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# Aquatic invertebrates of Lake Gregory, northwestern Australia, in relation to salinity and ionic composition

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**Abstract**

Lake Gregory is a large semi-permanent lake system in arid north-western Australia. Its catchment extends into humid areas and as a result the lake has dried only twice in the last 25 years. Although the system is mostly fresh, parts of it become saline as they dry. We identified aquatic invertebrates and undertook chemical analysis of water samples from several sites at Lake Gregory in 1989, when the main water-body was saline, and in 1991 and 1993, after the system had flooded and was fresh. During the period 1989–1993, salinities varied from 0.1‰ to 82‰, and ionic composition ranged from strong sodium chloride dominance, in saline water and fresh water of the eastern part of the system, to bicarbonate dominance in fresh water of the western area. At least 174 invertebrate species were recorded, including two mollusc species that were never collected live. This species richness is much higher than that recorded from other Australian arid zone lakes, probably owing to long periods of inundation with fresh water. The fauna was dominated by insects (42 per cent of total species richness), crustaceans (27 per cent) and rotifers (22 per cent). Most species (160) were restricted to fresh water; only 12 species were found in saline water. Only one ostracod occurred in saline conditions, although ostracods are a dominant group in Australian saline lakes. Among species restricted to fresh water, the proportion of rotifer and protozoan fauna that occurred in bicarbonate-dominated water was greater than the proportion of insect, crustacean and hydracarine fauna that did so.

## Introduction

Salinity is one of the important factors affecting the distribution of aquatic invertebrate species in Australian lakes and its relationship with species richness and community composition has been examined by several authors (Williams et al., 1990). As a general rule, invertebrates inhabiting inland waters can be divided into four groups: those restricted to fresh water, usually with salinities $\ll$ 3‰ (Timms, 1987; Hart et al., 1991); salt-tolerant freshwater species that extend into salinities up to ca. 15‰; halophilous species occurring mostly in saline water up to ca. 50‰ but sometimes in fresh waters; and halobiont species restricted to salinities of 50–300‰ (Beadle, 1959; Bayly, 1972).

More attention has been paid to the osmoregulatory abilities and salinity tolerance of halobiont and halophilous species than freshwater species but it is known that the occurrence and salinity tolerance of some freshwater species is influenced by ionic composition (Bayly, 1972; Bayly & Williams, 1973). Virtually all salt lakes and many fresh water-bodies in Australia are dominated by sodium chloride (Bayly & Williams, 1973; De Deckker, 1983a) and, for most salt-tolerant freshwater species, prior adaptation to relatively high proportions of sodium chloride may be the reason they can withstand elevated salinities. Ratios of other ions may also have a role in salinity tolerance, e.g. the salinity tolerance of *Boeckella triarticulata* is greater when large amounts of (bi)carbonate as well as low amounts of calcium and magnesium occur (Bayly, 1969). The salinity tolerance of some North American ostracods is similarly influenced by the ratio of (bi)carbonate to calcium (Forester, 1986). Other factors with a substantial effect on species occurrence include turbidity, pH, temperature, water

regime, existence of nearby sources of colonisation, and biological interactions such as competition and predation (Williams, 1998).

Lake Gregory is a large semi-permanent lake system in the monsoonal arid zone of north-western Australia (Bowler, 1981; Halse, 1990) that was originally named Gregory Salt Lake and often mistakenly regarded as saline. In fact, it is a freshwater system containing some large water-bodies that are hypersaline at low water levels. Such substantial variation in salinity of a lake is unusual. In this paper, we present data on flooding cycles, salinity and ionic composition of Lake Gregory and list the aquatic invertebrates collected. We examine the occurrence of invertebrates in relation to salinity and ionic composition, compare the fauna of Lake Gregory with that of ephemeral arid zone lakes elsewhere in Australia and discuss why the Lake Gregory fauna was depauperate when the lake was saline.

## Study area

Lake Gregory is on the edge of the Great Sandy Desert, north-western Australia (Figure 1). It is part of a palaeoriver system that became blocked, probably during the late Tertiary (Halse, 1990). The lake has an area of 380 $km^2$ when flooded to its normal boundary and a catchment area of 65 000 $km^2$, which lies to the north-east in an area receiving monsoonal rainfall. All significant inflow comes via Sturt Creek. Median annual rainfall at Halls Creek, ca. 250 km north of the lake and just outside the catchment, is 514 mm with most rain in January and February. Temperatures are highest prior to the wet season (average daily maximum in November and December, 38 °C) and lowest in the middle of the dry season in July (average daily maximum, 27 °C, and minimum, 12 °C). Annual evaporation is ca. 4000 mm.

Lake Gregory consists of three parallel chains of lakes. Sturt Creek breaks into a series of anastomosing channels near the lake and empties into all three chains, often by sheet flow (Figure 1). The eastern chain consists of Mulan, the largest and deepest waterbody, and Lera. Bulbi occurs at the southern end of the central chain and is connected to Mulan, except at low lake levels, by Djaluwon Creek. Delivery Camp makes up the southern part of the western chain, which is connected to Mulan only when the system is flooded far beyond the mapped boundary. Large numbers of waterbirds occur on the Lake Gregory system, especially on the eastern chain (Halse, 1990, 1998).

