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SALINE WATER

The biology of the saline lakes of central and eastern inland of Australia: a review with special reference to their biogeographical affinities

Brian V. Timms

Abstract In 1984 when Bill Williams highlighted the regionalization of salt lakes in Australia, little was known about lakes in the remote inland. It was thought the invertebrate fauna of such lakes was depauperate due to their being poor evolutionary loci associated with extreme episodicity. However, work in the last two decades, has shown the fauna of many inland lakes is relatively rich. Part of the reason for restricted faunas in the larger lakes is habitat homeogeneity. Nevertheless there is little diversification at the species level, indicating restrictions on speciation. There are also limits on diversity imposed by the harsh environment, as indicated by the lack of forms unable to survive severe desiccation, e.g. higher crustaceans. Lakes in central and the eastern inland are dominated by characteristic lower crustaceans such as *Parartemia minuta*, *Daphniopsis queenslandensis*, *Moina baylyi*, *Trigonocypris globulosa* and a new mytilocyprid ostracod, as well as some forms widespread in Australia and in salt lakes on other continents. This invertebrate fauna is just as distinct as those of other salt lake districts in southern Australia, further reinforcing the concept of regionalization in Australia. The fish fauna of central and eastern salt lakes is also largely specific, but the waterbirds are not as they have responded to the episodicity by nomadism and habitat flexibility.

Keywords Geomorphology · Hydrology · Water chemistry · Aquatic macrophytes · Invertebrates · Fish · Waterbirds · Regionalization of fauna

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Saline Waters and their Biota

B. V. Timms (✉)
School of Environmental and Life Sciences,
University of Newcastle, Callaghan, NSW 2308,
Australia
e-mail: brian.timms@newcastle.edu.au

Introduction

The Australian salt lake fauna is highly regionalized, unlike that on other continents. Williams (1984) in a study of 39 halobiont and halophilic crustaceans showed the distinctiveness of faunas in the southwest of Western Australia, Eyre Peninsula, South Australia, the Coorong, and also in South Australia, western Victoria and the midlands of Tasmania. The explanation lies in past climatic events, linking and dividing these areas and the assumption that lakes in episodic desert environments are poor evolutionary loci. At the time little was known of the fauna of lakes of the arid inland, but data on Lake Eyre (Bayly, 1976) suggested a depauperate fauna of widespread forms.

During the 1980s to the present, taxonomic resolution of some groups has improved and information has become available on many lakes of the inland. Initially these data supported the contention that the episodic desert lakes had a limited fauna vis-a vis saline lakes in the more reliable climate of southern Australia, but that elements of this fauna were characteristic of inland lakes (e.g. Williams & Kokkinn (1988) on Lake Eyre) or had some tropical affinities (e.g. Timms (1987) on Lake Buchanan).

In 1993, I showed that the fauna of saline lakes in the Paroo was almost as diverse as in more climatically benign western Victoria (Timms, 1993) and later (Timms, 1998a, 2002) suggested that much of the simplicity of the fauna of large inland lakes was associated with habitat homeogeneity, rather than it being explained by episodicity limiting diversification in arid-zone lakes.

It is now opportune to re-examine and review the salient features of the saline lakes of inland Australia, using a greater data set of taxa and lakes. Information is still scant on lakes in the remote inland of Western Australia (S. Halse, pers. com.; J. Johns, pers. com.) and on some taxonomic groups (Protista, Nematoda), so both are excluded, but sufficient information is available on lakes of the central and eastern inland. Particular attention will be given to consideration of this area as a unique saline lake area in Australia, equivalent to those suggested by Williams (1984), and also to possible reasons for their supposedly depauperate fauna.

