Seasonal Fauna of Ephemeral Saline Lakes near the Coorong Lagoon, South Australia

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Abstract

Twenty-three ephemeral athalassic saline lakes near the Coorong lagoon, South Australia, were sampled monthly over 10 months in 1978–79. The numbers of species found were 16 ostracods, nine copepods, two anostracans, two cladocerans, one amphipod, one isopod, one gastropod, one nematode, one polychaete, two foraminiferans, one rotifer, and in addition ciliates, dipteran larvae, aquatic grasses and a charophyte.

Ecological notes and data on salinity range for each species are presented. The affinities of the fauna and the means by which the species persist when a lake dries out are discussed.

Introduction

Most studies of Australian salt-lake faunas (Bayly and Williams 1966; Bayly 1970; Geddes and Brock 1978) are based on samples taken at one time. Geddes' (1976) study of the seasonal fauna of 16 ephemeral saline lakes in western Victoria provided information on the richness of fauna in lakes of various salinities and on the salinity tolerance of the species. Similar studies in other parts of the world are few and incomplete, concentrating on particular animal groups (Hartland-Rowe 1966; Scudder 1969), or not making full identifications of the microfauna (Rawson and Moore 1944; Hammer *et al.* 1975). Several reviews consider salt-lake faunas and comment on salinity tolerance (Beadle 1943, 1959; Löffler 1961; Macan 1963; Bayly 1972; Williams 1978).

In the present study collections were made from 23 ephemeral saline lakes in south-eastern South Australia (Fig. 1). Some occupy depressions around Lake Albert, but most lie in a corridor between two semiconsolidated calcrete-encrusted sand barriers, parallel to the south-eastern coast. These barriers were stranded during Pleistocene glacio-eustatic sea-level oscillations and represent high sea-level stillstands of the last interglacial period (von der Borch 1976). The Coorong lagoon occupies much of the interdune area and is connected to the sea via the mouth of the River Murray. One lake (Fig. 1, locality 18) is connected to the Coorong lagoon in winter. The other lakes in depressions adjacent to, or south of, the lagoon are filled either by rainfall or when the unconfined aquifer rises above the lake beds in the wet winter months. In summer these lakes dry due to evaporation and the lowering of the water table. Most lakes near the Coorong lagoon are at a maximum of 1 m above mean sea level, and were connected to the Coorong and hence the sea a few thousand years ago. Underlying fresh and saline ground waters control the salinity and chemical composition of the lakes (von der Borch 1976). Lakes of a range of salinities were selected but, in general, this series is less saline than that studied by Geddes (1976).

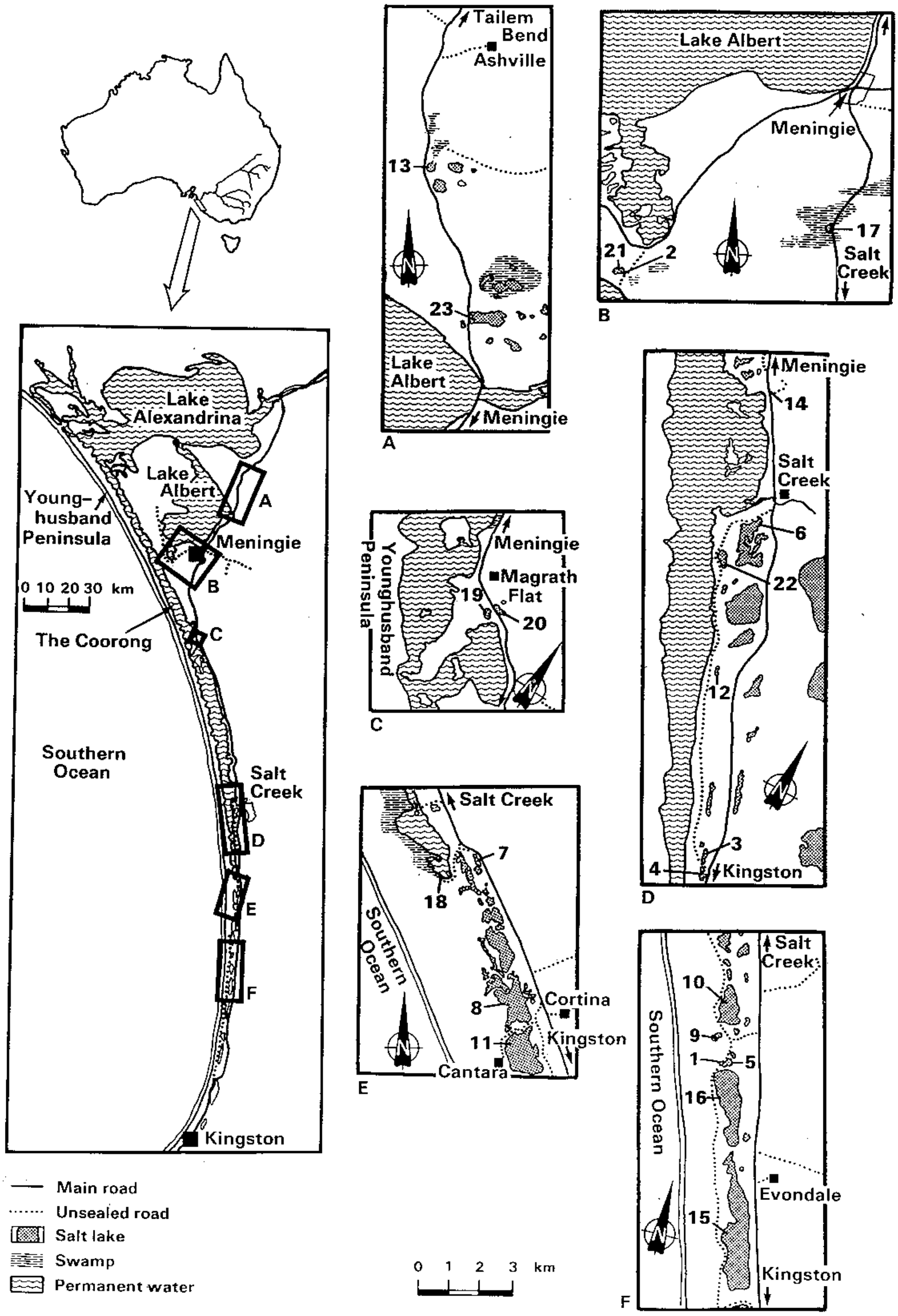

Fig. 1. Maps showing the location of the 23 lakes studied.