## Materials and methods

Aquatic invertebrates were collected from 12 sites in the Lake Gregory system, including two temporary claypans north of Mulan (Figure 1). We sampled sites 1, 2, 4, 5 and 6 at Mulan, 3 at Lera, 7 at Bulbi, 8 and 9 at temporary claypans and 10 at Delivery Camp in October 1989; 1, 3, 4, 5, 6, 7 and 10 in May/June 1991; and 1, 4, 5, 7, 10, and two additional Mulan sites, 11 and 12, in August 1993. Zooplankton and benthos were sampled separately at each site using pondnets with 50 $\mu$m and 160 $\mu$m mesh, respectively, in 1989 (except for site 10). In 1991 and for site 10 in 1989, 110 $\mu$m mesh was used for both samples; in 1993, 50 $\mu$m and 110 $\mu$m mesh were used. Zooplankton was preserved in 5% formalin and benthos was preserved in 70% alcohol. We set a gill net for fish in 1989. In 1991 and 1993 fish were collected in dipnets and in the gut contents of birds collected for dietary analysis.

Water depth was measured at the deepest part of Mulan each sampling period. Conductivity and pH were measured *in situ* and water samples were taken at each site for laboratory determination of ionic composition, total dissolved solids (TDS) by gravimetry, and silica. Turbidity was measured only in 1991 and 1993. Standard analytic techniques were used (APHA, 1989). Conductivity measurements were used to check the results obtained for TDS but are not presented. We have used TDS as an indication of salinity. Additional sets of water samples were collected from some sites in September 1991, as well as in May/June 1991 when invertebrate collections were made. All available data on depth and salinity since 1971 were collated to provide information about water regime and salinity levels, although depths often had to be estimated.

## Results

### *Water levels and salinity*

Maximum depth in Mulan in October 1989 was only 1.5 m (Figure 2) when moderately high salinities were recorded around the margin of Lera (27‰), Mulan (18–46‰) and Bulbi (82‰), and Djaluwon Creek connecting Mulan and Bulbi was dry. Delivery Camp and two claypans north of Mulan were fresh (< 1‰).

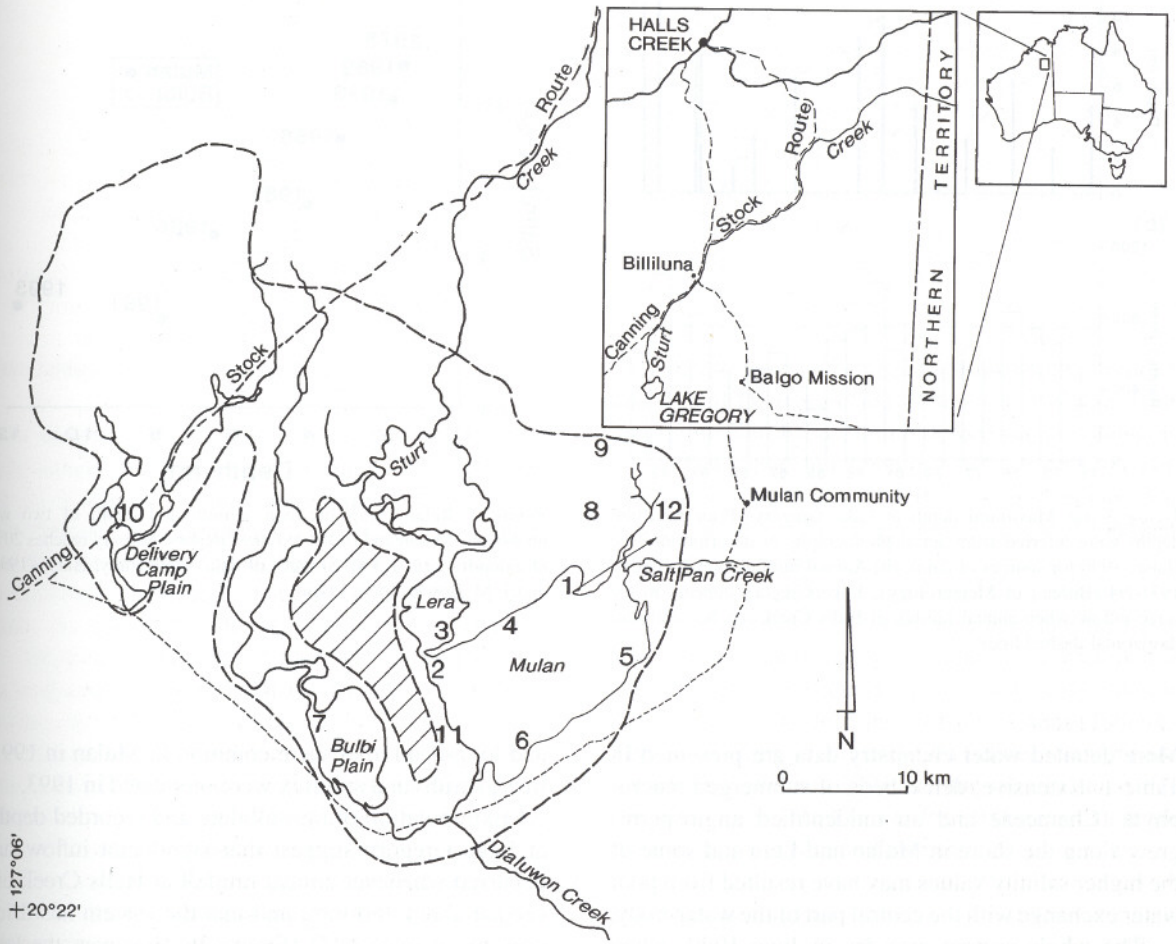


*Figure 1.* Major water-bodies at Lake Gregory. The dashed line indicates approximate boundary in 1993, after massive flooding (hatched area remained above water). Approximate positions of the 12 sampling sites are shown; arrow indicates the re-location of site 1 after the 1993 flood.

