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The biogeographical affinities of the fauna in episodically filled salt lakes: A study of Lake Eyre South, Australia

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Abstract

Lake Eyre South, a large and normally dry playa in central Australia, filled with water in January 1984. Water persisted until January 1985. Salinity rose between these dates from ~25‰ to >270‰. Monthly observations on the fauna were made to determine if it consisted of widely dispersed species, and thus to test the assumption that episodically filled salt lakes are unimportant as evolutionary loci for the fauna of salt lakes. It was concluded that most species in the lake were indeed widely dispersed. Particularly common components of the fauna were: *Craterocephalus eyresii* (Steindachner) (fish), an undescribed species of *Diacypris* (ostracod), *Moina baylyi* Forró (cladoceran), *Tanytarsus barbitarsis* Freeman (chironomid), *Parartemia minuta* Geddes (anostracan), and *Microcyclops platypus* (Kiefer) (copepod).

Introduction

The fauna of Australian salt lakes displays marked regional differences. An explanation for these has recently been put forward (Williams, 1984) and involves two assumptions. First, episodically filled salt lakes are unimportant as evolutionary loci for the fauna of salt lakes. The inundation of such lakes has a strong element of unpredictability, and they contrast with regularly filled salt lakes where inundation generally occurs on a seasonal basis each year with a strong element of predictability. Second, the most important environmental determinant within salt lakes is the seasonal (or predictable) temporal pattern of interaction between salinity, temperature and the presence of water. Salinity by itself is relatively unimportant.

If episodically (irregularly) filled salt lakes are poor evolutionary loci, they should contain many widely dispersed species and few endemics. Further, De Deckker (1983) has suggested that fewer species are present in episodically filled salt lakes than in predictably filled ones (a feature which *perhaps* reflects the greater importance of predictably filled lakes as evolutionary loci).

An opportunity to test these ideas arose in 1984 when Lake Eyre South, a large and usually dry playa in South Australia, filled after the occurrence of unusually heavy rain in the area in January. It was only the second time this century that Lake Eyre South had filled, the previous occasion being in 1974. Lake Eyre North, an even larger playa to which Lake Eyre South connects, also filled in 1949–1950. The present paper documents and discussed the results of a study of the lake between February 1984 and January 1985. It does so with a view to examining only the first of Williams's (1984) assumptions.

Materials and methods

Lake Eyre South lies *ca.* 625 km north of Adelaide, South Australia; the general setting is indicated in Fig. 1. It is within an arid climatic zone with an an-

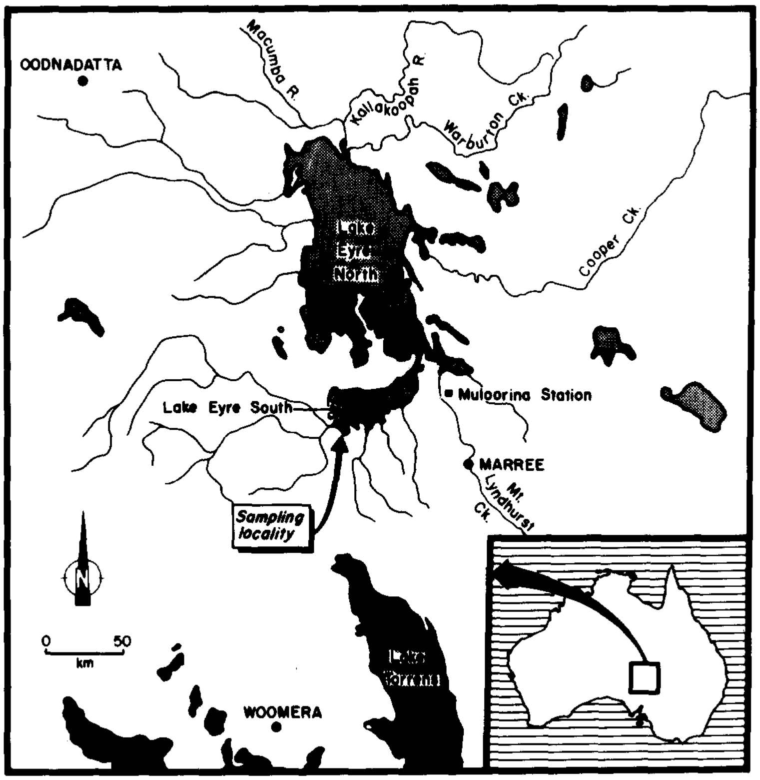

Fig. 1. Location of Lake Eyre South, sampling position, and position of stations from which meteorological information has been obtained.

nual median rainfall of <15 cm and an annual average evaporation over twenty times as great, viz. ~ 360 cm. The incidence of rain is highly unpredictable, and, using Gaffney's variability index, rainfall variability is regarded as very high (Gaffney, 1975).