This study aims to provide further information on the autecology of saline-lake animals, especially the little-known ostracods. The knowledge of taxonomy of microcrustaceans inhabiting saline lakes has improved in recent years and in the present study all crustaceans have been identified to species level. It is of particular interest to investigate the composition and derivation of the fauna of lakes in close proximity to the sea and yet with athalassic characteristics such as ephemerality and seasonal variation in salinity. The lakes span a wide salinity range and so the relationship between salinity and species richness can be considered.

Methods

Physicochemical Aspects

Data on rainfall at Meningie and Kingston and temperature at Meningie and Murray Bridge were provided by the Australian Bureau of Meteorology. Water temperature was measured, generally between 0830–1500 h, with a mercury bulb thermometer.

Salinity expressed as total dissolved solids (TDS) was calculated from conductivity according to Williams (1966). Highly saline waters were diluted to a conductivity (K_{18}) of less than 0·10 S cm^{-1} and the calculated TDS multiplied by the dilution factor. On one occasion (4.xi.1978) pH measurements were made on water samples in the laboratory.

Faunal Aspects

The 23 localities were sampled approximately monthly between June 1978 and February 1979; some were also sampled in May 1978. Some samples were collected using a circular plankton net of mesh size 158 μm, but most were collected using a rectangular net of 210-μm mesh mounted on sleds. This net was towed for about 10 m and filtered about 1 m^3 of lake water. From observation of zooplankton volume, each collection was given a zooplankton abundance ranking on a scale of 1 to 5 with 1 representing < 5 ml of settled zooplankton; 2, 5–10 ml; 3, 10–20 ml; 4, 20–40 ml; and 5, > 40 ml.

Zooplankton species were recorded numerically as dominant (over 40% of total zooplankters), subdominant (10–40%), common (5–10%), uncommon (1–5%) or scarce (< 1%). For each species notes were made on the size, developmental stage, presence and nature of eggs. Animals that were not true zooplankters were often collected. They were identified and their developmental stage was noted but no information on abundance was recorded. Aquatic macrophytes also were noted.

Mud samples were collected from dry lakes in February 1979. In the laboratory, these were placed in distilled water. Salinity was monitored and at various intervals the species present and their stages of development noted.

Results

Physicochemical Aspects

All lakes were dry or contained shallow pools of brine in March and April 1978. Rains in mid May and between 28 May and 12 June (Fig. 2) provided the first free water for some lakes and resulted in considerable dilution of others. Rainfall exceeded evaporation during the winter and early spring and lakes remained full. In October the lakes began to dry but heavy November rainfall caused some near-dry lakes to fill again.

Fig. 3 shows the monthly rainfalls at Kingston and Meningie for 1978–79, compared with the long-term averages. Total rainfall at Kingston was close to average but March, April and May were drier than average and June and November wetter. At Meningie, rainfall was above average, particularly in July.

Daily maximum and minimum air temperatures at Murray Bridge, north of Meningie, are plotted in Fig. 4. Minimum water temperatures occur earlier than 0830 h, and actual minima probably were similar to minimum air temperature. Table 1 shows that maximum water temperatures may be significantly higher than maximum air temperatures, especially in the warmer months of the year. In shallow margins of lakes (or in near-dry lakes) temperatures may be even higher, with 32 °C recorded in water 5 cm deep on 27 November 1978 (air temperature 23 °C). On 24 and 25 November, air temperatures reached 33 and 37 °C and water temperatures would have approached 40 °C.

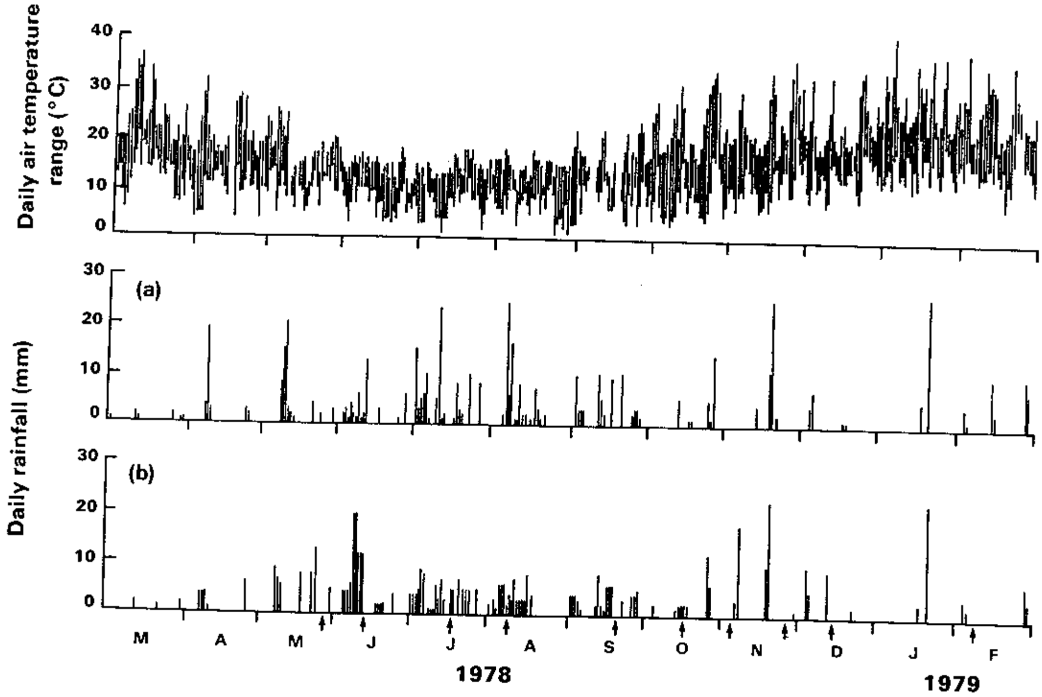

Fig. 2. Daily air temperature ranges at Meningie and daily rainfall recorded at Meningie (*a*) and Kingston (*b*) for the period March 1978–February 1979. Arrows indicate sampling dates. (Gaps in the temperature diagram are days for which no temperature was recorded.)

Seasonal fluctuations in salinity at each locality are plotted in Fig. 5. The salinity directly after filling (in May or June) was lower than subsequent salinities in some lakes

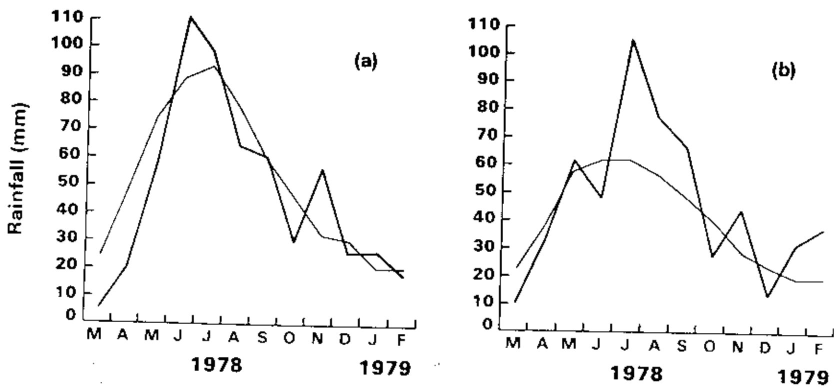

Fig. 3. Monthly rainfall from March 1978 until February 1979 (———) and long-term mean monthly rainfall (———) at Kingston (*a*) and Meningie (*b*).