*Table 1.* Total dissolved solids (mg $L^{-1}$), pH, ionic composition (mg $L^{-1}$), silica (mg $L^{-1}$) and turbidity (NTU) at selected sites at Lake Gregory

| Site | Date | TDS | pH | Na | K | Ca | Mg | Cl | $SO_4$ | $HCO_3$ | $CO_3$ | $SiO_2$ | Turbidity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 5 | 10.x.89 | 25100 | 9.5 | 8450 | 548 | 47 | 421 | 13300 | 2200 | 180 | 58 | 3 | – |
| 5 | 17.viii.93 | 460 | 9.7 | 131 | 14 | 16 | 9 | 198 | 51 | 43 | <2 | 16 | 26 |
| 7 | 10.x.89 | 81800 | ~ 7.5 | 26300 | 1120 | 1150 | 1700 | 41100 | 10400 | 81 | <2 | 21 | – |
| 7 | 2.vi.91 | 220 | 9.0 | 46 | 9 | 14 | 5 | 68 | 31 | 46 | <2 | 19 | 280 |
| 10 | 14.x.89 | 400 | – | 104 | 30 | 7 | 9 | 99 | 26 | 150 | <2 | 33 | – |
| 10 | 3.vi.91 | 110 | 8.1 | 10 | 7 | 5 | 4 | 7 | 6 | 37 | <2 | 26 | 380 |

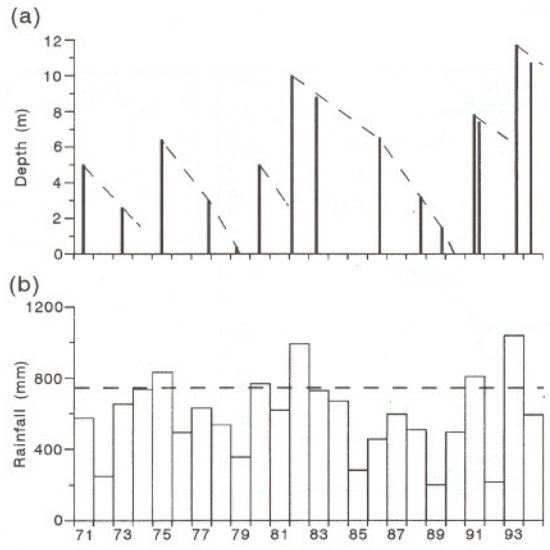


*Figure 2.* (a) Maximum depth at Lake Gregory. Prior to 1986, depths were inferred from aerial photographs or descriptions (see Halse, 1990 for sources of data). (b) Annual rainfall at Halls Creek 1971–94 (Bureau of Meteorology). Lake Gregory appears to receive inflow when annual rainfall at Halls Creek reaches 750 mm (horizontal dashed line).

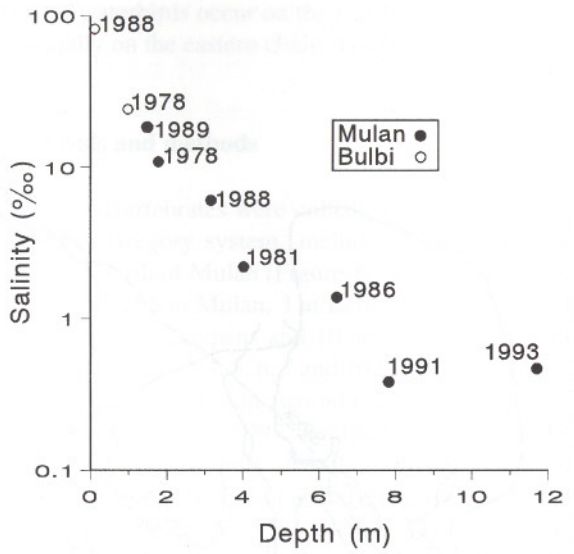


*Figure 3.* Relationship between salinity and depth of two water-bodies, Mulan and Bulbi, at Lake Gregory. Salinity reaches 20‰ at a depth of ca. 1.3 m. Sources of data – this study, Halse (1990) and J. M. Bowler (pers. comm.).

More detailed water chemistry data are presented in Table 1. Extensive, dense beds of submerged macrophyte (Characeae and an unidentified angiosperm) grew along the shore in Mulan and Lera and some of the higher salinity values may have resulted from poor water exchange with the central part of the water-body.

The whole system was dry in June 1990, when SAH visited, but re-flooded in February 1991 beyond the mapped boundary, which is reached at ca. 5 m depth. The maximum depth in Mulan in May/June 1991 was 7.8 m and salinities throughout the system were 0.1–0.4‰. By September 1991, salinities had increased by almost one-third at sites in Mulan and Lera and by almost four-fifths in Bulbi, although water level had dropped only 0.5 m. After 784 mm of rain in January and February 1993, there was massive flooding around the lake, which reached an area of 1300 $km^2$ (Figure 1). The depth in August 1993 was 11.8 m and salinities were 0.1–0.5‰ although, perhaps owing to poor water exchange around the edge of the lake, salinities at the same shoreline sites were about one-third higher in Mulan and two-fifths higher in Bulbi than in May/June 1991. Extensive beds of *Myriophyllum verrucosum* Lindley occurred along the shore of Mulan in 1991 and 1993, as well as *Marsilea mutica* Mettenius in shallow water in 1993. Inundated shrubs and long-dead trees were common in Mulan in 1991; trees, shrubs and spinifex were inundated in 1993.

Extrapolation of rainfall data and recorded depths at Lake Gregory suggest that significant inflow has occurred whenever annual rainfall at Halls Creek exceeded about 750 mm, and that the system has dried only twice since 1971 (Figure 2). However, the lake was probably dry most of the time between 1930 and 1968 because rainfall at the old Halls Creek townsite from 1930–43, and at the new townsite since 1944, exceeded 750 mm only in 1959. Data from old Halls Creek suggest the lake filled six times between 1896 and 1926, which is a similar water regime to that of the past 25 years. Several small claypans north of the major water-bodies, including sites 8 and 9, were filled by local rainfall in 1989 without inflow into the lake system and they retained water for about 6 months.

