

Drivers restricting biodiversity in Australian saline lakes: a review

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Abstract. Inland saline lakes are well known to be less biodiverse than fresh waters. In Australia, the most important driver affecting biodiversity is salinity that imposes an inverse linear relationship. However, in detailed studies across a wide salinity spectrum, the relationship is scale dependent. This is mediated in part by the range of salinity tolerated becoming broader as the maximum tolerated salinity increases. Other factors of importance sometimes include hydrology, habitat heterogeneity, season, pH and oxygen, but these are usually not easy to quantify. Even rarer is the influence of colonisation by marine organisms, which is applicable only at some sites near the coastline and the influence of ionic proportions on the presence of some species and, hence, diversity. The contribution of predation or competition on diversity, reported in some overseas salinas, is suspected but yet to be proved in Australia. The crustacean component in saline lakes is more influenced by these drivers than is most of the insect fraction.

Keywords: crustaceans, habitat heterogeneity, hydrology, insects, oxygen, pH, salinity, season.

Received 30 June 2020, accepted 8 September 2020, published online 13 November 2020

Introduction

Diversity is a basic ecological characteristic of every community. It is particularly relevant in drier climates where species are restricted by many adverse environmental conditions, as in Australian inland waters of dryland regions (Davis *et al.* 2018). These authors consider quantitatively various drivers in 10 types of aquatic habitats, but omit saline waters (those $>3 \text{ g L}^{-1}$). For this later grouping, Williams *et al.* (1990) provided some data on the role of salinity and, later, Williams (1998) considered the influence of various factors but without quantification. It is now appropriate to consider these drivers and others in more detail and, where possible, to quantify them.

Early investigations in Australian salinas (Bayly and Williams 1966; Bayly 1970) emphasised water chemistry and the unusual fauna but did not consider the role of a salinity scale or any other factors on diversity. It took a few decades for researches to consider these factors and to try to quantify them (Bayly 1969, 1970, 1976; Timms 1973, 1981, 1987, 1993, 1996, 1998a, 1998b, 2001a, 2001b, 2007, 2008, 2009a, 2009b, 2018; Geddes 1976; De Deckker and Geddes 1980; Geddes *et al.* 1981; Williams 1981, 1984, 1998; Williams and Kokkinn 1988; Williams *et al.* 1990; Pinder *et al.* 2002, 2004, 2005). In many of these studies, the conclusions are clearly enunciated, but in others a re-analysis of the data is necessary. This review will consider these drivers arguably in their order of importance. The location of sites included in these various studies are shown in Fig. 1.

Materials and methods

Even though this is a review paper and, thus, utilises already published information, data presented in some papers are re-analysed.

This applies to fig. 4 and 5 in Geddes (1976), table 17.2 in Geddes *et al.* (1981), various tables in Timms (1973, 1981), figures designated as fig. 2 in Timms (1993) and also fig. 2 in Williams (1990). Fortunately, in these studies, species richness in various sites arranged by salinity can be ascertained from these figures. Note that in choosing sites, a wider salinity range was used at the higher salinity, in keeping with the statement by Williams (1990) that tolerances were greater at higher salinities. Serendipitously, this approach enabled enough sites to be chosen to make the comparisons more robust.

The following three aspects of diversity were used: α diversity, which is the momentary species richness; β diversity, which is used in the sense of cumulative species richness over time at a nominated site; and γ diversity, which is the total list of species recorded in many sites within a defined district. All quoted salinities refer to the total concentration of inorganic ions.