(e.g. localities 3, 5, 9, 10, 15) and higher in others (e.g. localities 7, 12, 14, 22). The former group is entirely of low to moderate salinities while the latter includes lakes across the salinity spectrum. By July, salinities had stabilized and in most lakes remained fairly constant through August and September (the mean salinity for this 3-

month period has been used to order the lakes from 1 to 23 in ascending salinity). In October to December, salinities increased. In the lakes of higher salinity the waters approached salt saturation and salt crusts formed. In the less saline lakes, salinity did not rise so high, presumably because salts percolated through the lake floor with the descending water table.

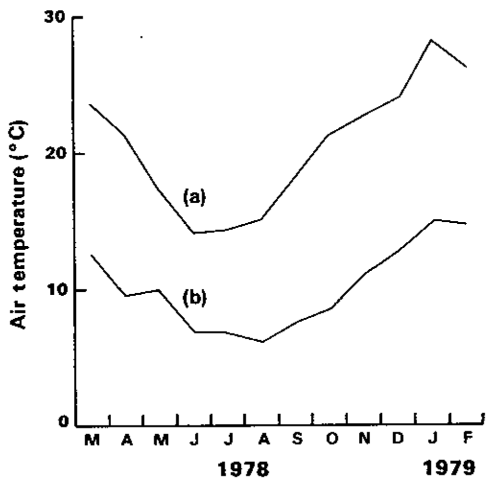

Fig. 4. Monthly average maximum (*a*) and minimum (*b*) air temperatures recorded at Murray Bridge for the period March 1978–February 1979.

Williams and Buckney (1976) analysed seven of the present localities and found ionic dominances to be

$$Na^+ > Mg^{2+} > Ca^{2+} \geqslant K^+$$

among the cations and

$$Cl^- \gg SO_4^{2-} > HCO_3^-$$

among the anions. Sodium accounted for 72–84% of the cation equivalent percentage,

Table 1. Comparison of maximum and minimum air and lake-water temperatures on 5 days when lakes were sampled

	Date of sampling				
	17.vii.1978	8.viii.1978	3.xi.1978	27.xi.1978	15.xii.1978
Water temperature (°C)					
Maximum	13	13	29	27	29
Minimum[A]	10	7	17[B]	16	20[B]
Air temperature (°C)					
Maximum	13	10	27	23	24
Minimum	10	3	9	16	12

[A]These water temperatures were recorded at 0830 h and are probably somewhat higher than true daily minimum.
[B]Taken rather later than 0830 h.

magnesium 10–23%, calcium 1–7% and potassium 1–3%. Chloride always accounted for more than 90% of the equivalent percentage of anions. The Coorong itself has high Mg^{2+} and Ca^{2+} concentrations (similar to seawater); these are lower in the lakes in the Coorong–Kingston chain, and there is less Mg^{2+} and Ca^{2+} again in the adjacent lakes (von der Borch 1965; Williams and Buckney 1976). These variations in ionic proportions are fairly minor and certainly the lakes are within the ranges of ionic proportions of those included in Bayly and Williams (1966) and so would fit the relationship between conductivity and TDS derived by Williams (1966).

The pH of the lakes measured on 4 November 1978 were all between 7·5 and 9·9. The extreme pH values were recorded in isolated lakes. The lakes south of the Coorong lagoon were between 8·0 and 9·4. This is consistent with von der Borch's (1965) finding that pH of lakes within the Coorong chain (i.e. south of the Coorong lagoon) ranged to 9·1, compared with 10·2 in isolated lakes.

Biological Aspects

The floral and faunal composition of the lakes is represented in Fig. 5. The aquatic grasses *Ruppia* sp. and *Lepilaena* sp. and the alga *Lamprothamnium papulosum* formed dense beds in most of the lakes. This is a major difference between the present lakes and those studied by Geddes (1976) which had no macrophytes. The fauna was dominated by crustaceans (Fig. 6). Twenty-eight species, 16 of them ostracods, were recorded. The standing crops of zooplankton generally were high in winter and early spring, being more than 20 ml m^{-3} in many localities, and fell as the lakes began to dry and salinity rose.

In the less-saline lakes (minimum salinities of about 30‰ or less), the faunal assemblage consisted of *Parartemia cylindrifera*, *Daphniopsis pusilla*, *Boeckella triarticulata*, *Calamoecia clitellata*, *Microcyclops dengizicus*, *Microcyclops* sp. 1, *Microcyclops* sp. 2, *Australocypris robusta*, *Australocypris* sp. nov. 1, *Diacypris* sp. nov. 1, *Mytilocypris ambiguosa*, *M. praenuncia* and *Austrochiltonia australis*. Some species (*Boeckella triarticulata*, *Limnocythere* sp., *Austrochiltonia australis*) may be considered to be salt-tolerant freshwater forms but most are truly halophilic. At salinities above 35‰, the faunal assemblage included *Parartemia zietziana*, *Diacypris fodiens*, *D. whitei* and *Australocypris rectangularis*. Other species which occurred across wide salinity ranges included *Microcyclops* sp. 3, *Mesochra baylyi*, *Diacypris compacta*, *D. dietzi*, *Diacypris* sp. nov. 2, *Reticypris herbsti*, *Reticypris* sp. nov. 1, *Australocypris hypersalina*, *Platycypris baueri* and *Haloniscus searlei*.

Fig. 6 details the salinities at which collections of the various species were made, and indicates collections where the species was dominant, subdominant or common and those where it was uncommon or scarce. Although collections of a species may be made at extreme salinities, when changes in zooplankton abundance and dominance ranking are considered (Fig. 5) the records at extreme salinity may represent survival of only a very small proportion of the population.