Study area and climate

The central and eastern inland (Fig. 1) has salt lakes in two main areas, the lower Lake Eyre basin in South Australia and the middle Paroo in northwestern New South Wales and adjacent southwestern Queensland. The first area contains Lake Eyre North and Lake Eyre South, with a combined area of 9,690 km^2 and the largest salina in Australia, and also numerous smaller lakes mainly to the north and east of Lake Eyre. The Paroo has many small saline lakes with Lake Wyara the largest at 34 km^2. In addition to these foci, the study sites also include the large Lake Torrens (5,923 km^2) to the south of Lake Eyre, a string of salinas ringing the northern Flinders Ranges, including Lake Frome (A = 2,625 km^2), some lakes north of Broken Hill (e.g. Salt Lake, Lake Altibouka), the Lake Bindegolly complex northwest of Lake Wyara, and the outlier Lakes Buchanan (A = 117 km^2) and Galilee far to the northeast in the Queensland highlands. It is not known whether lakes to the south of Broken Hill, to the west of Lake Torrens (e.g. L. Gairdner), and unnamed salt lakes between Lake Eyre and Lake Amadeus, have similar characteristics to those within the main area, so they are excluded for the time being. This salt lake region is similar in size to that in Western Australia and much larger than others in Australia (Fig. 1), though the total number of lakes is fewer than in Western Australia, and probably also in western Victoria.

The region exhibits a range of climate types—hot desert in the western two-thirds, hot grassland in eastern quarter, and a small area of subtropical with a moderately dry winters in the far northeast (Stern et al., 2000). Average maximum temperature in July (winter) ranges from 18°C in the south to 24°C in the north, while average January maxima vary from 36 to 39°C (Bureau of Meteorology, 2002). Mean annual rainfall varies from <100 mm northeast of Lake Eyre to 500 mm in the northeast, with most of the region receiving less than 250 mm (Bureau of Meteorology, 2002). Significantly, rainfall variability is greatest for any area in Australia, with Gaffney indices (90 rainfall percentile minus 10 rainfall percentile, over 50 rainfall percentile—see Gaffney, 1975) greater than 1.5 (and reaching 2) in the western and central areas (Brown, 1983). Mean annual evaporation is also greatest in Australia, exceeding 3,600 mm around Lake Eyre and greater than 3,000 mm almost everywhere else (Kotwicki, 1986).

Geomorphology and hydrology

The larger lakes are old and ultimately of tectonic origin. Lake Torrens lies in a graben with basal lacustrine sediments of Cainozoic age (Twidale & Campbell, 1993), Lake Eyre has been present in some form since the middle Jurassic but its