Plotting available salinity data from Mulan and Bulbi against depth data showed an inverse relationship between salinity and lake depth (Figure 3). Salinity in the centre of the Mulan exceeded 20‰, and the system became truly saline, only when depth was less than ca. 1.3 m (Figure 3). This occurred during the last 6 months of the drying phase of the lake in 1989/90 and probably less than one-tenth of the time the system has contained water since 1979 (Figure 2).

*Table 2.* Salinity (‰) and ionic composition (percentage milliequivalents) of the four categories of water chemistry recognized at Lake Gregory

| Category | Salinity | Na | K | Ca | Mg | Cl | $SO_4$ | $HCO_3$ | $CO_3$ |
|---|---|---|---|---|---|---|---|---|---|
| Aa[1] | 18–46 | 87–88 | 3 | 1 | 8 | 87–90 | 9–12 | 1–2 | 0.1–0.2 |
| Ab[2] | 82 | 84 | 2 | 4 | 10 | 84 | 16 | 0.1 | – |
| Ba[3] | 0.3–0.5 | 70–75 | 5–6 | 10–13 | 10–12 | 72–80 | 14–15 | 5–14 | – |
| Bb[4] | 0.2–0.4 | 61–67 | 4–6 | 17–21 | 12–13 | 54–68 | 15–23 | 16–25 | – |
| C[5] | 0.4–1.2 | 68–83 | 8–25 | 3–8 | 2–12 | 35–50 | 8–11 | 36–51 | – |
| D[6] | 0.1 | 32–37 | 12–15 | 21–32 | 23–28 | 20–39 | 9–17 | 53–62 | – |

[1] Lera and Mulan sites in 1989; [2] Bulbi in 1989; [3] Mulan and Bulbi sites in 1993; [4] Mulan and Bulbi sites in 1991; [5] Delivery Camp and claypan sites in 1989; [6] Delivery Camp site in 1991 and 1993

*Ionic composition and turbidity*

Sites sampled at Lake Gregory can be grouped into four categories on the basis of water chemistry (Table 2). Category A sites were saline, with sodium and chloride the dominant ions. Categories B, C and D sites were all fresh but differed in their patterns of ionic dominance. Patterns of ionic dominance were: A, $Na \gg Mg > K \approx Ca$, $Cl \gg SO_4 > HCO_3$; B, $Na \gg Ca \geq Mg > K$, $Cl > SO_4 \geq HCO_3$; C, $Na \gg K = Mg > Ca$, $Cl \approx HCO_3 \gg SO_4$; D, $Na \geq Ca \approx Mg > K$, $HCO_3 > Cl > SO_4$.

Sites at Mulan, Lera and Bulbi (1, 2, 3, 4, 5, 6 and 7) in October 1989 were regarded as category A, i.e. saline, with sodium and chloride ions accounting for approximately 85 per cent of total cation and anion milliequivalents. The calcium/(bi)carbonate ratio was < 1 at the Mulan and Lera sites (category Aa) but > 1 at Bulbi (category Ab).

When the whole system became fresh after the 1991 flood, sodium chloride continued to account for 60–80 per cent of total cation and anion milliequivalents at the Mulan, Lera and Bulbi sites (category B). Bulbi had the lowest sodium chloride concentration and its chloride value of 54 per cent milliequivalents in 1991 made it an outlier in category Bb (Table 2). The 30–40 per cent increase in salinity between May/June 1991 (category Bb sites) and September 1993 (category Ba) was accompanied by a 15–20 per cent increase in the milliequivalent proportion of sodium chloride and a 40–50 per cent decrease in calcium and bicarbonate. The proportion of other ions also declined (Table 2). The 30–80 percent increase in salinity between May/June and September 1991 was accompanied by changes in ionic proportions that were about half the magnitude of changes between 1991 and 1993. The largest changes in ionic composition occurred at Bulbi.

In 1989 the two claypans north of Mulan (sites 8 and 9) and Delivery Camp Plain (site 10) were fresh and dominated by sodium chlorocarbonate (category C). At Delivery Camp Plain in 1991 and 1993, the percentage milliequivalents of divalent and monovalent cations were similar. Bicarbonate was the dominant anion (category D).

Water was clear at saline sites and, although not measured precisely, turbidity was low. During freshwater phases, high turbidity values were recorded at Lake Gregory, especially at the least saline sites in the central and eastern parts of the system (Table 1). There was a negative correlation between salinity and turbidity in 1991 and 1993 over the salinity range 0.1–0.6‰ ($r_s = -0.766, n = 18, P < 0.001$). Silica levels were usually very high (Table 1).

*Invertebrates and fish*

At least 174 invertebrate species were collected (Appendix), including dead specimens of two mollusc species *Velesunio wilsoni* and *Glytophysa (Oppletora) jukesii,* excluded from further analyses. Twelve species were collected from seven saline sites (category A), 137 species from 12 sodium chloride-dominated freshwater site/date combinations (B), 38 species from three freshwater sites with similar chloride and bicarbonate activity (C), and 59 species from two sampling occasions at a bicarbonate-dominated freshwater site (D). The numbers of species at individual sites ranged from one (*Tanytarsus barbitarsus*) at site 7 in 1989 when salinity was 82‰ to 67 at site 1 in 1993. One species of fish *Leiopotherapon unicolor* (Günther) was abundant during all sampling periods.