Qualitative faunal collection of the zooplankton and benthos were made at one location on the southern shore of the lake with a net of mesh aperture 160μm at monthly intervals beginning February 1984. Samples were preserved in formalin. February–May samples were collected by one of us (W.D.W.); all later samples were collected by W. Chandler, Roxby Management Services.

Water samples were collected at the same time as faunal samples and stored in black polyethylene bottles. Standard analytical techniques more or less as outlined by Geddes *et al.* (1981) were used to determine the major ions, and salinity was defined as the total weight of major ions.

Meteorological information was obtained from the Engineering and Water Supply Department of South Australia (Muloorina rainfall data) and the Commonwealth Bureau of Meteorology (all other data).

Results

Meteorological data are not available for the lake itself, but some important data are available for Muloorina, Oodnadatta and Woomera (see Fig. 1 for locations). A combination of these data provides a reasonable approximation of the meteorological conditions that would have prevailed at the lake during the rainfall and subsequently as the lake dried out. Appropriate data are indicated in Fig. 2. Heavy rain fell on the 12–14 January (21.1 cm) followed by a lighter downfall (4.8 cm) later the same month (25 January). Extensive flooding resulted and local runoff filled the lake. This is the first recorded instance

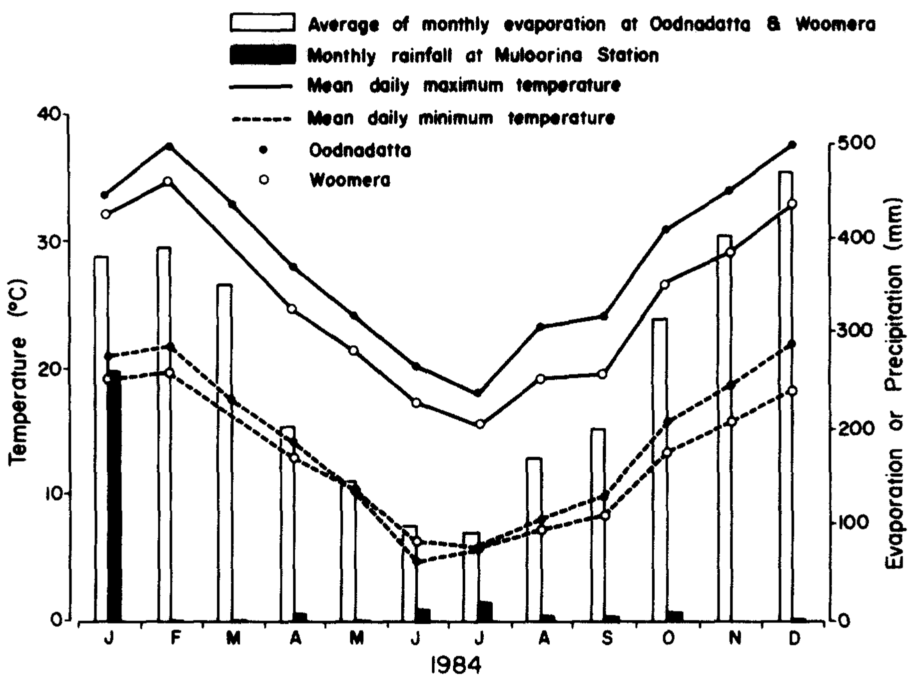

Fig. 2. Meteorological conditions in the Lake Eyre region during 1984. Data from Commonwealth Bureau of Meteorology and The Engineering and Water Supply Department of South Australia.

of filling by local floods; on previous occasions when the lake was filled (1974 and in the last century), Lake Eyre South was filled by overflow from Lake Eyre North which received heavy inflows from its catchment in Queensland.