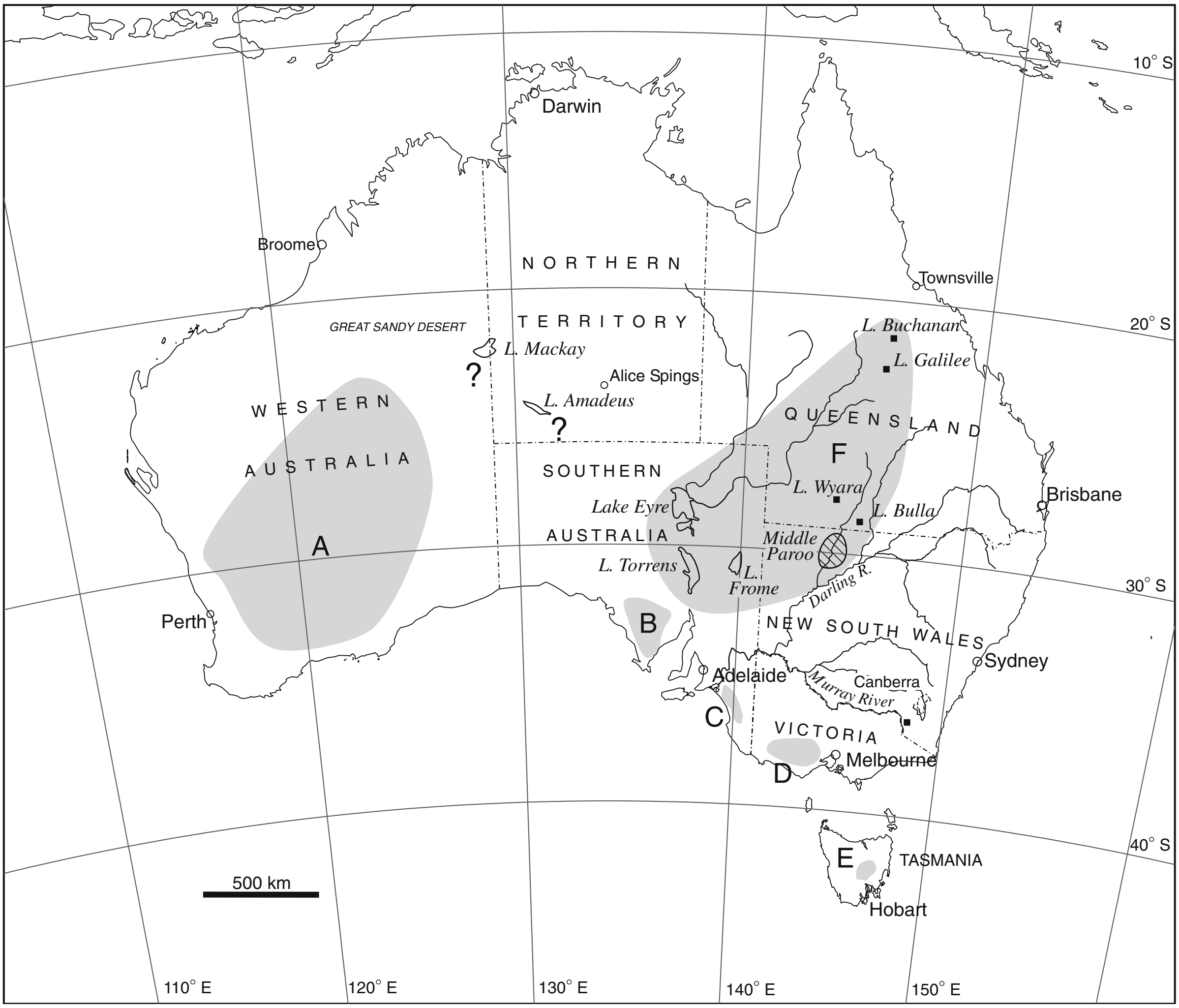

Fig. 1 Map of Australia showing known salt lake regions. A–E following Williams (1984), F, this study. A = south-western Western Australia, B = Eyre Peninsula, SA, C = Coorong, SA, D = western Victoria, E = midland Tasmania, F = central and eastern inland, including the lower Lake Eyre basin, the Paroo, and central upland Queensland

present basin was created by epeirogenic earth movements in the last 30,000 years (Kotwicki, 2000). Lake Wyara lies on a Tertiary fault (Timms, 1998a), and Lake Buchanan lies along a fault line in an intermontane basin and dates back in some form to the early Tertiary (Chivas et al., 1986). Presently, these lakes are shallow (<2 m deep) playas, though episodic fillings raise their levels to flood surrounding country and are marked by stranded beaches. Pleistocene floodings were extensive and are well documented for Lake Eyre (Kotwicki, 1986). Most of the lake basins are modified by wind action, with Lake Wyara having the most smoothed eastern shore and much degraded lunette dune (recognisable only on satellite images; present form and augering suggest it lacks younger lunettes homologous with those of surrounding lakes—Timms, 1998a).

Smaller saline lakes in the inland are also shallow (<1 m deep) and invariably were formed by wind action. In the Paroo most have old (Pleistocene?) gypseous lunette dunes and younger clay lunette dunes (Timms, 1993);

lake ages are >40,000 years (Pearson et al., 2001).

All of the lakes fill from major episodic rainfall events, more often than not associated with unreliable summer monsoons. Lake Torrens has the most parsimonious filling regime, having significant water only once since white settlement (early 1800s) (Williams et al., 1998). At the other extreme Lake Wyara more often than not has water and dries only in severe El Niño events (Timms, 1998a). Lake Eyre has some water every 2–3 years but major fillings are much longer apart (e.g. 1949, 1974, 1990) (Kotwicki, 2000). The shallow lakes of the Paroo fill and dry irregularly during La Niña years and then remain mostly dry during El Niño years with some having a more propitious hydrologic regime than others (Timms, 1993, 1998b). Nothing is known of the hydrology of the smaller lakes of the Lake Eyre region, but probably they contain water much less frequently than the Paroo lakes.