The aquatic invertebrate fauna of Lake Gregory was dominated by insects, crustaceans and rotifers, which comprised 42, 27 and 22 per cent of the fauna, respectively. The 110 $\mu$m mesh used to sample zoo-

plankton in 1991 was too coarse for many rotifers and this group was undoubtedly undersampled. Cladocerans made up 57 per cent of the crustaceans, and chironomids 28 per cent of the insect fauna. With the exception of the coleopterans *Cybister tripunctatus* and *Eretes australis* and some anisopterans, the invertebrate fauna consisted of comparatively small animals.

Only one species, the ostracod *Heterocypris gregarius*, occurred in all water categories. Its absence from category A sites with salinity > 27‰ and occurrence at only one of the sites with salinity of 27‰ (although valves of dead animals were present at the other) suggest 27‰ is near its upper salinity tolerance. This is a wide salinity range for a freshwater species (Bayly, 1972) although a similar range has been recorded for an undescribed congener (Timms, 1993).

Other species at category A sites were restricted to saline water. The rotifer *Brachionus plicatilis*, cladoceran *Moina baylyi*, copepod *Apocyclops dengizicus* and chironomid *Tanytarsus barbitarsus* are known to be halophilous or halobionts, as are some species of ceratopogonid and the coleopteran genera *Berosus* and *Megaporus* (Williams, 1984; Timms, 1987, 1993; Williams & Kokkinn, 1988). *Cletocamptus dietersi* has previously been collected in southern Australia at a salinity of 16‰ and in north-western Australia at 12‰ (Hamond, 1973; S. A. Halse unpubl. data); it occurred at 46‰ at Lake Gregory. Little is known about salinity tolerance of the coleopteran *Hydroglyphus leai* or rotifer *Brachionus* aff. *nilsoni* recorded at 18 and 20‰, respectively. *Brachionus nilsoni* occurs in saline waters in parts of south-eastern Australia at lower salinities than its congener, *B. plicatilis* (I. J. Powling, pers. comm).

Forty-eight per cent of the species restricted to fresh water were collected only from sodium chloride-dominated water (category B), 16 per cent were collected only from water with a substantial amount of bicarbonate (categories C, D) and 36 per cent occurred in both types of fresh water (Table 3). Insects and crustaceans had similar distributions with respect to water category but a significantly higher proportion of rotifer species were confined to bicarbonate-rich sites ($\chi^2 = 13.1$, 1 df, $P < 0.01$, comparing rotifers with combined insects and crustaceans). Protozoan species also appeared to prefer bicarbonate-rich sites, while hydracarine species occurred mostly at sodium chloride-dominated sites (Table 3).

*Table 3.* Number of freshwater species at Lake Gregory restricted to sodium chloride-dominated sites (B), bicarbonate-rich sites (C,D) or occurring at both (B/C,D)

| Taxon | Water category | | | |
|---|---|---|---|---|
| | Fresh | B | C,D | B/C,D |
| Protista | 5 | – | 3 | 2 |
| Rotifera | 36 | 15 | 10 | 11 |
| Hydracarina | 5 | 4 | – | 1 |
| Crustacea | 41 | 16 | 3 | 22 |
| Insecta | 69 | 40 | 7 | 22 |
| Others | 4 | 3 | 1 | – |
| Total | 160 | 78 | 24 | 58 |

## Discussion

Bowler (1990) considered that evaporation and a decanting process from north-western and central waterbodies towards Mulan largely accounted for the ionic composition of water in Lake Gregory during saline phases, although the high pH resulting from photosynthesis was also important and was associated with the production of carbonate (Table 1). Bowler (1990) recorded a pH of 11.0 in Mulan. Saline water in Lake Gregory had similar ionic composition to that recorded in salt lakes of south-western Australia, except that bicarbonate levels were elevated (Geddes et al., 1981). Lakes Buchanan and Eyre, the other large arid-zone salt lakes in Australia that have been studied (Timms, 1987; Williams & Kokkinn, 1988), had a higher proportion of chloride and calcium and a lower proportion of bicarbonate than Lake Gregory.

Most water samples from Lake Gregory were fresh. Anions in water of the western chain soon after flooding (category D) were dominated by bicarbonate. Williams & Buckney (1976) found the same for a pool near Inverway, in the eastern part of the Lake Gregory catchment, and for Lake Woods after it had flooded. Lake Woods lies 650 km east of Lake Gregory and is a similar type of lake, although it contains water less often (Bowler, 1981). Magnesium was the dominant cation in the Inverway pool and Lake Woods, whereas equal amounts of magnesium, calcium and sodium occurred in the western chain at Lake Gregory.

The number of invertebrate species (174) collected at Lake Gregory is high for an Australian arid zone lake. Timms (1987) collected 53 species from Lake Buchanan and surrounding pools during eight visits. Lake Buchanan, in eastern Australia at the same lat-

itude as Lake Gregory, usually contains water for only a few months each year. Salinities recorded by Timms (1987) ranged from 1–200‰, although water at most sampling sites varied from slightly saline to hypersaline. Williams & Kokkinn (1988) collected 16 species of invertebrate from the episodically filled Lake Eyre, the largest lake in Australia, during 12 visits over one year after the lake had flooded. Lake Eyre is in central southern Australia and salinities varied from 25–>270‰. Three smaller episodically filled freshwater lakes in the Gibson Desert, Western Australia, contained 13–15 species each when sampled on a single occasion (S.A. Halse, unpubl. data). The number of species recorded in 25 lakes in the Paroo, an arid inland region of eastern Australia, varied from 6–66 after 12 occasions with an inverse relationship between salinity and species richness (Timms, 1993). Among Paroo lakes with similar salinities, more species were collected from lakes with longer, more regular periods of inundation, although the greater species richness was partly attributable to them being sampled more often because they contained water for longer periods (Timms, 1993).