Figure 3, a Landsat image taken on 21 January 1984, gives an indication of the extent and distribution of water in the region shortly after the major rainfall. The figure shows that both Lake Eyre South and Lake Eyre North filled within two weeks of the rain. A large number of small water-bodies peripheral to the lakes are also well shown. Figure 4 provides an indication of the general appearance of the lake near the sampling point in May 1984. At the sampling point, the substratum was coarse mud, and water depth decreased progressively over the time of sampling from ~ 0.5 m. A general account of the natural history of the lake has recently been given by Serventy (1985).

Only small quantities of rain fell after January 1984, and the intense evaporation and overall high temperatures which followed (Fig. 2) led to the desiccation of Lake Eyre South (and most other waters in the region) by January 1985.

The detailed results of the chemical analyses are given in Table 1. To indicate more clearly the relative changes that took place, the results are also shown in Fig. 5 where the concentrations of the major ions are shown as percentage equivalents. With regard to salinity, it appears that the lake was probably never fresh (i.e. with salinity $< 3\ g \cdot l^{-1}$); at least, it appears likely never to have been so for long, for within one month of filling salinity was already 25.3‰. Salinity rose steadily from 25.3‰ but at a reatively slow rate until September by which time it had reached 86.7‰. Thereafter its rate of increase accelerated, so that in the remaining four months of the lake's existence salinity rose to at least 272‰. Over almost the entire salinity range, relative ionic proportions remained more or less constant, with Na and Cl the dominant ions. It was only at the very highest salinities that some small change in dominances occurred; it principally involved Mg and Ca.

The results of the faunal collections are shown in Fig. 6. At least 17 species were recorded, comprising fish (1 species), insects (1 species of chironomid, 1