Results

Salinity

In Australia, the earliest published role of the proportional influence of salinity is seen in Geddes *et al.* (1981) and Timms (1973, 1981), both being made clearer by a re-analysis of their data. Timms (1981) made a comprehensive study of just three Victorian lakes, namely, Purumbete (0.4 g L^{-1}), Bullenmerri (8 g L^{-1}) and Gnotuk (58 g L^{-1}). In all five communities studied, there was a marked difference between the fresh and the two saline lakes and then a decrease with an increased salinity in the latter (Table 1a). No mathematical relationship was suggested (Timms 1973). The study of Geddes *et al.* (1981) of 54 Western Australian lakes showed a significant

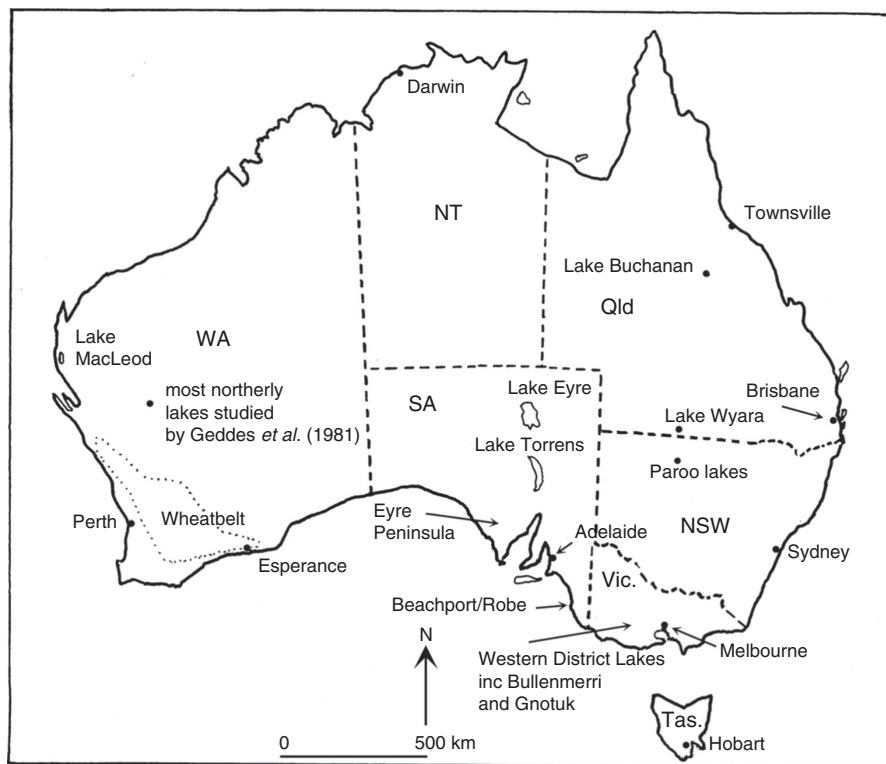


Fig. 1. Map of Australia showing most of the locations mentioned in the text.

Table 1. Species diversity in permanent and seasonal saline lakes
Data from Geddes (1976) and Timms (1981, 1993, 1998a).

Lake	Salinity (g L ⁻¹)	Mean α diversity \pm s.e.
Permanent lakes		
Bullenmerri	8	18.2 \pm 2.5
Gnotuk	58	10.1 \pm 1.5
Temporary lakes		
4 Victorian	5–20	7.0 \pm 0.4
11 Paroo	5–10	14.4 \pm 2.5
6 Victorian	50–75	5.8 \pm 0.2
7 Paroo	50–75	5.3 \pm 1.6

negative relationship between α diversity and salinity ($r = 0.695$, significant at $P < 0.01$; calculated from table 17.2 of Geddes *et al.* 1981), but of variable intensity among regions (see later in the paper). The aquatic fauna of saline Lake Buchanan and associated pools in northern Queensland showed a significant negative relationship between α diversity and salinity (Timms 1987). Again, Timms (1993, 1998a) showed a linear relationship between salinity and α diversity for a series of lakes in the Paroo in north-western New South Wales, but of different slope under different rainfall scenarios (see later in the paper; Fig. 2). In a thorough study of many Western Australian sites, Pinder *et al.* (2005) proposed a complicated mathematical relationship between diversity and salinity; the equations varying for various salinity ranges. Contrary to the above