Although we sampled with smaller sized mesh than used in most studies and, therefore, collected a higher proportion of the microfauna, it seems likely that the main reasons for the comparatively high species richness at Lake Gregory were that it contained fresh water during two of the three sampling periods and that it has regular and prolonged inundation. According to De Deckker (1983a), episodically filled saline lakes contain fewer species than regularly filled ones and we suggest this also applies to freshwater arid zone lakes.

Though it has a high species richness when fresh, Lake Gregory has a depauperate fauna when saline. Twenty species were collected at Lake Buchanan at salinities $\geq$ 20‰ and 16 at Lake Eyre compared with 12 at Lake Gregory (Timms, 1987; Williams & Kokkinn, 1988). The difference in species richness was mostly attributable to differences in ostracod faunas: one species occurred at Lake Gregory when it was saline compared with seven and six, respectively, at Lakes Buchanan and Eyre. Ostracods are usually a major component of the fauna of saline lakes in Australia (Geddes et al., 1981; Williams et al., 1990) and ten species were collected at Lake Gregory when it was fresh (Appendix). However, the calcium/bicarbonate ratios of <1 that occurred at all saline Lake Gregory sites, except Bulbi with a salinity of 82‰, are unusual in Australian salt lakes. Bayly & Williams (1966) collected few ostracods from moderately saline bicarbonate-rich salt lakes in Victoria.

Another possible explanation for the paucity of ostracod species in Lake Gregory during saline phases is that the lake is mostly a fresh water-body when flooded; it becomes saline for only the last six months or so of the flooding/drying cycle. This contrasts with the pattern of salinity change in Lakes Eyre and Buchanan; water is almost always saline in those lakes. The long periods of freshwater occurrence, the incremental increase in salinity, the temperature pattern in relation to water level and salinity, and competition from freshwater animals at the upper range of their salinity tolerance may combine to make Lake Gregory an unfavourable habitat for most of the ostracods inhabiting saline lakes (see also De Deckker, 1983b). Other lakes in the arid zone of north-western Australia fed by surface sources are fresh, episodically filled and ephemeral. The few saline lakes that do occur are not suitable sources of colonisation for Lake Gregory, because these lakes dry before Lake Gregory becomes saline. Of relevance in this context, too, is that all the species recorded from Lake Gregory when saline appear to be widespread forms, not endemic to the lake. This accords with the views of Williams & Kokkinn (1988) who point to the need for seasonally predictable occurrence of saline waters as a prerequisite for the development of regionally endemic species in salt lake faunas.

The study demonstrated that Lake Gregory has unusual physico-chemical behaviour and that it is a significant site in the arid zone of Australia in terms of the number of invertebrate species it contains. These factors, together with the large numbers of waterbirds the lake supports (Halse, 1998), make Lake Gregory an important area for conservation. Our sampling was not intensive enough to draw conclusions about the effect of ionic composition on species occurrence at the lake, although a greater proportion of the rotifer and protozoan faunas occurred at bicarbonate-rich freshwater sites than the insect, crustacean or hydracarine faunas, suggesting that there may be differences between invertebrate groups in their response to ionic composition. These apparent trends should be treated cautiously, because there were probably positive relationships between bicarbonate dominance, lack of submerged macrophytes and turbidity. Macrophyte distribution and turbidity can have substantial effects on community composition (Williams, 1998).

## Acknowledgements

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**Appendix**

Aquatic invertebrates recorded in different water categories at Lake Gregory (see text for explanation of categories). Values represent the number of times taxa were recorded at sites belonging to each water category, molluscan taxa that were collected dead are indicated by 'd'.

| Taxon | Water category | | | |
|---|---|---|---|---|
| | A | B | C | D |
| PROTISTA | | | | |
| LOBOSEA | | | | |
| ARCELLINIDA | | | | |
| Arcellidae | | | | |
| *Arcella* sp. | | 1 | 1 | |
| Centropyxidae | | | | |
| *Centropyxis spinosa* Cash | | | 2 | |
| Difflugiidae | | | | |
| *Difflugia corona* Wallich | | | 1 | 2 |
| *Difflugia oblonga* Ehrenberg | | 1 | 1 | |
| **FILOSEA** | | | | |
| GROMIIDA | | | | |
| Euglyphidae | | | | |
| *Euglypha* sp. | | | 1 | |
| PLATYHELMINTHES | | | | |
| TURBELLARIA | | | | |
| TRICLADIDA | | | | |
| Dugesiidae | | | | |
| ? *Mesostoma* sp. | | 2 | | |
| NEMATODA | | | | |
| Nematoda sp. | | | | 1 |
| ROTIFERA | | | | |
| DIGONONTA | | | | |
| BDELLOIDEA | | | | |
| Bdelloidea sp. | | 1 | | 1 |
| MONOGONONTA | | | | |
| FLOSCULARIACEA | | | | |
| Filiniidae | | | | |
| *Filinia australiensis* Koste | | 1 | | |
| *Filinia longiseta* (Ehrenberg) | | 2 | | |
| *Filinia pejleri* Hutchinson | | | 2 | |
| Hexarthridae | | | | |
| *Hexarthra mira Hudson* | | 6 | 2 | 1 |
| Testudinellidae | | | | |
| *Testudinella patina* (Hermann) | | 3 | 1 | |