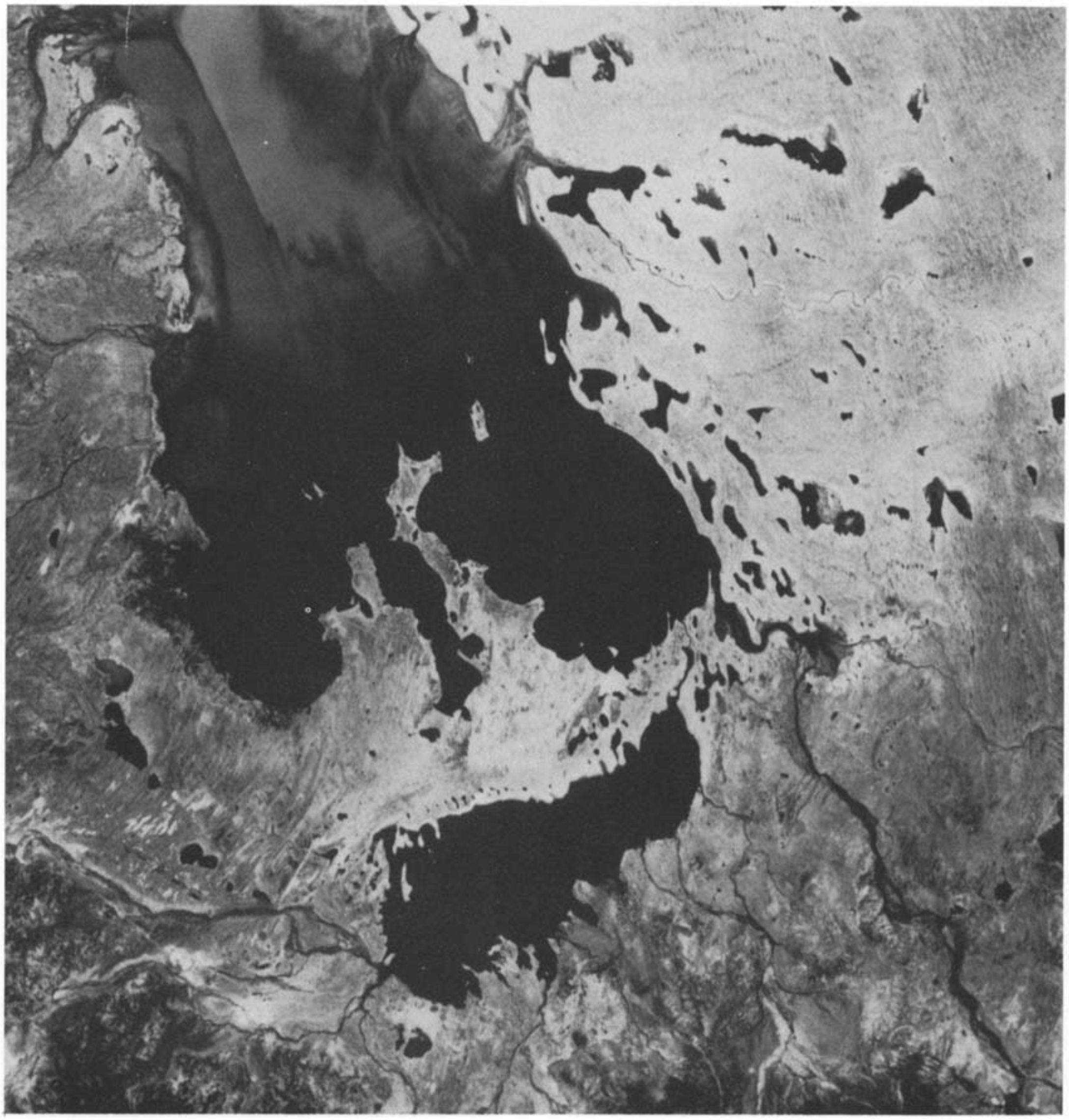

Fig. 3. Lake Eyre South and adjacent regions as photographed by Landsat on 21 January, 1984. Landsat imagery provided by the Australian Landsat Station, Division of National Mapping, Department of Resources and Energy.

or 2 beetle species, and 1 ephydrid species), rotifers (1 species), brine shrimp (1 species), cladocerans and copepods (2 species each), and ostracods (6 species). Crustaceans were numerically dominant at all times.

Discussion

The chemical observations on the lake provide information on the pattern of change in one of the major physicochemical features of the lake, viz. salinity, and confirm that patterns of ionic dominance and constancy in Lake Eyre South were similar to those found in regularly filled Australian salt lakes (that is, chemical differences were not the cause of any possible faunal differences between Lake Eyre South and regularly filled lakes). The pattern of ionic dominance and constancy observed is characteristic of

Fig. 4. Lake Eyre South. Aerial view of sampling position, 7 May, 1984.

Table 1. Results of chemical analyses of water samples. All data expressed as $mg \cdot l^{-1}$.

Date	Salinity	Na	K	Ca	Mg	Cl	SO_4	HCO_3	CO_3
14 Feb. 1984	25331	9114	< 1	545	53	14290	1274	55	0
28 Mar.	40989	14620	70	876	150	23000	2140	35	7
30 Mar.	42355	15150	93	887	143	23350	2700	32	0
30 Apr.	49023	17520	70	1050	171	27220	2950	42	0
7 May	51301	18400	46	1040	187	28300	3280	48	0
28 May	57728	20640	48	1240	193	31880	3670	57	0
25 June	61278	21970	49	1350	173	34360	3310	66	0
21 July	64969	23230	92	1350	236	35910	4070	81	0
27 Aug.	71248	25500	136	1450	264	39640	4170	88	0
24 Sept.	86710	31200	68	1680	310	48100	5290	62	0
28 Oct.	117797	42600	111	2050	451	65700	6820	65	0
30 Oct.	120067	43800	111	1820	473	67500	6300	63	0
26 Nov.	162697	60300	129	1650	725	93100	6720	73	0
17 Dec.	217350	82000	208	1220	874	126200	6800	48	0
16 Jan. 1985	272819	101300	555	459	2500	155600	12300	105	0

almost all Australian salt lakes so far investigated (see, for example, Williams and Buckney, 1976).