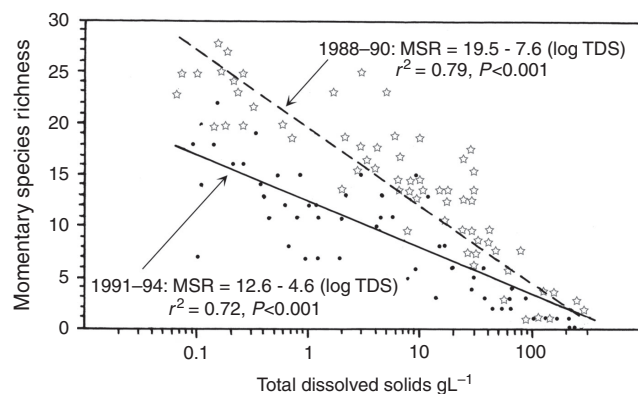


Fig. 2. Diversity v. salinity in Paroo Lakes. Modified from Timms (1993, 1998a). Data points are shown in open stars for 1988–90 and in solid circles for 1991–94. To enhance clarity, in both cases, some are omitted if the same or too close to others.

studies, Timms (2009a) on Eyre Peninsula lakes failed to find a significant relationship between diversity and salinity as (1) there were few hyposaline lakes to give high diversity at low salinities, (2) there were many marine springs at ~ 35 g L⁻¹, thus increasing mesosaline species and (3) there were many (66%) hypersaline lakes so that their euryhaline species did not show much decrease in diversity over a wide salinity range. Finally, a study of reasonably homogenous lakes in the Esperance area of Western Australia had a more classical significant relationship between salinity and β diversity (Timms 2009b). The overall conclusion is inescapable,

namely, that generally the salinity factor is dominant in determining diversity in saline lakes across Australia.

However, the relationship is not necessarily linear as implied in the most of the above studies. In a study of 79 lakes in the western district of Victoria, Williams *et al.* (1990) reported variable levels of correlation between salinity and diversity over different salinity ranges and a hand-drawn sigma-shaped curve between the two. They concluded that 'an appreciation of scale is fundamental.' Furthermore, they stated that species living at low salinities have the narrowest range of salinity tolerance, those at intermediate salinities, a broader range and those at the highest salinities, the widest tolerance to salinity. Pinder *et al.* (2002, 2005) reported similarly for their detailed Western Australia studies, but found no relationship between salinity and richness at salt concentrations of $<3 \text{ g L}^{-1}$.

Hydrology

There are indications that permanent saline lakes have more species at similar specific salinities than do seasonal waters, and that among the latter with shorter hydroperiods, species richness is even lower.

A re-analysis of the data for two permanent lakes, namely, Bullenmerri and Gnotuk, and sets of seasonal lakes showed that the former were more species rich than were the latter (Table 1). This difference is an expression in the permanent lakes of the greater depth and, hence, more benthic species and also the presence of vegetated littorals and rocky shorelines in the permanent lakes vis-à-vis seasonal lakes; i.e. habitat heterogeneity is the basic reason for the differences (see later), but other explanations are possible, such as in permanent lakes species have more time to accumulate. Divergence between permanent and seasonal lakes is less at higher salinities, no doubt being associated with the restricted species pool. One example is the dominance of 'giant' ostracods in Australian higher-salinity lakes (Halse 2002; Halse and McRae 2004) and the presence of just a few species in most hypersaline communities simplify whole-lake diversity.

Two sets of data are available on hydrological influence in seasonal lakes. The study of Geddes *et al.* (1981) of 54 lakes across a large area of Western Australia referred to above (Fig. 1) showed differences among regions, the wetlands of the far northern area (α diversity of 2.9) being less diverse than those of southern areas (α diversity of 6.2–7.5), with the assumed shortest water presence in the northern salinas in a zone of lower rainfall and higher evaporation. This hydrological briefness is confirmed by a study on rock pools (gnammas) across much the same area (Timms 2012; Brendonck *et al.* 2015), thus providing the environmental data needed to support the conclusion. However, also influencing diversity in these northern sites could be less frequent filling and, so, a less diverse egg bank, although eggs can remain viable in sediments for many years, commonly a decade, and so, mitigate for infrequent fillings (Boulton and Lloyd 1992; Katajisto 1996).