Physical limnology

Lake waters are dominated by Na and Cl ions (Na >> Mg > Ca > K and Cl >> SO_4 > HCO_3) due to long accumulation of marine aerosols (Herczeg et al., 2001), though in a few hypsosaline lakes in the Paroo SO_4 and occasionally Ca dominate (Williams and Kokkinn, 1988; Williams et al., 1998; Timms, 1993, 1998a). Lake Buchanan has unusual water chemistry in that Ca ≈ Mg due to local catchment influences (Chivas et al., 1986). Salinities fluctuate widely (e.g. in Lake Torrens—Williams et al., 1998); however, many have characteristic salinity ranges when holding water and not near the drying phase. For instance in Lake Wyara salinity is often in the range 10–30 g l^{-1}, whereas Lake Nichebulka in the Paroo is always > 50 g l^{-1} (Timms, 1993, 1998a). Meromictic solar hot pools (with fresh rainwaters on remnant saline waters) occur near Lake Buchanan (author, unpublished data), and are probably common, at least transitorily. Waters are all alkaline with pH generally in the range 8–10.

All lakes contain clear waters, except when first filled or very shallow and wind stirred. Thermal stratification has not been observed (but see above), which contrasts with many turbid freshwater riverine waterholes and claypans in the area (e.g. Timms, 1997a, b). Because of the continental climate and waters that are shallow and clear, water temperatures fluctuate widely daily and seasonally. Daily ranges of 15°C are common and seasonal ranges of 8–39°C have been recorded in the Paroo lakes (Timms, 1993), with more extreme temperatures known (at least 3–44°C, author unpublished), but no ice has been recorded.

Flora

Little data are available on macrophytes and almost none on phytoplankton. Larger episodic lakes (Lake Eyre, Lake Torrens) apparently have little or no aquatic plants as the environment is too harsh (Williams, 1990). For lakes in the Paroo and Bulloo that hold water permanently or semipermanently the list includes the charophytes *Chara* spp., *Nitella* spp. and *Lamprothamnion* spp. and the angiosperms *Lepilaena* spp. and *Ruppia* spp. (Table 1). There is a change in species composition and a decrease in species richness with increasing salinity and ephemerality. Dense stands of submergent macrophytes in these lakes can support up to 10 times the number of waterbirds and invertebrates as comparable freshwater lakes (Kingsford & Porter, 1994; J. Porter, pers. com.). Non-dormant seedbanks can be dense, with for example 18,000 seeds m^{-2} in Lake Wyara (J. Porter pers. com). Of phytoplankton, only a very incomplete species list is available for Lake Eyre (Williams, 1990). It includes a few diatoms, the green alga *Dunaliella* spp. (inc. *D. salina*) and various bluegreens including *Nolularia spumigena*, *Anabaenopsis* sp. and *Glaucocystopsis* sp. Except for two charophytes (Casanova et al., 2003; A. Garcia, pers. com.), these are all widespread genera and species.

Invertebrates

Littoral and planktonic macroinvertebrates have been extensively studied, and lists of halobiont, halophilic and tolerant freshwater species are

Table 1 Aquatic macrophytes in five saline lakes in northwestern NSW and southwestern Qld (J. Porter pers. com.)

Lake[a]	*Chara australis*	*Chara fibrosa*	*Chara vulgaris*	*Lamprothamnium papulosum*	*Lamprothamnium succinctum*	*Nitella lhotzkyi*	*Nitella sonderi*	*Myriophyllum verrucossum*	*Lepilaena bilocularis*	*Lepilaena preissii*	*Ruppia maritima*	*Ruppia tuberosa*	Duration of inundation (y)	Mean TDS (g/l)
1	x	x	x		x	x	x	x					2.3	5.8
2				x		x			x		x	x	2.2	7.1
3				x					x	x	x	x	1.0	17.8
4	x			x		x			x	x	x	x	2.0	24.1
5				x						x		x	0.5	72.2