Fig. 7 shows the number of co-occurring species (species richness) in the plankton and epibenthos of the lakes in late winter and early summer in relation to prevailing salinities. This count included anostracans, cladocerans, copepods, ostracods, amphipods, isopods and gastropods but not benthic forms such as nematodes, foraminiferans and polychaetes or nannoplanktonic forms such as ciliates. Species richness generally was high with up to 13 co-occurring species in winter. Variation in the number of species in lakes evidently is not attributable to salinity alone. Thus at salinities of 16 and 27‰ species richness was only 7 and 8. The lower species richness (7 at 16‰) was recorded in the most turbid of the lakes studied. As salinity rises during the drying phase of a lake, the species richness may be maintained as most of the fauna is quite salt tolerant. In late spring and early summer species richness was as high as 11, 8 and 7 at 96, 104 and 130‰, respectively. Above 150‰ species richness fell

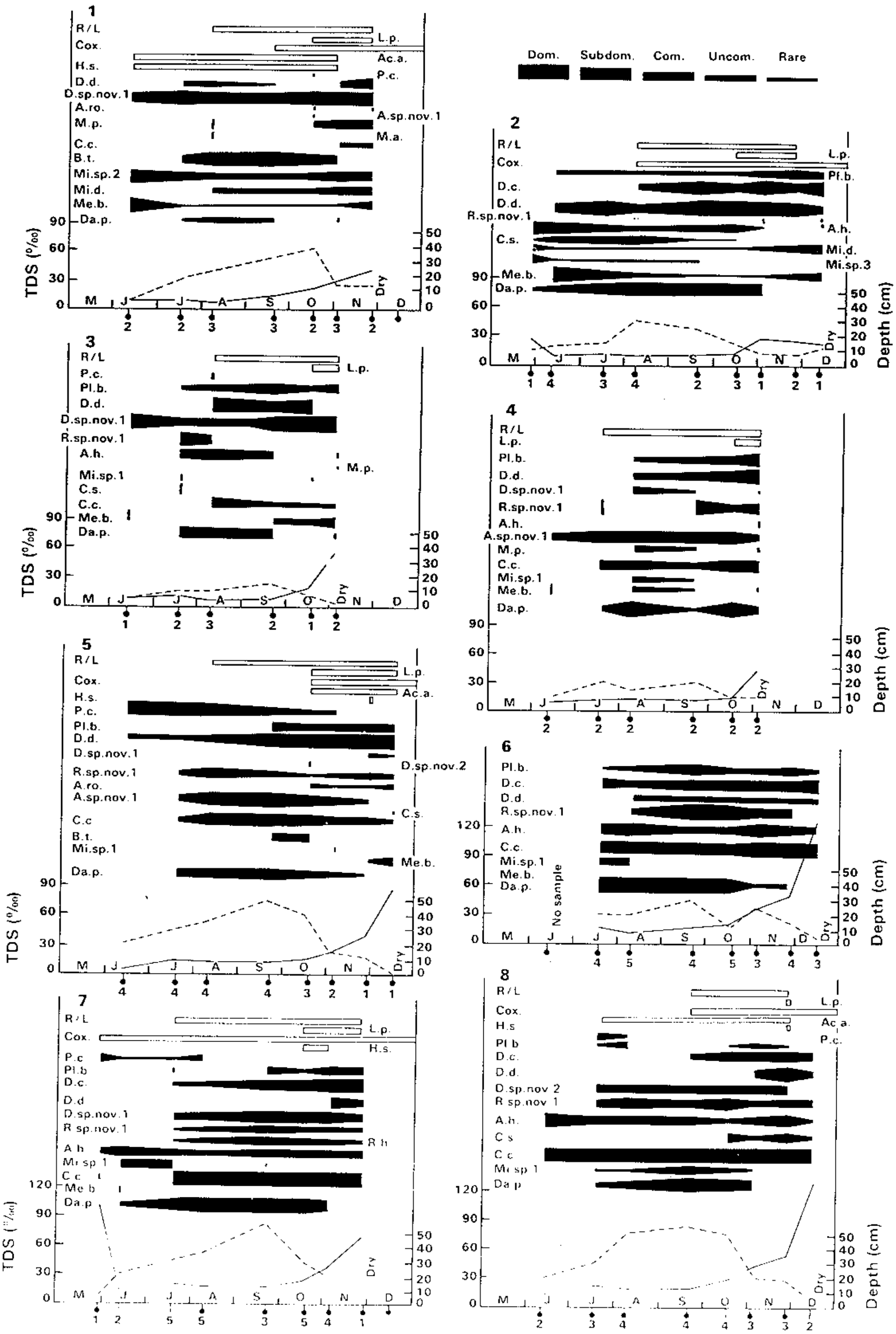

Fig. 5.

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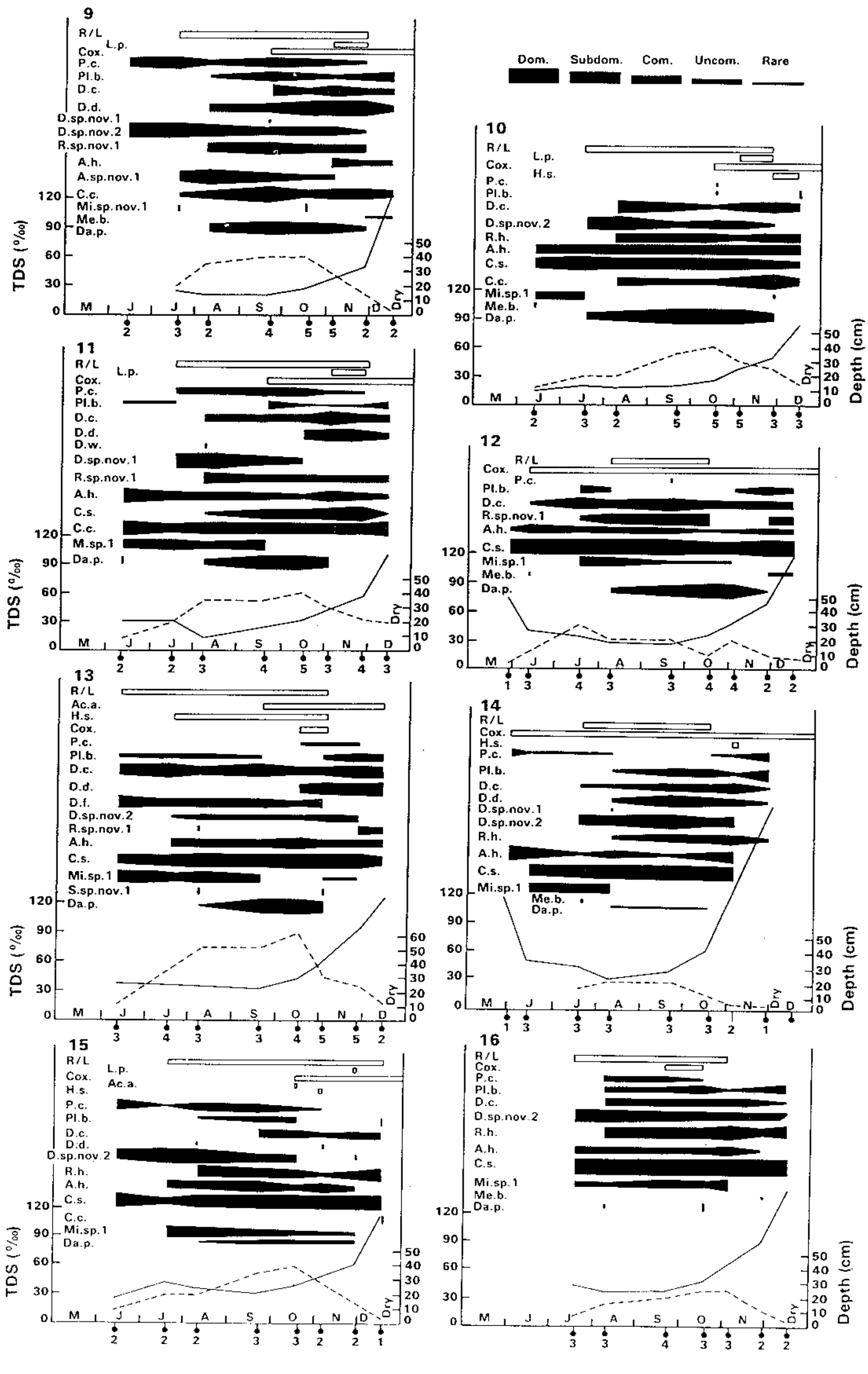
Fig. 5. contd