| Taxon | Water category | | | |
|---|---|---|---|---|
| | A | B | C | D |
| *Euchlanis dilatata* Ehrenberg | | 6 | | 1 |
| Trichotriidae | | | | |
| *Macrochaetus collinsi* (Gosse) | | 1 | | |
| MOLLUSCA | | | | |
| BIVALVIA | | | | |
| EULAMELLIBRANCHIA | | | | |
| Hyriidae | | | | |
| *Velesunio wilsoni* (Lea) | 7d | | 2d | |
| *Glyptophysa (Oppletora) jukesii* (Adams) | | 2d | | |
| ANNELIDA | | | | |
| OLIGOCHAETA | | | | |
| TUBIFICIDA | | | | |
| Naididae | | | | |
| *Allonais ranauana* (Michaelsen & Boldt) | | 3 | | |
| *Pristina longiseta* Ehrenburg | | 2 | | |
| ARTHROPODA | | | | |
| ARACHNIDA | | | | |
| HYDRACARINA | | | | |
| Hydracarina sp. | | 3 | | |
| Eylaidae | | | | |
| *Eylais* sp. | | 1 | | |
| Limnesiidae | | | | |
| *Limnesia* sp. | | 2 | | 1 |
| Unionicolidae | | | | |
| *Neumania* sp. | | 3 | | |
| Pionidae | | | | |
| *Piona* sp. | | 4 | | |
| Arrenuridae | | | | |
| *Arrenurus* sp. | | 5 | | |
| CRUSTACEA | | | | |
| CLADOCERA | | | | |
| Sidiidae | | | | |
| *Diaphanosoma* aff. *unguiculatum* Gurney | | 4 | 3 | 1 |
| *Latonopsis australis* Sars | | 1 | 1 | |
| Chydoridae | | | | |
| *Alona diaphana* King | | 9 | | 1 |
| *Alona* sp. A | | 1 | | 1 |
| *Alona* sp. B | | 5 | | |
| *Alona* sp. C | | 1 | | 2 |
| *Alona* sp. D | | 3 | | |

| Taxon | Water category | | | |
|---|---|---|---|---|
| | A | B | C | D |
| *Alona* sp. E | | 1 | | 1 |
| *Biapertura rigidicaudis* Smirnov | | 10 | | 2 |
| Aff. *Biapertura* sp. | | | | 1 |
| *Chydorus* sp. | | 5 | | 2 |
| *Leydigia* sp. | | 3 | | |
| Aff. *Monospilus* sp. | | | 1 | 1 |
| *Rak* sp. | | 2 | | |
| *Celsinotum* sp. | | 2 | | |
| *Ephemeroporus* aff. *barroissi* (Richard) | | 2 | | |
| Chydorinae sp. | | 1 | | |
| Macrothricidae | | | | |
| *Macrothrix* aff. *pectinata* (Smirnov) | | 3 | | 1 |
| Moinidae | | | | |
| *Moina baylyi* Forro | 5 | | | |
| *Moina* aff. *micrura* Kurz | | 8 | 1 | 1 |
| Bosminidae | | | | |
| *Bosmina meridionalis* Sars | | 3 | 1 | 1 |
| Daphnidae | | | | |
| *Ceriodaphnia cornuta* sensu lato Sars | | 4 | | |
| *Ceriodaphnia quadrangula* sensu lato (Müller) | | 4 | | |
| *Ceriodaphnia* sp. C | | 1 | | |
| *Ceriodaphnia* sp. | | | | 1 |
| *Daphnia carinata* King | | 7 | 3 | 1 |
| *Scapholeberis kingi* Sars | | 4 | | |
| *Simocephalus latirostris* Stingelin | | 3 | | |
| OSTRACODA | | | | |
| Limnocytheridae | | | | |
| *Limnocythere dorsicula* De Deckker | | 5 | 12 | |
| Ilyocyprididae | | | | |
| *Ilyocypris australiensis* Sars | | 1 | | 1 |
| Cyprididae | | | | |
| *Ampullacypris oblongata* (Sars) | | 1 | | |
| *Bennelongia barangaroo* De Deckker | | 1 | 2 | |
| *Cypretta baylyi* McKenzie | | 5 | 2 | |
| *Cyprinotus kimberleyensis* McKenzie | | 12 | 1 | |
| *Cypericercus* aff. *salinus* De Deckker | | 8 | 1 | 2 |
| *Heterocypris gregarius* Skoksberg | 4 | 8 | 1 | 1 |
| *Heterocypris* sp. B | | 1 | | |
| *Zonocypretta kalimna* De Deckker | | | 1 | |

| Taxon | Water category | | | |
|---|---|---|---|---|
| | A | B | C | D |
| CONCHOSTRACA | | | | |
| Cyzicidae | | | | |
| *Cyzicus* sp. | | 1 | | |
| COPEPODA | | | | |
| Centropagidae | | | | |
| *Boeckella triarticulata* (Thompson) | | 12 | 3 | 2 |
| *Calamoecia canberra* Bayly | | 11 | 3 | 2 |
| *Calamoecia lucasi* Brady | | 1 | 1 | |
| Centropagidae sp. A | 1 | | | |
| Cyclopoidae | | | | |
| *Apocyclops dengizicus* (Lepeschkin) | 6 | | | |
| *Mesocyclops notius* Kiefer | | 1 | 1 | 2 |
| *Microcyclops varicans* (Sars) | | 5 | | 2 |
| Canthocamptidae | | | | |
| *Cletocamptus dietersi* (Richard) | 3 | | | |
| INSECTA | | | | |
| EPHEMEROPTERA | | | | |
| Caenidae | | | | |
| *Tasmanocoenis arcuata* Alba-Tercedor & Suter | | 3 | | 1 |
| Baetidae | | | | |
| *Cleon* sp. | | 2 | | 1 |
| ZYGOPTERA | | | | |
| Coenagriidae | | | | |
| ?*Austrogrion* sp. | | 4 | | |
| *Ischnura heterosticta* (Burmeister) | | 5 | | |
| *Xanthagrion erythroneurum* Selys | | 3 | | |
| Coenagriidae sp. | | 3 | | |
| ANISOPTERA | | | | |
| Aeshnidae | | | | |
| *Hemianax papuensis* (Burmeister) | | 3 | | |
| Aeshnidae sp. | | 1 | | |
| Corduliidae | | | | |
| *Hemicordulia tau* Selys | | 1 | | 1 |
| Libellulidae | | | | |
| *Diplacodes bipunctata* (Brauer) | | 6 | | 1 |
| *Orthetrum caledonicum* (Brauer) | | 3 | | 1 |
| *Macrodiplax cora* (Brauer) | | 1 | | |
| HEMIPTERA | | | | |
| Gerridae | | | | |
| *Limnogonus fossarum skusei* Bueno | | 2 | | |