[a] Code to lakes: 1 = Lake Altibouka, 2 = Lake Bindegolly, 3 = Salt Lake, 4 = Lake Wyara, 5 = Clifton Downs Lake

available in Williams et al., 1988, 1998; Williams, 1990; Timms, 1993, 1997a; 1998a, b; 2002. Several points arise from an examination of this extensive literature:

1. At least 76 taxa are present, although the real number of taxa present is unknown, because many represent multiple species (e.g. *Daphnia* spp, *Microcyclops* spp). This is comparable with the faunal list for western Victoria (89 species from Bayly & Williams, 1966; Geddes, 1976; Williams 1981, pers. com.; Timms, 1983), more than for the Coorong region (36 species from Bayly & Williams, 1966; Bayly, 1970; De Deckker & Geddes, 1980), Eyre Peninsula (23 species in Williams, 1984) and Tasmania midlands (22 species in De Deckker & Williams, 1982), but considerably fewer than is known in southwestern Western Australia (107 species from Geddes et al., 1981; Pinder et al., 2002). Though faunas for some notable individual lakes are depauperate, the conclusion that the fauna overall is relatively rich is inescapable.
2. Some species are new, including a fairy shrimp *Branchinella* sp., a clam shrimp *Eocyzicus parooensis* sp. and the cladoceran *Daphnia* sp. all from hyposaline waters. New species in mesosaline waters include *Microcyclops* spp, and some ostracods.
3. The list includes some worldwide species (e.g. *Brachionus plicatilis*, *Apocyclops dengizicus*) and many widespread Australian species (e.g. *Boeckella triarticulata*, *Diacypris compacta*, *D. dietzi*, *D. whitei*, *Platycypris baueri*, *Reticypris walbu*, *Austrolestes annulosus*, *Anisops thienemanni*, *Necterosoma penicilatum*, and *Tanytarsus barbitarsis*). However the dominants such as *Parartemia minuta*, *Daphniopsis queenslandicus*, *Moina baylyi*, *Mytilocypris splendida*, *Trigonocypris globulosa*, a new mytilocyprid ostracod and *Berosus munitipennis* are characteristic (not necessarily endemic) of the inland and north (Williams, 1990; Timms, 1993, 1998a, b; Williams et al., 1998).
4. Many insects are listed, arguably more than in other districts in Australia, but this partially reflects better taxonomic resolution. Anyhow,

most are unimportant ecologically and restricted to hyposaline waters, so that crustaceans are the dominant group across the salinity spectrum, as elsewhere in Australia.

5. Although there is a general decrease of diversity with increasing salinity (e.g. Timms, 1993, 1998b), most salt-tolerant species have a wide salinity range, so that there is little change in species composition in mesosaline and hypersaline conditions (Williams et al., 1990). It is only at very high salinities (>ca. 150 g l^{-1}) where the fauna is restricted to brine shrimps and a few ostracod species. This means that with salinity increase associated with a lake drying, temporal succession of species is minimal. However lakes with a long hyposaline stage like L. Bulla (author unpublished) and to as lesser extent L. Wyara (Timms, 1998a), not surprisingly, have an early hyposaline fauna quite distinct from that which develops much later. This often includes a clam shrimp *Eocyzicus parooensis* n. sp. which is unique to inland Australia (Timms, 1993, 1998b as ''*Limnadia* sp. a''). For Lake Torrens with a short hyposaline stage this fauna includes only two species (*Triops australiensis* and *Branchinella* n. sp.) and their presence was brief (Williams et al., 1998) while in Lake Eyre with no detected hyposaline stage, only one species, *Heterocypris* sp., was restricted to initial stages (Williams, 1990).
6. The fauna lacks crustaceans without a stage resistant to severe desiccation. Thus the isopod *Haloniscus searli*, and the amphipods *Austrochitonia australis* and *Austrochiltonia subtenuis*, which are occur throughout southern Australia, are absent (though one specimen of *A. australis* was found in L. Eyre South—Williams, 1990). Interestingly, perhaps the snail *Coxiella gilesi* is near the limit of survival capabilities as it apparently only occurs in sites with a more propitious water regime (Lakes Buchanan, Bulla and Wyara). While the copepods *Calamoecia clitellata* and *C. salina* do have resistant eggs, these are either not resistant enough for inland conditions or some other factor excludes them from the eastern inland.
7. Many of the genera characteristic of saline lakes in Australia are represented by a single species in the inland as against two or more in many other districts. The most notable examples are *Parartemia*, *Daphniopsis*, and *Mytilocypris.* Certainly there is a contrast to the spectacular speciation in Western Australia seen in *Parartemia*, *Coxiella* and some ostracods (Pinder et al., 2002). Some genera common in the central and eastern inland also occur in Western Australia, but not in other salt lake regions e.g. *Celsinotum*, *Trigonocypris* and the undescribed new mytilocyprid genus. Halse and McRae (2004) have described two new genera of mytilocyprid ostracods from WA. The genera are *Lacrimicypris* and *Repandocypris*.