9
10
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Dom.
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Ac.a.
P.c.
Pl.b.
D.c.
D.d.
D.f.
D.w.
D.sp.nov.1
D.sp.nov.2
R.sp.nov.1
R.h.
A.h.
A.sp.nov.1
C.c.
C.s.
Mi.sp.nov.1
Mi.sp.1
M.sp.1
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Fig. 5. contd

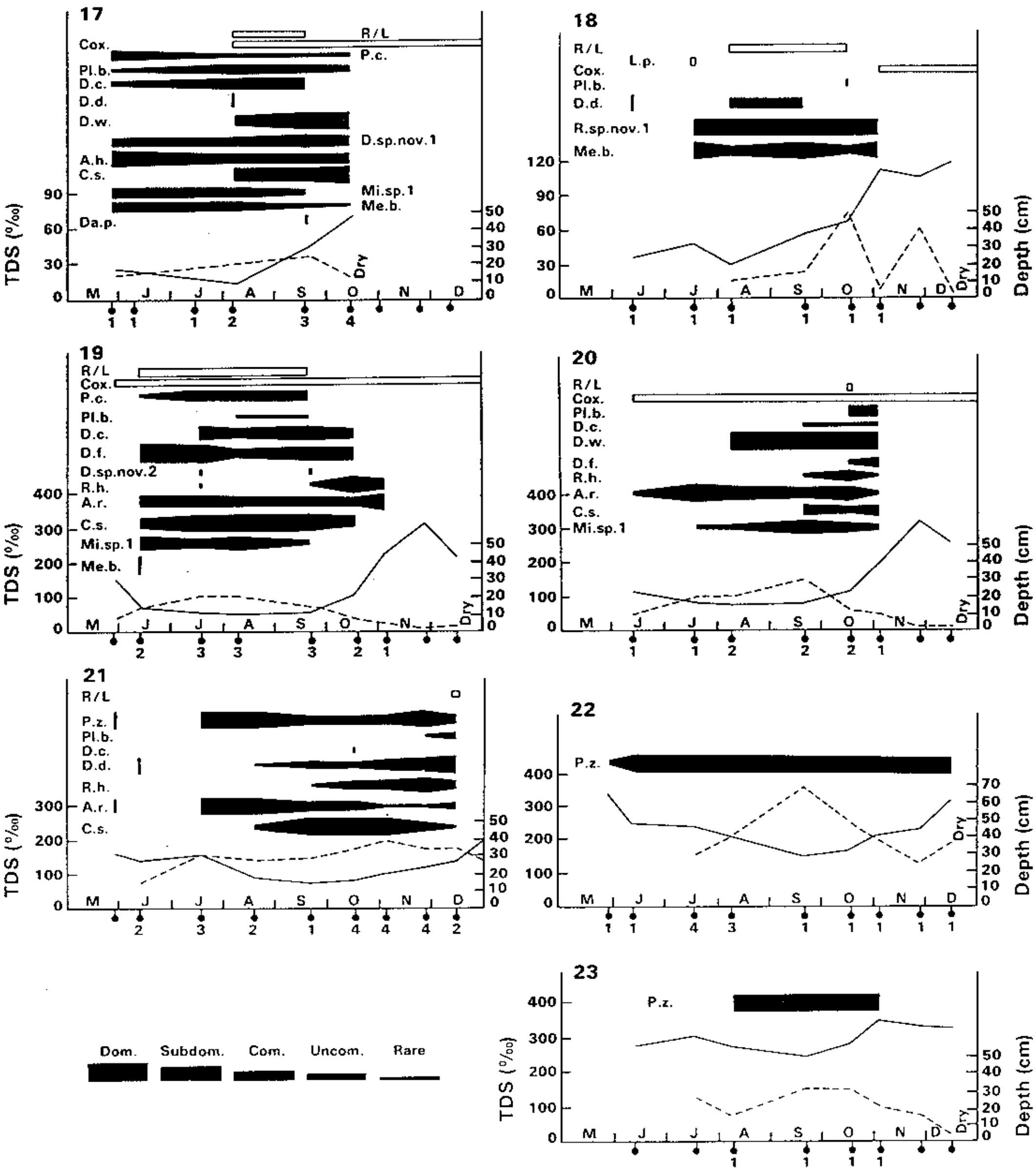

Fig. 5. Seasonal variations in the salinity (———), water level (------), and floral and faunal compositions of localities 1–23. The horizontal black bars indicate the presence of the species and the appropriate thickness relates to species dominance (Dom., dominant; subdom., subdominant; com., common; uncom., uncommon; rare). The horizontal white rectangles indicate presence of species for which abundance was not estimated. At the bottom of each diagram, solid black circles indicate dates of sampling and the numbers below them represent abundance indices (5, > 40 ml of settled zooplankton; 4, 40–20 ml; 3, 20–10 ml; 2, 10–5 ml; 1, < 5 ml). Abbreviations of species: R/L, *Ruppia*/*Lepilaena*; L.p., *Lamprothamnium papulosum*; Cox., *Coxiella striata*; Ac.a., *Australochiltonia australis*; H.s., *Haloniscus searlei*; P.c., *Parartemia cylindrifera*; P.z., *P. zietziana*; Lim.sp., *Limnocythere* sp.; Pl.b., *Platycypris baueri*; D.c., *Diacypris compacta*; D.d., *D. dietzi*; D.f., *D. fodiens*; D.w., *D. whitei*; D.sp.nov.1 and 2, *Diacypris* sp. nov. 1 and 2; R.h., *Reticypris herbsti*; R.sp.nov.1, *Reticypris* sp. nov. 1; A.ro., *Australocypris robusta*; A.h., *A. hypersalina*; A.sp.nov.1, *Australocypris* sp. nov. 1; A.r., *A. rectangularis*; M.p., *Mytilocypris praenuncia*; M.a., *M. ambiguosa*; C.c., *Calamoecia clitellata*; C.s., *C. salina*; B.t., *Boeckella triarticulata*; Mi.d., *Microcyclops dengizicus*; Mi.sp.1, 2 and 3, *Microcyclops* sp. 1, 2 and 3; Me.b., *Mesochra baylyi*; S.sp.nov.1, *Schizopera* sp. nov. 1; Da.p., *Daphniopsis pusilla*.