Before considering the fauna of Lake Eyre South in particular, some general points may be made. First, we believe it unlikely that resistant bodies of the fauna of episodically filled lakes persist for extended periods (tens of years) in the dry sediments of such lakes. Thus, second, the fauna of episodically filled lakes during periods of inundation will originate from (perhaps small) loci within the local en-

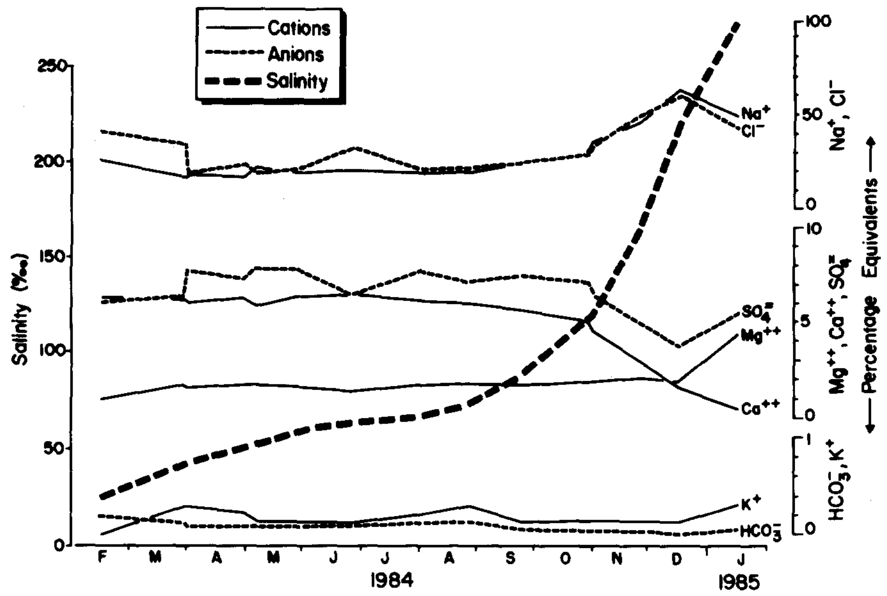

Fig. 5. Salinity and percentage equivalents of major ions in Lake Eyre South, February 1984–January 1985.

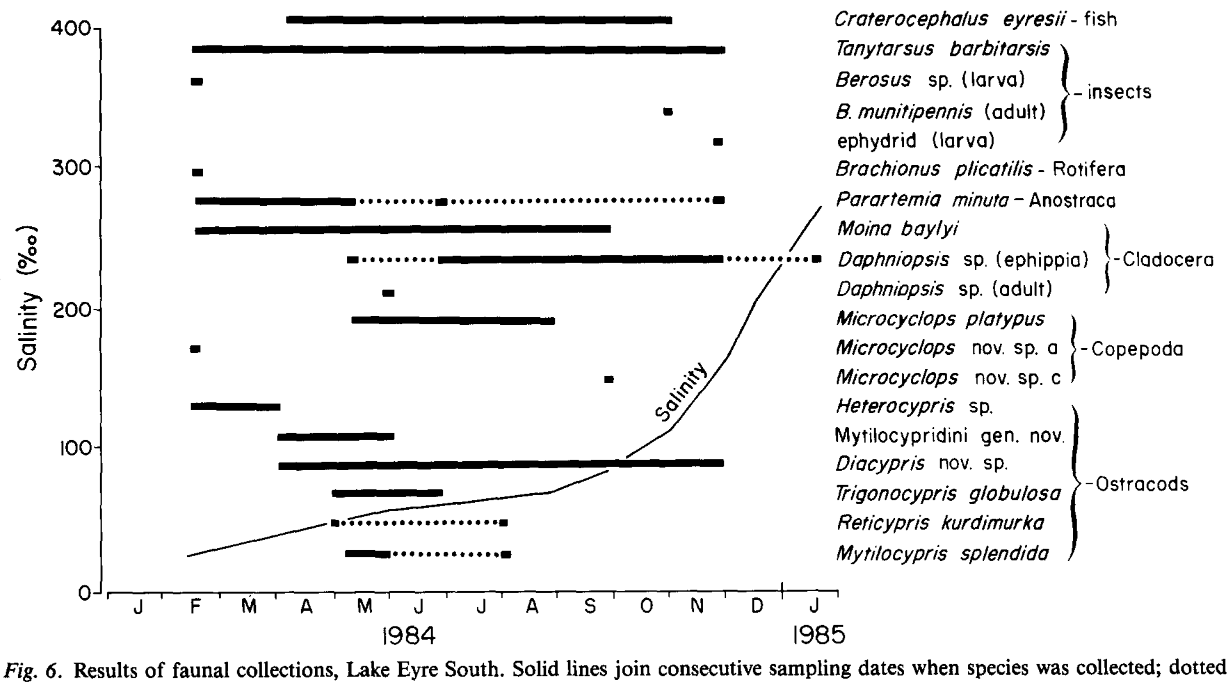

Fig. 6. Results of faunal collections, Lake Eyre South. Solid lines join consecutive sampling dates when species was collected; dotted lines join dates when species was collected but not recorded during intervening dates (species presence is here assumed).