The graphs for two separate studies in the Paroo (Timms 1993, 1998a) show different slopes for the relationship in wet years v. dry years, with a lower diversity at low to moderate salinities in dry years (Fig. 2). There were eight wettings in the

3 dry years v. 12 in the 3 wet years, almost all wettings being of shorter duration in the dry years as suggested by rainfall records. The difference is due largely to the lack of insects in the dry years, probably indicating their lower resilience to generally dry conditions than for crustaceans, which hatch easily from resistant eggs and, generally, need a shorter time to complete their life cycles (Timms 1998a).

Habitat heterogeneity

This subject is not often raised in saline-lake studies, no doubt owing to the difficulty to quantify it. However, sometimes the influence of a varied structured habitat, as in a large inlet to a lake, can be compared with the homogeneity of wave-washed shores in large lakes. Such an example is the Werewilka Inlet to Lake Wyara in south-western Queensland (Timms 1998b, 2001a). The inlet has much greater variation in its sediment than do the shores of the lake (see fig. 3 in Timms 2001a). The invertebrate data from both lake and inlet were reworked (Table 2) to show the clear difference in diversity between the two sites. This table was then further extended by the analysis of diversity in some large saline lakes compared with that in small salinas in inland Australia. There was an adverse effect on the diversity of wave-washed, relatively homogeneous shores of large lakes, compared with somewhat heterogeneous shores of small lakes (Table 2; Timms 2001a). For organisms with tolerance to low salinity ($<5 \text{ g L}^{-1}$), the difference was significant at $P = 0.08$ ($r = 0.084$); however, for the saline species (salinity of $>20 \text{ g L}^{-1}$) and of $>50 \text{ g L}^{-1}$), the difference was not significant ($r = 0.4687$ and $r = 0.5269$ respectively). The difference is explained by low-tolerance insects being more common among littoral rocks and debris than on pure muddy sand, whereas there was little difference between saline organisms (mainly crustaceans) inhabiting largely the pelagic zone of both types of waters.

An adjunct to habitat heterogeneity is the presence of macrophytes. Generally, these are not eaten (a notable herbivorous exception is moth larvae), but plants (e.g. *Ruppia*, *Lepileana*, *Chara*) provide physical habitat and are particularly attractive to damselflies and microfauna. No doubt the presence of macrophytes at lower salinities enhances diversity, but there are no Australian studies.

Season

Generally, saline lakes are more biodiverse in summer than in winter, the difference largely being due to the abundance of insects in summer. This is most apparent in inland salinas in the Paroo where one study recorded 38 species in summer but only 24 species in winter (Timms 2018). Summer and winter crustacean species were almost identical, but very few insects were found in winter. Two seasonal studies in southern Australia did not record insects where water was present only in winter and spring (Geddes 1976; De Deckker and Geddes 1980). In a study at Esperance, the insect and crustacean lists were of similar length (30 v. 36 taxa respectively); however, a re-examination of their seasonality showed that insects were recorded mainly, but not exclusively, in non-winter collections (Timms 2009b; and B. V. Timms, unpubl. data). Most winter presences were of dipteran larvae.

Table 2. Beta species richness in large and small saline lakes in Australia

Lake	Number of species			Lake salinity (g L ⁻¹)	Sampling frequency	References
	>10 g L ⁻¹	>25 g L ⁻¹	<35 g L ⁻¹			
Large inland lakes						
Lake Eyre, SA	19	17	13	25–270	21 visits over 2 separated years	Williams and Kokkinn 1988; Bayly 1976; Williams 1990
Lake Torrens, SA	29	27	5	13–249	10 visits over 1 year	Williams <i>et al.</i> 1998
Lake Buchanan, Qld	32	17	15	4–128	8 visits over 10 years	Timms 1987
Lake Wyara, Qld	35	17	4	3–350	36 visits over 10 years	Timms 1998b
Small Paroo ‘lakes’						
Werewilka Inlet	66	36	10	1–70	26 visits over 13 years	Timms 2001a
Lake Mere	38	20	4	4–82	18 visits over 8 years	Timms 1993, 1998a; unpubl. data
Gidgee Lake	44	22	14	2–180	18 visits over 7 years	Timms 1993, 1998a, 2018
Lake Bulla	55	18	10	2–262	33 visits over 10 years	Timms 2008
Mid Blue Lake	61	15	7	1–103	35 visits over 10 years	Timms 2008
North Blue Lake	56	16	0	1–31	29 visits over 10 years	Timms 2008