sharply with only the brine shrimp *P. zietziana* at salinities above 200‰. Further, zooplankton standing crop (Fig. 5) can be high, up to 120‰, with abundance indices of 4 and 5 recorded at localities 4 (96‰) and 21 (114‰).

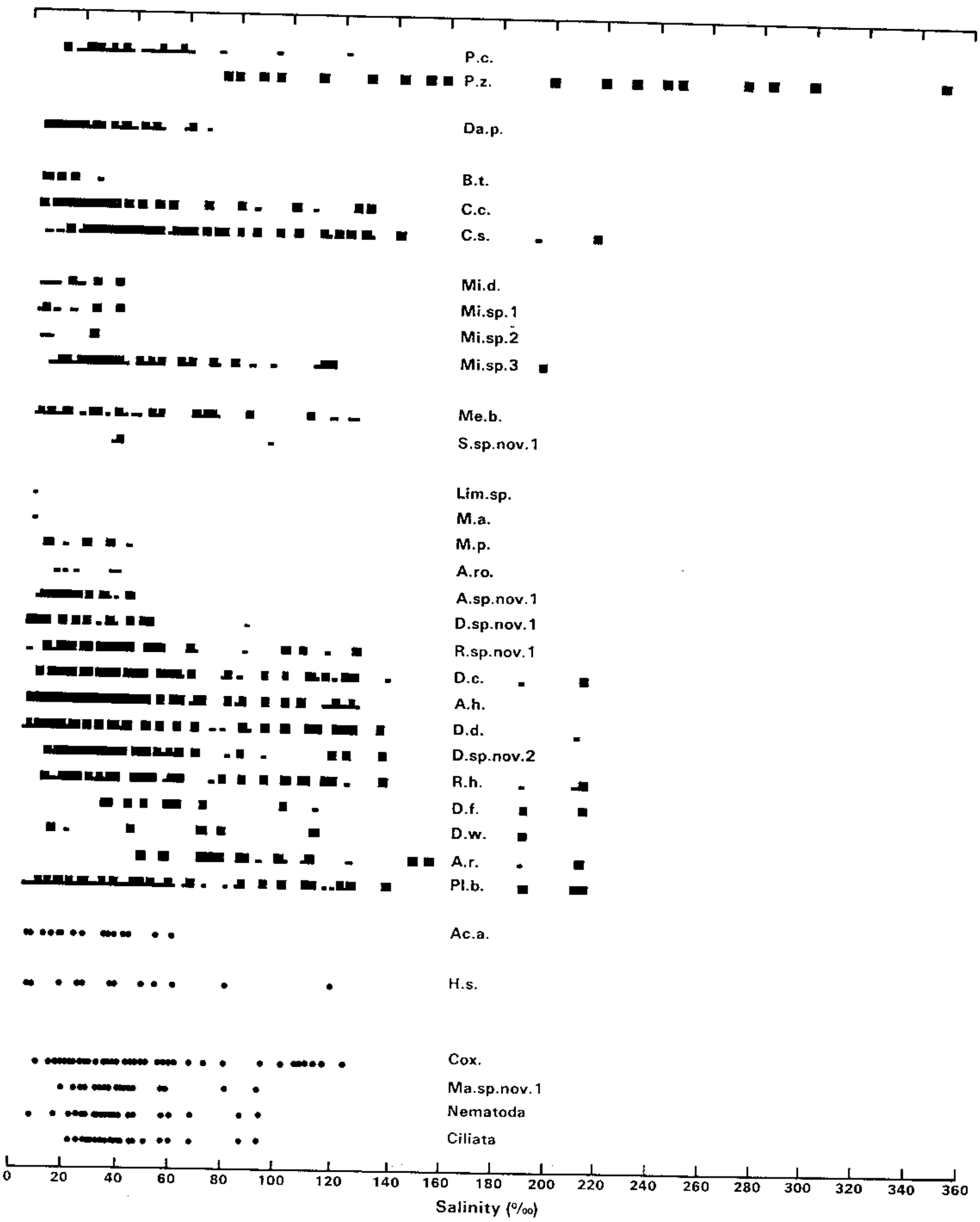

Fig. 6. Salinities at which various species were recorded. Low rectangles indicate when the species were rare or uncommon in the samples; squares indicate when species were common, subdominant or dominant. Solid circles indicate the presence of species for which abundance was not estimated. Abbreviations as for Fig. 5; Ma.sp.nov.1, *Manayunkia* sp. nov. 1.

The fauna which emerged from mud samples after the addition of distilled water is shown in Table 2. Mud samples were from localities 1, 2, 5, 8–10, 12, 13, 17 and a small pool near locality 22, and salinities ranged from 22 to 95‰. This list is incomplete when compared with the fauna of the lakes and it seems that proper conditions for emergence of many members of the fauna were not provided. It might be noted that many of the muds in the experiment became anoxic. Several small members (ciliates, nematodes) of the salt-lake fauna not in field samples were seen in the laboratory experiments.

Each species now is discussed with reference to Figs 5 and 6 and Table 2.

Flora

The charophyte *Lamprothamnium papulosum* (Wallroth) and the aquatic grasses *Ruppia* and *Lepilaena* spp. were commonly encountered. *L. papulosum* was recorded in localities 1–5, 7–11 and 14–18. It was absent from localities 6 and 12 which were highly turbid, and from the most saline lakes. Zygotes can germinate in fresh water and seawater but not in one and a half or twice seawater salinity (Burne *et al.* 1980) and this would explain the absence of *L. papulosum* from localities 19–23. *L. papulosum* appeared later than *Ruppia* sp. and *Lepilaena* sp., consistent with the observation that this alga requires a higher temperature for germination (Lucas and Womersley 1971). The habit of *L. papulosum* varied extensively with salinity and water depth. The highest salinity recorded for healthy specimens was 82‰. Often, as water level dropped, the charophytes were either 'burned' or dried. They seemed to survive longer if shaded (e.g. by *Melaleuca* sp. trees).