dorheic drainage basin or from further afield. It will be washed in by flooding creeks or carried in by the wind, by birds, or by other means. These loci may be numerous, but most will be ephemeral and unpredictably filled. A few will be more or less permanent and fed by subsurface water originating from better watered parts of the Lake Eyre drainage basin (e.g. pools in the bed of Cooper Creek). The fauna of the ephemeral localities must comprise easily dispersed, opportunistic species. It may well also comprise species which are less easily dispersed but which have adapted to the irregular periodicity of the presence of water in the region or which have come from the few more or less permanent waters of the basin. These less easily dispersed species could have evolved in the region or have entered from outside. Whatever the case, we believe it unlikely that they would represent the majority of species found in such water-bodies.

With regard to Lake Eyre South in particular, the central question, then, is: how widely dispersed are the animals found there? To what degree are they endemic and found only in Lake South or in the Lake Eyre region? In this matter the data are equivocal, or at least would appear so at first glance. Thus, several species recorded are new, and therefore, it would seem, probably endemic to the lake. Close examination, however, suggests a somewhat different picture. Consider each element of the fauna *seriatim.*

Of the ostracods, *Mytilocypris splendida* (Chapman) is clearly widespread; it also occurs, for example, in many salt lakes in western Victoria (De Deckker, 1983). *Reticypris kurdimurka* De Deckker, although originally described from material collected from Lake Eyre North, is also known to occur in Lake Annean, near Meekathara, Western Australia, some 2000 km to the west of Lake Eyre (De Deckker, 1981). *Trigonocypris globulosa* De Deckker is a species of northern and central Australia; it has, for example, been found at Lake Buchanan, Queensland, and in a salt lake in the northwestern corner of New South Wales (De Deckker, 1978). The new genus of the Mytilocypridini, likewise, has a mainly northern and central distribution according to De Deckker (personal communication), and is in fact the same taxon recorded by Geddes *et al.* (1981) from Lake Annean in Western Australia. The species of *Heterocypris,* whilst apparently new, has already been recognised by De Deckker (personal communication) from other localities in central Australia (e.g. Lake Napperby). Amongst all the ostracods, therefore, it is only the new species of *Diacypris* which can presently be regarded in the current state of our knowledge of ostracod taxonomy as endemic to Lake Eyre South; all other ostracods occur well beyond the Lake Eyre catchment.

Of the copepods, *Microcyclops platypus* (Kiefer) is known from several localities in southwestern Western Australia (Geddes *et al.,* 1981). Similarly, both of the other species within the genus are known to occur elsewhere (Morton, unpublished data).

The identity of the species of *Daphniopsis* (a cladoceran) is difficult to determine because only a single adult specimen was found; all other material was ephippial. The extent to which ephippia of *Daphniopsis* are species specific remains uncertain, although there is good evidence to suggest that they are (Kokkinn and Williams, 1987). If they are, then the species present in Lake Eyre South is definitely not *D. pusilla* Serventy, a species formerly thought to be widespread in predictably filled salt lakes in southern Australia (see discussion in Sergeev and Williams, 1983). Examination of the ephippia using scanning electron microscopy suggests that they belong to either a new species endemic to Lake Eyre South or a taxon most closely related to one found in Lake Buchanan, Queensland. A full description of ephippia of *Daphniopsis* from Lake Eyre South and from Lake Buchanan is given by Kokkinn and Williams (1987).