pH

Not many Australian saline lakes are acidic, but there are some in Western Australia (Pinder *et al.* 2002, 2004, 2005; Timms 2009b), and on Eyre Peninsula, South Australia (P. Hudson, pers. comm., July 2016). Pinder *et al.* (2004) found that pH was strongly correlated with the composition of salt-lake communities. Most such lakes have *Parartemia* spp. characteristic of such waters. For *P. contracta*, Conte and Geddes (1988) showed that it is able to live at a low pH because of a unique biochemical ability to access CO₂ from sources other than HCO₃⁻ at pH of <6.3. In their study, it was the only invertebrate in localities of low pH. The Esperance area has many lakes of pH <7 (for these, there was a positive relationship with a decreasing pH of $r = 0.367$, $P < 0.05$; Timms 2009b). At a pH of <4, the only invertebrates present were *Parartemia acidiphila* (noted as *Parartemia* sp. F in the study) and the ostracod *Australocypris bennetti* (acid form).

Oxygen

Given that the solubility of oxygen in water decreases linearly with an increasing salinity, its effect on diversity is likely to be similar to that of salinity. However, it is not likely to affect air-breathing insects, nor small crustaceans relying on diffusion for gas exchange, just larger crustaceans and, then, more probably at the lower oxygen tensions characteristic of higher salinities. The only documented Australian example was reported by Mitchell and Geddes (1977) for solar salt ponds near Adelaide. In these, *Artemia* was the only brine shrimp in the most saline ponds because of its haemoglobin, whereas the ecologically similar *Parartemia*, with no or very little haemoglobin, was restricted to ponds of lower salinity and, hence, higher oxygen tensions.

Marine influence

It is rare to find marine-derived species in inland saline lakes, no doubt owing to the lack of resistant stages in marine species to withstand seasonal or episodic desiccation. However, examples

are known in lakes close to the coast, but physically separated, such as along the Beachport–Robe coast of south-eastern South Australia (Bayly 1970), on Eyre Peninsula, South Australia (Timms 2009a), in north-western Western Australia (Halse *et al.* 2000) and also in south-western Australia (A. Pinder, pers. comm., May 2020). At least in the case of polychaetes and copepods in the Beachport–Robe series, existence is precarious and recolonisation, possibly by birds, is probably necessary (Bayly 1970). In the Eyre Peninsula series, the presence of 18 species (of 88 in total) is apparently relictal and relies on permanent near-seawater salinities (Timms 2009a). There are no quantitative data on any effect on α diversity, but γ diversity for a region is raised a little.

Ionic composition

Australian saline lakes are somewhat homogeneous in their ionic composition, almost all being dominated by sodium (Na) and chloride (Cl) ions. At very high salinities (at $> \sim 300$ g L⁻¹), microorganisms can be negatively affected by high magnesium concentrations (Baas-Becking 1931; Borowitzka 1981); however, almost no multicellular organisms live at such salinities. At more common hypersaline and mesosaline conditions, Radke *et al.* (2003) showed that ionic composition can influence ostracod communities, and in hyposaline waters (~ 22 g L⁻¹), the presence of carbonates can increase the tolerance to salinity by the copepod *Boeckella triarticulata* (Bayly 1969). No data are available on the effect on diversity, but such would be minor.

Discussion

Studies on world saline lakes usually report a generalised inverse relationship between salinity and species richness (Hammer 1986); however, the relationship has been quantified only recently by some studies, much like the Australian studies mentioned above. Examples include McCulloch *et al.* (2008) on the Sua Pan, Botswana, Waterkeyn *et al.* (2008) on the

Camargue wetlands in southern France, Horváth *et al.* (2014) on soda pans of the Carpathian Basin of eastern Europe, and Anufriineua and Shadrin (2018) on Crimean lakes. These authors try to quantify other factors too such as ionic composition, pH and hydroperiod.