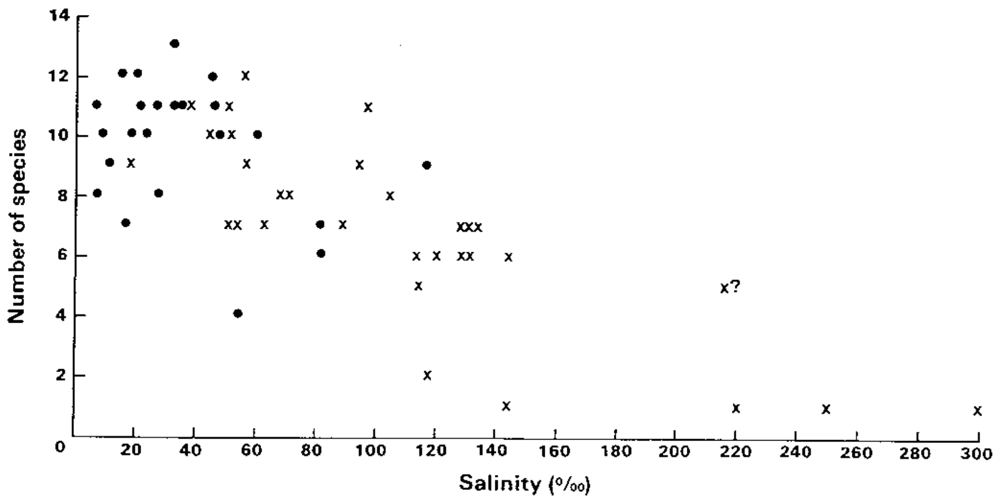

Fig. 7. Species richness *v.* salinity for all samples collected in late winter (20.ix.1978, ●) and early summer (27.xi. and 15.xii.1978, ×). Validity of the point ×? is questionable as most individuals in this collection were moribund. (Species richness includes anostracan, cladoceran, copepod, ostracod, amphipod, isopod and gastropod species.)

The vegetative forms of the aquatic grasses *Ruppia* and *Lepilaena* spp. are indistinct and considered together here as *Ruppia*/*Lepilaena*. Aquatic grass was present in localities 1–19 with dense beds of healthy grass recorded from 6·2 to about 50–60‰. The upper salinity limit was difficult to establish as the plants gradually succumbed to rising salinities and desiccation. Dry lakes were covered with dense beds of brown and white grass. Two very high records of *Ruppia*/*Lepilaena* were at localities 20 and 21 where a few new shoots of grass were seen at over 100‰ in October and December, respectively. Further information on halophilic macrophytes in some of these lakes is provided by Brock (1979).

Fauna

Anostraca

Two species of *Parartemia* were collected: *Parartemia cylindrifera* Linder and *Parartemia zietziana* Sayce. *P. cylindrifera* occurred in most localities up to locality 19, although previously known only from the type locality in Western Australia (Linder 1941). The record of *Parartemia* sp. by Geddes and Brock (1978) was, in fact, *P. cylindrifera*. *P. zietziana* occurred in the three most saline lakes; it is the common brine shrimp in south-eastern Australia (Geddes 1976, 1981).

Table 2. Fauna and flora emerging from mud samples in laboratory experiments after distilled water had been added

Species	Stage observed	Salinity range of emergence (‰)	Salinity range observed (‰)	Time until first active specimens observed (days)
Fauna				
Ciliata	Adult	27–95	22–95	1
Foraminifera				
Elphidium sp.	Adult	25–58	22–58	1
Nematoda	?Adult	34–95	22–95	1
Polychaeta				
Manayunkia sp. nov. 1	Adult	27–95	27–95	1
Gastropoda				
Coxiella striata	Adult	58–95	27–95	0[A]
Crustacea				
Calamoecia sp.	Nauplius	27–42	27–42	10
Mesochra baylyi	Adult	27	27–34	3[B]
Australocypris sp.	Nauplius	25–51	22–51	8
Platycypris baueri	Nauplius	32	32	15
Diacypris sp.	Nauplius	25–51	22–51	8
Haloniscus searlei	Adult and juvenile	27–34	27–34	0[A]
Flora				
Ruppia sp. and/or *Lepilaena* sp.	Shoot	22–42	22–42	17
Lamprothamnium papulosum	Shoot	28	28	17

[A]Seen moving a few hours after water had been added.
[B]Active specimens may have been overlooked on previous days as this species was not easily seen due to its brisk and rapid motion and common habit to hide.

Most populations of *P. cylindrifera* were small; generally they were ranked uncommon or scarce except those in locality 5 where the species was dominant when juvenile in July and August and in locality 9 where it was common until October. Even in these latter localities few individuals reached adulthood, as for *P. zietziana* in western Victorian lakes (Marchant and Williams 1977). In other lakes often only one or two adult individuals were collected; the reasons for the very low abundance of this species are not clear. In locality 5 nauplii hatched in June and adults were first collected in September, suggesting a development time of about 3 months (average water temperatures ~12°C). In some localities development must have been faster as adults were found in July, less than 2 months after filling. In all lakes it seemed there was only a single cohort of *P. cylindrifera* with females laying only resting eggs. In this respect this species differs from *P. zietziana* which generally produces subitaneous and resting eggs (Geddes 1976). It is also clear that *P. cylindrifera* prefers much less saline water; the salinity range was 6–123‰ and generally salinities below 50‰ were preferred.

Populations of *P. zietziana* were relatively larger, although in localities 22 and 23 the species occurred alone. In locality 21 individuals were first observed in May at 161‰; adults were present by July and nauplii were seen until November indicating that at lower winter salinities subitaneous eggs were produced. In locality 22 hatching occurred in June at 244‰ and adults were present by August. In locality 23 individuals were first observed in August at 277‰; some were already adult indicating that development had been completed in less than 1 month. Only a single cohort was observed and that persisted until November when salinity was 353‰. It appears that the present populations are more salt tolerant than those in western Victoria studied by Geddes (1976). He recorded 202‰ as the highest salinity at which individuals were first observed and 298‰ as the upper salinity tolerance; the corresponding values in the present study are 277 and 353‰. As in western Victoria, development is hastened at high salinity.

Cladocera

The only cladoceran commonly collected from the lakes was *Daphniopsis pusilla* Serventy. A single collection of *Macrothrix* sp. was made from locality 1 in September when salinity was 12·2‰. *D. pusilla* is common in salt lakes in south-eastern and south-western Australia (Bayly and Edward 1969).