Moina baylyi Forró, the only other cladoceran found, on present evidence does seem to be endemic. However, using scanning electron microscopy again, the ephippia of this species, too, are similar to moinid ephippia found in Lake Buchanan, Queensland. *Moina baylyi,* likewise, therefore, may eventually prove to be more widespread than its present distribution suggests. Note that the moinids from Lake Eyre collected by Bayly (1976) were originally thought to be *M. mongolica* Daday, an Asian species. It is now known that this identification (by N. N. Smirnov) is erroneous, and the species involved is new (Forró, 1985). The taxonomic position of *Moina salina* Daday, another halobiontic moinid and said to occur in Australia, remains confused (cf. Negrea, 1984, and Forró, 1985). Whatever the case, huge populations of *M. baylyi* built up in Lake Eyre South during the period of inundation. To all intents, it was the only cladoceran present in the lake.

With regard to the brine shrimp, this was initially thought to be similar to an undescribed species known from the Yorke Peninsula of South Australia (M. C. Geddes, personal communication). Subsequent examination showed that it was *Parartemia minuta* Geddes, a species previously known from Lake Buchanan in Queensland (M. C. Geddes, personal communication).

All remaining taxa recorded (Fig. 6) are either impossible to identify to species level in the current state of our taxonomic knowledge of the group involved (the larvae of *Berosus* and the ephydrid), or are clearly very widespread species in the salt lakes of southern Australia or elsewhere (*Craterocephalus eyresii* (Steindachner) (a fish), *Tanytarsus barbitarsis* Freeman (a chironomid), and *Brachionus plicatilis* Müller (a rotifer)).

Of the total 17 or 18 taxa recorded from Lake Eyre South, therefore, only two (*Moina baylyi,* and *Diacypris* nov.sp.) can be regarded unequivocally as restricted to the lake in the present state of our knowledge. It is possible that this is really the case. It is also possible, however, and, indeed, considered more likely, that these species, if at all restricted in their distributions, are endemic to the *region* rather than to Lake Eyre itself, and will be found to occur in the numerous small pools associated with the creeks which drain into Lake Eyre. Such saline pools are likely to contain water much more regularly than does the lake, and thus would provide a series of saline water-bodies in the region of a sort in which evolution could take place and which could provide refuges during the long periods of desiccation experienced by Lake Eyre, as indicated earlier in our general remarks. These pools, many inaccessible, have not yet been thoroughly investigated, but in a series of them located along the Cooper Creek (9 localities in all) salinities ranged from 7.3‰ to 303‰. Unfortunately, the only faunal material collected consisted of the eggs of *Parartemia,* cladoceran ephippia, and some larvae of *Tanytarsus barbitarsis.* The collections were made by Mr. F. Badman on our behalf in April and June 1985 (at which time Lake Eyre had been dry for some months).

It is also possible, of course, given the extremely poor state of our knowledge concerning the fauna of the episodic salt lakes in the very dry interior of central and northern Australia (no lake in this region has been thoroughly investigated apart from Lake Eyre), that the two taxa apparently endemic to Lake Eyre South will eventually prove, like the other species present, to be widespread forms.

It appears, then, that a first glance at the faunal list for Lake Eyere South may *not* provide an accurate picture of the degree of endemicity prevailing. Most species are indeed widespread. Only a few are apparently endemic, and even these may turn out to be widespread on further investigation. This view is sustained by a consideration of the fauna observed by Bayly (1976) in Lake Eyre (South and North) during the 1974–75 filling. Althought his data overall are less comprehensive than those recorded in 1984, he did record some species not found by us, viz. *Boeckella trarticulata* (Thomson), *Apocyclops dengizicus* (Lepeschkin), *Hexarthra fennica* (Levander), and three species of *Diacypris.* None of these is endemic to the lake or the region; most are best regarded as widely occurring halophiles and halobionts.

On balance, the evidence suggests that the assumption concerning the relative unimportance of episodically filled salt lakes as evolutionary loci is correct: unpredictably filled lakes are dominated – if not entirely populated – by widespread forms.