| Taxon | Water category | | | |
|---|---|---|---|---|
| | A | B | C | D |
| Mesoveliidae | | | | |
| *Mesovelia orientalis* Kirkaldy | | 1 | | |
| Corixidae | | | | |
| *Agraptocorixa* sp. | | | | 1 |
| *Micronecta gracilis* Hale | | 8 | | |
| *Micronecta robusta* Hale | | 4 | | 1 |
| *Micronecta* sp. | | 2 | 1 | |
| Notonectidae | | | | |
| *Anisops gratus* Hale | | | 1 | |
| *Anisops hyperion* Kirkaldy | | | 2 | |
| *Anisops nasuta* Fieber | | 1 | | |
| *Anisops paraexigera* Lansbury | | 2 | | |
| *Anisops semita* Brooks | | 2 | | |
| *Anisops stali* Kirkaldy | | | 1 | |
| *Anisops thienemanni* Lundblad | | 3 | | |
| *Anisops* sp. | | 3 | | 1 |
| Pleidae | | | | |
| *Plea* sp. | | 1 | | |
| **Tipulidae** | | | | |
| Tipulidae sp. | | 1 | | |
| Culicidae | | | | |
| *Anopheles (Cellia) amictus* Edwards | | 3 | | |
| *Culex annulirostris* Skuse | | 1 | | |
| Chironomidae | | | | |
| *Ablabesmyia* aff. *notabilis* Skuse | | 1 | | |
| *Chironomus* sp. | | 3 | | |
| *Cladotanytarsus* aff. sp. K4 | | 8 | | 2 |
| *Coelopynia pruinosa* Freeman | | | 2 | |
| *Cricotopus* aff. *albitarsis* Hergstrom | | 9 | | 2 |
| *Crytochironomus* aff. *griseidorsum* Kieffer | | 5 | | 1 |
| *Dicrotendipes* aff. *jobetus* Epler | | 4 | | 2 |
| *Dicrotendipes* sp. K8 | | 11 | | 1 |
| *Larsia albiceps* (Johannsen) | | 9 | | |
| *Nanocladius* sp. | | 3 | | 1 |
| *Parachironomus* sp. | | 1 | | 1 |
| *Paracladopelma* aff. sp. M3 | | 5 | | |
| *Polypedilum leei* Freeman | | 4 | | 1 |
| *Polypedilum nubifer* Skuse | | 2 | | |
| *Procladius paludicola* Skuse | | 7 | | 2 |
| *Tanytarsus barbitarsus* Freeman | 4 | | | |

| Taxon | Water category | | | |
|---|---|---|---|---|
| | A | B | C | D |
| *Tanytarsus* aff. *bispinosus* Freeman | | 5 | | 1 |
| *Tanytarsus* aff. *manlyensis* Glover | | 4 | | |
| *Tanytarsus* aff. *richardsi* Glover | | | | 1 |
| *Tanytarsus* aff. sp. B1 | | | | 1 |
| *Tanytarsus* aff. sp. K10 | | 1 | | |
| Ceratopogonidae | | | | |
| Ceratopogonidae sp. | 1 | | | |
| Stratiomyidae | | | | |
| Stratiomyidae sp. A | | 4 | | |
| Stratiomyidae sp. B | | 1 | | |
| Stratiomyidae sp. C | | 1 | | |
| TRICHOPTERA | | | | |
| Hydroptilidae | | | | |
| *Orthotrichia* sp. | | 1 | | |
| Ecnomidae | | | | |
| *Ecnomus* sp. A | | 2 | | |
| *Ecnomus* sp. B | | 1 | | |
| Leptoceridae | | | | |
| *Oecetis* sp. | | 3 | | 1 |
| *Triplectides australis* Navas | | 3 | | |
| COLEOPTERA | | | | |
| Carabidae | | | | |
| *Platycoelus prolixus* (Erichson) | | 2 | 1 | |
| Carabidae sp. | | 1 | | |
| Dytiscidae | | | | |
| *Allodessus bistrigatus* (Clark) | | 1 | | |
| *Cybister tripunctatus* (Oliver) | | 1 | | |
| *Eretes australis* (Erichson) | | 4 | 1 | |
| *Hydroglyphus grammopterus* (Zimmerman) | | 3 | | 1 |
| *Hydroglyphus lea* (Guignot) | 1 | | | |
| *Hyphydrus lyratus* Swartz | | 2 | | 1 |
| *Megaporus* sp. | 1 | | | |
| Hydrophilidae | | | | |
| *Berosus australiae* Mulsant | | 1 | | |
| *Berosus debilipennis* Blackburn | | 1 | | |
| *Berosus josephenae* Watts | | 1 | | |
| *Berosus pulchellus* MacLeay | 1 | 1 | | |
| *Enochrus elongatulus* MacLeay | | 2 | | |
| *Enochrus deserticola* Blackburn | | 6 | | 1 |
| *Paracymus pygmaeus* MacLeay | | 1 | | |
| Hydrophilidae sp. | | 1 | | |