Vertebrates

Like Australia as a whole, saline lakes in the central and eastern inland have a fish fauna restricted to a few species of generally limited salinity tolerance. What is remarkable in large inland lakes is the abundance of fish at low to moderate salinities and their importance in supporting piscivorous birds. When hyposaline, Lake Wyara has boney bream (*Nematolosa erebi*), yellowbelly (*Macquaria ambigua*), and carp (*Cyprinus carpio*), which support large rockeries of pelicans and cormorants (Timms, 1998a). Even more spectacular is Lake Eyre which can have prodigious numbers of Lake Eyre hardyhead *Craterocephalus eyresii* and boney bream as well as yellowbelly, Australian smelt (*Retropinna semoni*), and spangled grunter (*Leiopotherapon unicolour*); likewise these support even greater numbers of piscivorous birds (Williams, 1990). All species survive dry times in waterholes of inflowing creeks, have good dispersal abilities and have high fecundity when lake water is present. Most of these species survive in waters to ca. 35 g l^{-1}, though the Lake Eyre hardyhead is tolerant of 110 g l^{-1} (Glover & Sim, 1978; Merrick & Schmida, 1984). However fish kills are usually not due to salinity tolerance being exceeded but to algal toxins, gill clogging by algae, or water deoxygenation (Ruello, 1976; Glover, 1990; author unpublished data).

Until recently, it was thought the arid inland, including its saline lakes supported few waterbirds (Frith, 1982). However regular aerial surveys over the last two decades (Kingsford, 1995; Kingsford and Halse, 1996) have found large numbers on many lakes, particularly saline waters, for example peaks of 325,000 on Lake Eyre North and greater than 280,000 on Lake Wyara and nearby freshwater Lake Numalla. Over a 3-year period these later lakes averaged 42,000 birds with 10 times more individuals in the saline lake than in the freshwater lake, but a few less species (31 compared with 39, and 41 overall) (Kingsford & Porter, 1994). Lake Wyara is more attractive to waterbirds because its clear waters encourage luxuriant plant growth and it abundance of invertebrates was six times greater than in the nearby freshwater lake (Kingsford & Porter, 1994). No bird is restricted to the saline lakes of the inland, but they are important feeding and breeding sites for many species. Eurasian coot (*Fulica atra*) and Black swan (*Cygnus atratus*) eat the abundant plants, Grey teal (*Anas gracilis*) and various waders consume invertebrates, Australian pelicans (*Pelecanus conspicillatus*) and cormorants feast on the fish and Pink-eared duck (*Malacorhynchus membranaceus*) consume zooplankton. Among breeding birds, Australian Pelicans, cormorants, Black swans, Silver gulls (*Larus novaehollandiae*), Caspian terns (*Hydroprogne caspia*), Red-necked avocets (*Recurvirostris novaehollandia*) and Banded stilts (*Cladorhynchus leucocephalus*) are the most common (Reid et al., 1990; Kingsford & Porter, 1994; Williams et al., 1998). Many other species, especially the ducks, breed in ephemeral fresh waters nearby and congregate on the saline lakes as waters dry (Kingsford, 1995; Timms, 1997b). All species are nomadic, especially the Pink-eared duck, so that lakes are usually colonized quickly after filling. An exception to this occurred in early 2000 when widespread rains filled many lakes in central and the eastern inland—saline lakes in the Paroo had few waterbirds as it seems they preferred the wetlands associated with Lake Eyre (author, unpublished data). Generally at any one time somewhere in inland Australia, there is water, often saline, supporting many waterbirds (Roshier et al., 2001). The danger is that water resource development on the allogenic rivers will dry alternative habitats in the arid zone and leave the birds nowhere to go (Kingsford, 2000).

