]. The species swarm of *Parartemia* in Australian saline lakes is unparalleled elsewhere in the world. WA has about 14 species in the wheatbelt and Goldfields areas, though diversity is much less in eastern Australia, with generally only one species per geographical area, though SA has a few.

Beyond *Artemia* and *Parartemia*, the other common anostracans in mesosaline lakes are *Phallocryptus spinosa* in Mediterranean, Europe, Spain, Ukraine, the Middle East and North Africa[18] and references therein, and *Branchinella* (*Branchinella*) *simplex* and *B. buchananensis* in Australia. All three species occasionally cooccur with *Artemia*/*Parartemia*, e.g. *P. spinosa* and *A. parthenogentica* in Italy[36] and *B. simplex* and *Parartemia* n. sp. x in Australia[11]. Many anostracans have been recorded in hyposaline lakes throughout the world, including *B. campestris*, *B. lateralis*, *B. gigas*, *B. mackini*, *P. subletti* and *Streptocephalus texanus* in North America[19,37–41] (D. Christopher Rogers, pers. commun.), *P. wrighti*, *D. cervicornis* and *T. salinarum* in South America[14–16] and *B. media*, *Branchipus schaefferi*, and *Chirocephalus salinus* in Europe and the Mediterranean[42,43]. Diversity is similar in Australia, with five species found commonly at salinities >3 ppt and a few more near this salinity. When the higher anostracan diversity in other continents vis-a-vis Australia is considered[44], the proportion of Australian species penetrating saline waters is higher. Except for *P. spinosa*, overseas species generally are not hyposaline specialists, but freshwater species with the ability to penetrate hypsosaline waters, whereas in Australia at least four species (*B. buchananensis*, *B. nana*, *B. simplex* and *Branchinella* n. sp.) are salt-water specialists. In Australia, all halophilic species belong to the one genus (*Branchinella*), which on reflection is not that remarkable given that most Australian anostracans other than *Parartemia* are of this genus[22].

Salt tolerance in anostracans is most prominent in three evolutionary groups. Foremost is the suborder Artemiina containing the haliobionts *Artemia* and *Parartemia*[45]. Second is the thamnocephalid genus *Phyllocryptus* containing three halophilic species scattered across much of the world[18], and the third group is from another thamnocephalid genus, *Branchinella* and consists mainly of members of group I of Geddes[9]. Of these four genera, only *Phyllocryptus* is not represented in Australia.

Spinicaudatans in North American hyposaline waters include *Eocyzicus diguetti* and *Leptestheria compleximanus*[38,46], *Cyzicus tetracerus*, *Leptestheria cortieri* and *L. mayeti* in Europe and northern Africa[42,43], and *Eocyzicus politus* in India[47]. Australia has four species, with *E. parooensis* common, widespread and seemingly with the highest salinity (ca. 24 ppt) penetration of all spinicaudatans[20]. Unlike overseas where two species often co-occur, Australian records are usually of just the one species, but often co-occurring with an anostracan, as in Gidgee Lake in the Paroo (Figure 2).

There are even fewer records of notostracans in saline waters, e.g. the widespread *Triops cancriformis* is occasionally found in mesohaline waters[42,48]. In contrast, *Triops* sp. (near *australiensis*) is common in mesosaline and even in hypersaline waters in WA (Table 4).

In summary, penetration of large branchiopods into saline waters in Australia is either more or less equivalent to that overseas (anostracans other than *Artemia*/*Parartemia*; spinicaudatans), or is much expanded (the *Parartemia* species swarm, *Triops*, *Branchinella* hyposaline specialists, high penetration of *E. parooensis*). Most of this has occurred in the wheatbelt and goldfields of WA. Here an unusual combination of great age of the landscape, super abundant saline waters, climatic fluctuations and isolation has resulted in speciation and adaptation to saline waters in many crustacean groups, including the copepod genus *Calamoecia*[49], *Daphnia* (*Daphniopsis*)[50] and Myticyprinid ostracods[3], as well as various large branchiopods. It seems also that molecular evolution may be hastened in crustaceans in athassalic conditions[51]. In the spectacular case of *Parartemia*, eggs which sink and stick to clayey muds rather than float and easily spread probably have aided the speciation process by restricting dispersal. However, this factor alone has not resulted in speciation in eastern Australia with just two widespread species (*P. minuta* in the north and *P. zietziana* in the south). SA, especially the Eyre Peninsula, has some unique geological and climatic characteristics of southwestern WA[52,53]. Interestingly, it has a higher diversity of *Parartemia*, but hardly equal to that in WA.

Only a broad outline is available of how these large branchipods survive the adverse osmotic environment of these saline waters. *P. zietziana* is a hypersomotic regulator in dilute waters and a strong hypoosmotic regulator at high salinities, much like *Artemia* spp[54]. Presumedly other species of *Parartemia* behave similarly, but *P. contracta*, which lives in acid saline waters, has a problem[31]. *P. zietziana* and *Artemia* rely on large quantities of ATP to support their sodium pumps, the CO_2 for the aerobic glycolysis C-4 dicarboxylic shunt coming from dissolved bicarbonate/carbonate ions in their medium. But such ions are absent in the acid saline lakes inhabited by *P. contracta*, which would need to have an additional proton pump and get its CO_2 from endogenous substrates. The same probably applies for *Parartemia* sp. f, as it also lives in acid saline lakes (unpublished data).

The species of *Branchinella* found in hyposaline lakes probably survive by being osmoconformers. For instance, *B. australiensis* and *B. compacta* are hyperosmotic at low salinities but *B. australiensis* cannot survive in waters above its isosmotic point of about 140 mOsmol kg water (and hence hardly penetrates hyposaline waters), while *B. compacta*[55] osmoconforms from 160 to 460 mOsmol and so can survive in waters to about 16 ppt. Interestingly, *B. campestris* which lives in hyposaline waters to about 19–25 ppt in North America is also an osmoconformer, but to higher body fluid levels[40] of 660 mOsmol. The four clam shrimps in hypsosaline waters probably survive by being osmoconformers like *B. compacta*, but it would be remarkable if that too was the explanation for the survival of *B. simplex* in hypersaline waters to 62 ppt and *Triops* near *australiensis* in hypersaline waters to 93 ppt.

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