What can now be said about the relative numbers of species in episodically and predictably filled salt lakes? Do episodically filled salt lakes have fewer species as suggested by De Deckker (1983)? Before addressing this question, an important point needing consideration is the extent to which the results from Lake Eyre South can be compared with results from predictably filled salt lakes. Clearly, comparison with a set of data from many predictably filled salt lakes examined once is scarcely justifiable; likewise, comparison with several salt lakes examined as regularly as Lake Eyre South is scarcely justifiable. The most acceptable comparison is obviously with one salt lake examined in a manner similar to that of Lake Eyre South. A comparison of this sort can be made with Lake Cantara South, South Australia. This lake has been investigated in some detail over several seasons by De Deckker and Geddes (1981) and by one of us (W.D.W.; unpublished). It is typical of other salt lakes in the vicinity. Its fauna is listed in Table 2.

As can be seen by comparing the lists of the fauna in Table 2 and Fig. 6, approximately equal numbers of species have been recorded from the two lakes. It

Table 2. Fauna of Lake Cantara South, South Australia. Data from De Deckker and Geddes (1980) and Williams (unpublished).

Coxiella sp.
Parartemia cylindrifera Linder
Platycypris baueri Herbst
Diacypris compacta (Herbst)
D. dietzi (Herbst)
D. whitei (Herbst)
D. sp. nov. 1
Reticypris sp. nov. 1
Australocypris hypersalina De Deckker
Calamoecia salina (Nicholls)
C. clitellata Bayly
Microcyclops sp.
Daphniopsis sp.
Haloniscus searlei Chilton

seems, then, that this sort of comparison at least does not support the suggestion that episodically filled salt lakes have fewer species than predictably filled ones. It may be noted, however, that a wider comparison between the number of species found in Lake Eyre South and predictably filled salt lakes in all regions where such lakes occur in Australia (see Williams, 1984, for documentation of the supporting literature) provides a different answer: more species are known from the predictably filled lakes. For example, a comparison of this sort between Lake Eyre South and all of the lakes in the vicinity of Lake Cantara South gives an approximate ratio of 18:37. But this twofold difference could disappear if data were available for more localities in the vicinity of Lake Eyre and these data too were summed. For the present, all that can be said is that there is no firm evidence to support the suggestion that episodically filled salt lakes have fewer species than predictably filled ones.

The main purpose of this paper, as indicated, is to use the data to examine the assumption that episodically filled salt lakes are unimportant as evolutionary loci – as indicated by the presence of many widely dispersed species and few endemics. Having done that, however, some brief comments on certain other features of the data are apposite. In this regard, special interest attaches to the general nature of differences between the fauna of Lake Eyre South and that of more regularly filled salt lakes in southern Australia, and to the pattern of succession which occurred in Lake Eyre South as it dried.

Concerning the general nature of differences, several points are obvious. There is a complete absence in Lake Eyre of species which overcome the dry period as adults, viz. *Coxiella* spp. and *Haloniscus searlei* Chilton. Both of these taxa are abundant and widespread in the salt lakes of southern Australia. Lake Eyre also lacks calanoid copepods, species of which (*Calamoecia salina* (Nicholls) and *C. clitellata* Bayly) are ubiquitous and abundant within most salt lakes of southern Australia. The absence of calanoids from Lake Eyre is all the more noteworthy in that freshwater calanoids certainly do occur in the region; *Calamoecia zeidleri* Bayly, recently described by Bayly (1984), occurs in a number of standing freshwater bodies near Oodnadatta and Lake Eyre. Explanation probably lies in the fact that *Calamoecia* has poor powers of dispersal (Maly, 1984), and, typically, freshwater species of the genus inhabit permanent waters (Bayly, 1978). Finally, as noted previously by Bayly (1976) in connection with his observations of events in 1974, the absence of *Australocypris,* which commonly co-exists with species of *Diacypris* in southern salt lakes lacking fish, is noteworthy.

Patterns of succession were not well-defined. A few species are clearly tolerant to only relatively low salinities and were present during the first month or two of the lake's existence (*Heterocypris, Brachionus plicatilis, Microcyclops* sp.a.). Others occurred during almost all of the time water was present in the lake basin. Of these, especially important were *Craterocephalus eyresii, Tanytarsus barbitarsis, Moina baylyi,* and *Diacypris* sp.nov. There may have been a correlation between the presence of *Parartemia minuta* and the (apparent) absence of fish in the first few months after water appeared and towards the end of the time when free water was present. The presence of fish may also have played an important role in determining the presence of other species, as suggested by Bayly (1976).

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