Biogeographical affinities

In a comprehensive comparison of the salt lake invertebrate fauna of various areas in Australia, species lists of halobiont, halophilic and salt-tolerant fauna found in waters > 10 g l^{-1} were prepared by consulting Brock & Shiel (1983), Geddes et al. (1981), Halse (1981) and Pinder et al. (2002) for southwestern Western Australia; Williams (1984) for Eyre Peninsula, South Australia; Bayly (1970), Bayly & Williams (1966) and Geddes & De Deckker (1980) for the Coorong region, South Australia; Bayly & Williams (1966), Geddes (1976), Timms (1981, 1983), Williams (1978, 1981, 1995) and Williams et al. (1990) for western Victoria; De Deckker & Williams (1982) for midland Tasmania; and Timms (1993, 1998a, b, unpublished), Williams (1990), Williams & Kokkinn (1988) and Williams et al. (1998) for the central and eastern inland of Australia. In total, 226 species were found, many more than the 39 species used by Williams (1984), mainly due to the inclusion of taxa tolerant of considerable salt (> 10 g l^{-1}), but also to inclusion of more recent studies (particularly Pinder et al., 2002) and an extra region (the inland). It still suffers, however, from taxonomic uncertainty and uneven degree of study of the different areas.

The lists were compared using four similarity coefficients in all possible combinations of regions, separate and combined (Table 2). The resultant coefficients are all low indicating the regions have largely separate faunas. As Williams (1984) found using three similar and one different coefficient, the closest similarity was between Eyre Peninsula and Coorong, then western Victoria and Tasmania, all regions in southeastern Australia, and western Victoria and the Coorong. The inland region was not included in any of the top five of the four coefficients and southwestern Western Australia only occasionally occurred alone in any of the top coefficients. These two are

Table 2 Community coefficient analysis of salt lake fauna in six salt lake regions of Australia. A = southwestern Western Australia, B = Eyre Peninsula, SA, C = Coorong, SA, D = western Victoria, E = midland Tasmania, F = central and eastern inland. See Fig. 1 for locations

Rank	Cluster	Coefficient	Rank	Cluster	Coefficient
Jaccard's coefficient			Kulczynski's coefficient		
1	B–C	0.311	1	B–C	0.452
2	A–BCDE	0.289	2	D–E	0.410
3	BC–DE	0.271	3	CD–E	0.409
4	ABC–DE	0.263	4	A–BCDE	0.409
5	D–E	0.208	5	BC–DE	0.372
Sorensen's coefficient			Ochiai & Barkman's Coefficient		
1	BC–DE	0.426	1	B–C	0.326
2	D–E	0.342	2	A–BCDE	0.317
3	C–D	0.336	3	ABC–DE	0.295
4	B–C	0.322	4	BC–DE	0.281
5	BC–D	0.313	5	D–E	0.271

the most distinctive regions. For the inland, the community coefficients between the six study sites (Table 3) are much higher than those for between regions, suggesting strong internal relationships and hence a valid regional fauna.

Williams (1984) used the degree of similarity between regions as chronologically indicative of past associations and explained them by climatic fluctuations on the assumptions that (i) episodically filled lakes are of little value for evolution of fauna and (ii) the most important environmental determinant is the predictable pattern of salinity, temperature and presence of water. Thus in fluvial times all the salt lake regions of Australia were interconnected, but in arid times they were well separated to the southern extremities of the continent with the most benign and predicable climate. It was here the salt lake fauna survived and evolved. This being so, how then should the central and eastern inland feature as a separate salt lake region? According to the Williams theory the inland should not contain a separate fauna and not be species rich. In the early 1980s all that was known of the inland suggested an impoverished fauna of no special biogeographical relationships.