The eight abiotic factors affecting diversity in saline lakes itemised above are not a complete list, nor have all the factors been quantified. Biotic factors such as predation and competition have not been recorded in Australia and could be influential. Perhaps the biggest omission is how the presence of predators at middle salinities influences diversity. The example of the corixid *Trichocorixa verticalis* in Great Salt Lake is pertinent. It reduced *Artemia* populations and allowed two copepods and a rotifer, thus overall increasing diversity (Wurtsbaugh 1992). The effect of fish predation on *Artemia* is well known, so that should fish be removed, *Artemia* thrives and as do a few other invertebrates, so that diversity is increased. Although corixids (Knowles and Williams 1973) and the taxonomically similar *Parartemia* to *Artemia* occur widely in Australian saline lakes (Timms 2014), no study has recorded any biological influence. Campbell (1993) noted that the ostracod *Australocypris insularis* is a predator in some Australian salt lakes; however, its influence on diversity is also unknown.

The list of factors enunciated above is not the same as the ones mentioned by Williams (1998). His list is more inclusive and includes salinity, oxygen, ionic composition, pH, hydrological patterns, geographical position, palaeoclimatic events, chance, human interventions and biological interactions. His approach is more focussed on community structure rather than species diversity *per se*, and so is complementary to the present study. The Williams *et al.* (1990) paper is most relevant as it was the first to point out that the relationship between salinity and species richness is not linear but depends on the salinity scale. The linear relationships reported above are simplistic, and for a real understanding, scale should be involved. The same probably applies to other linear relationships reported for other factors. Obviously, factors influencing species composition and diversity are numerous and complex. Salinity is the easiest to quantify and, so, is often referred in saline-lake studies; however, it should be kept in mind that other factors are variously relevant.

In a comparison to other waters in the drylands of Australia (Davis *et al.* 2018), drivers of diversity in salt lakes are almost entirely different. Latitude and hydrologic connectivity so important in the waters Davis *et al.* (2018) studied, play no primary role in salinas; in fact, some can be in contradiction. For instance, the increase in diversity in saline lakes north to south in Western Australia (Geddes *et al.* 1981) is the antithesis of the situation in other aquatic communities in which diversity decreases with an increasing latitude (Davis *et al.* 2018); in this case, the explanation lies in rainfall differences, not in factors directly associated with latitude. However, as in other dryland aquatic communities, ecogeographic factors also influence community composition in saline lakes (Williams 1984; Timms 2007) but any diversity differences are explained by the factors enunciated above, not by the drivers for all of ecosystems in Davis *et al.* (2018). The hydrologically disconnected communities (springs and rockholes) of the arid biome have some drivers in common with saline lakes, particularly those pertaining to

dispersal; however, again, salt lakes are so distinctive from the norm because of the dominant role of just one driver, salinity.

Another aspect is clear. The insect component reacts differently to the drivers than do the crustaceans. Generally, insect diversity is more adversely affected by winter season and adverse hydrology than is the diversity of crustaceans; however, it is advantaged by heterogeneous habitat. The latter is partly explained by most crustaceans being planktonic and most insects being littoral. For the influence of salinity on diversity, chance plays a bigger role among insects than crustaceans, many insect occurrences in saline waters are haphazard, often involving only few dispersing individuals of a species (Timms 1993, 1998a). Adult aquatic insects are apparently not so much affected by the lesser factors of pH and oxygen, and certainly not by marine influence and ionic composition (Gillott 2005).

Conflicts of interest

The author declares that he has no conflicts of interest.

Declaration of funding

This research was self-funded and did not receive any specific other funding.

Acknowledgements

Adrian Pinder and two anonymous referees suggested many improvements to the manuscript for which I am most appreciative.

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Handling Editor: Rebecca Lester