First, this analysis has shown that the inland has almost as many saline lake species as in western Victoria and certainly more than midland Tasmania, the Coorong and Eyre Peninsula, other areas in more climatically predictable southern Australia (though some of this could be due to inadequate collecting in South Australian sites). The majority of inland richness resides in a cluster of various types of lakes in the middle Paroo of northwestern NSW (Timms and Boulton, 2001). Also adding to the richness is the huge area covered (see Fig. 1) which incorporates climatic

Table 3 Comparative community coefficient analysis between salt lake regions and the inland sites together with highest three pairings of inland sites. Wyara and For code to regions A–F see Fig. 1. Code to inland sites 1 = Lake Torrens, 2 = Lake Eyre, 3 = NSW Paroo lakes, 4 = Lake Wyara, 5 = Lake Bulla, 6 = Lake Buchanan. Note that Lakes Wyara and Bulla are Paroo lakes, but separated from them in this analysis in order to have lakes more directly comparable to sites 1,2, and 6

Coefficients	Jaccard		Sorenson		Kulczynski		Ochai & Barkman	
Means of regions A–F	0.178		0.267		0.245		0.203	
Means of inland sites 1–6	0.340		0.507		0.591		0.521	
Rank 1 of 1–6	4–5	0.643	4–5	0.783	4–5	1.800	4–5	0.789
Rank 2 of 1–6	3–5	0.524	3–5	0.687	3–5	1.100	3–5	0.697
Rank 3 of 1–6	3–4	0.433	3–4	0.604	3–4	0.764	3–4	0.634

differences of northern (L. Buchanan) and southern Australia (L. Torrens). Certainly the larger lakes (Buchanan, Wyara, Eyre, Torrens) have depauperate faunas, but this is hardly due to a restricted fauna being available for colonization, but more to a homogeneous environment presented by shallow wave washed shores. Thus for Lake Wyara in the Paroo, at least half of the difference between its fauna and the regional fauna is explained by habitat homeogeneity (Timms, 1998a). Furthermore in a study of the fauna of the major inlet which feeds this lake, 84 species occurred in the inlet, as against 34 in the lake (Timms, 2002). Again most of this difference was explained by habitat heterogeneity in the inlet, and little with its lower salinity.

The argument that the episodic lakes of the inland are of little value for evolution still has some validity. The above arguments do not explain all the difference and moreover evidence for such lakes being poor evolutionary loci is provided by the virtual absence of speciation within genera. Except for *Celsinotum*, *Microcyclops*, *Diacypris*, and possibly *Branchinella*, *Daphnia* and *Reticypris*, no crustacean is represented by multiple species as many are in southwestern Australia (Pinder et al., 2002) and some in western Victoria (Williams, 1981). The same applies for the snail *Coxiella* (Macpherson, 1957). The situation is a little different among the insects where many common genera have multiple species (e.g. *Aniops*, *Agraptocorixa*, *Necterosoma*, *Sternopriscus*, *Berosus*, *Tanytarsus*) but these are widespread throughout much of Australia and are relatively unimportant components of the salt lake fauna.

Given that the salt lake fauna of the central and eastern inland is relatively rich, how did it survive and differentiate in the uncertain environment of the inland especially during arid periods? I suggest the answer lies in the numerous small lakes in the middle Paroo. Almost all have attendant lunette dunes, indicating a more seasonal climate in the immediate past (Bowler, 1983). Even these days many of these lakes fill reliably in La Niña years (see above), so that the regularity of their presence is measured in decadal rhythms rather than annual rhythms. This has allowed a fauna to survive in an otherwise inhospitable environment, though of course animals which do not have a resistant stage in the life cycle or an unable to disperse as adults are excluded. So the fauna is a little impoverished without higher crustaceans and genera with multiple species. Lakes further away from this central cluster (Lakes Eyre, Buchanan) are not as species rich and as similar as the central Paroo group (Table 3). Lakes well west of the central inland, such as Lake Amadeus and Mackay and those in the remote inland of Western Australia may well be truly depauperate because their environment is markedly episodic as well as being homeogeneous.

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