D. pusilla was present in localities 1–17. It became dominant or subdominant in localities 2–13. This suggests that preferred localities are those in which winter salinities are between 9 and 30‰. Salinities at which populations were first recorded were from 12 to 36‰. Hatching of ephippial eggs seemed related to salinity rather than seasonal factors such as temperature or day-length as hatching occurred from May until November. The salinity range was 5·8–68·1‰ although few specimens were recorded at the latter salinity. In most localities populations produced subitaneous eggs during winter; no subitaneous eggs were produced at above 35‰.

The behaviour of *D. pusilla* in these lakes is similar to that in other areas (Bayly and Edward 1969; Hedley 1969; Bayly 1970; Geddes 1976) although the salinities tolerated are slightly higher. Factors such as temperature and acclimation history are probably important in determining the salinity tolerance of this species.

Copepoda

Nine copepod species were recorded in the lakes, making copepods the second most numerous group. Calanoids, cyclopoids and harpacticoids were represented.

Calanoida. The calanoids collected were *Boeckella triarticulata* Thomson, *Calamoecia clitellata* Bayly and *C. salina* (Nicholls). *B. triarticulata* was collected from locality 1 only. It appeared in July at 8·0‰, was dominant through winter, and was still common in early November at 27·1‰. This is a very high record for what is a predominantly freshwater species and exceeds the previous records of Bayly (1969) and Geddes (1976) (22 and 18·3‰, respectively). *C. clitellata* and/or *C. salina* were present in localities 1–17 and 19–21. They were absent from the Coorong lagoon, locality 18, and the most saline lakes. In most localities they became the dominant or subdominant zooplankter. *C. clitellata* was generally present in the less saline lakes (1, 3–11 and 15) and *C. salina* in the more saline (8 and 10–21; its occurrence in locality 2 may be explained by the contiguity of that small pool with the larger, deeper and saltier locality 21 where *C. salina* was the dominant zooplankter). Thus, although the physiological salinity tolerance of the two species is similar (Brand 1972), in the field they are differentially distributed with respect to salinity. A similar pattern of distribution of these two species was recorded by Geddes (1976) although there were no co-occurrences and the salinity of the lakes occupied by *C. clitellata* was somewhat higher. The restriction of *C. clitellata* to less saline localities and *C. salina* to more saline ones may be due to ecological factors such as interspecific competition. The salinity ranges of *C. clitellata* and *C. salina* were 6–132 and 7–195‰, respectively.

Cyclopoida. Four species of *Microcyclops* were collected. *Microcyclops dengizicus* (Lepeschkin) was in localities 1 and 2 at salinities ranging from 6 to 37‰. This cosmopolitan species has been collected previously in Australia from Lake Buchanan, Queensland (Bayly and Williams 1973), and is restricted to moderately saline water (Morton, personal communication). The other three species are designated *Microcyclops* sp. 1, 2 and 3. *Microcyclops* sp. 1 and 2 were each collected from one locality only: the former from locality 1 and the latter from locality 2. The salinity ranges of the species were 9–27 and 6–37‰, respectively. *Microcyclops* sp. 3 is the halobiont cyclopoid incorrectly identified as *Microcyclops arnaudi* by Bayly and Williams (1966) and Geddes (1976). It was present in localities 3–17, 19 and 20. The salinity range of *Microcyclops* sp. 3 was 6–200‰. In contrast to the calanoid copepods the initial collections of *Microcyclops* spp. generally included adult individuals, suggesting that these species can encyst at late juvenile or adult stages.

Harpacticoida. Two species of harpacticoids were collected. *Schizopera* sp. nov. 1 was in locality 13 at salinities ranging from 36 to 96‰. *Mesochra baylyi* Hamond was present in most localities up to locality 19 (excluding locality 13). It was the most persistent of the few species collected from locality 18, the southern end of the Coorong lagoon. Populations were generally small. The salinity range was 6–129‰ which is wider than 4–50‰ listed by Williams (1978). Like the *Microcyclops* species, *Mesochra baylyi* was usually adult when first collected. Laboratory hatching experiments confirmed that the species emerges as a late juvenile or adult.

Ostracoda

Sixteen species of ostracods from six genera have been collected. Of the large ostracods of the Mytilocypridini, three known species of *Australocypris* plus one new species and two species of *Mytilocypris* have been identified. The latter genus was recorded only at low salinity. Six species of *Diacypris* were identified, two of which are new. The recently described genus *Reticypris* (McKenzie 1978) was represented by two species, one of which is new. These two species were usually found on the lake floor whereas most of the other species were truly planktonic. *Platycypris baueri* was common but was never in high numbers. *Limnocythere* sp. was recorded only once. Typically a lake contained only one of the large mytilocypridinid species and several small species. The highest number of ostracods co-occurring was seven in locality 9; many lakes had five or six co-occurring ostracods. Only the two most saline lakes lacked ostracods; the lowest salinity in these was 144 and 250‰, respectively. Hatching of the various species often occurred at approximately the same time but the small species reached adulthood faster than the mytilocypridinids. The mytilocypridinids were the first to disappear as the lakes dried, indicating that their temperature and/or salinity tolerance is lower than that of some of the smaller species.

Limnocythere sp. The carapace outline of this species is very similar to that of *Limnocythere mowbrayensis* Chapman in possessing, on each valve, two laterodorsal protuberances, the posterior one being the largest. However, the lateral processes are not as prominent as in *L. mowbrayensis*, for which they are wing-like, as they do not extend, in dorsal view, past the anterior protuberance. This species was only recorded once, in locality 1 at 6‰. Valves of this species were found in the sediment of the lake suggesting that the species had occurred there previously. Although the genus *Limnocythere* is known mainly from permanent fresh waters, the record of the species mentioned above is not surprising since some species are recorded from 'brackish' waters in Europe (Klie 1938).

Mytilocypris. *Mytilocypris ambiguosa* De Deckker, and *Mytilocypris praenuncia* (Chapman) were recorded. *M. ambiguosa* was recorded only once, from locality 1 at 6‰. This is consistent with previous unpublished data and with the generally low salinity tolerance of *Mytilocypris* spp. compared with species in the allied halobiont *Australocypris*. *M. praenuncia* was more tolerant and was present in localities which reached almost 50‰. It was never found during the early stages of lake filling.

Australocypris. *Australocypris robusta* De Deckker, *Australocypris hypersalina* De Deckker, *Australocypris rectangularis* De Deckker, and *Australocypris* sp. nov. 1 were recorded. The generic affinity of *A. rectangularis* queried by De Deckker (1978) in the original description, is here validated. The new species is very similar in outline to *A. hypersalina* but females can be distinguished on the following features: both valves extend over one another in the anterodorsal area just before the hinge, and a depression occurs posterodorsally behind the hinge between the edge of the valve and the selvage which is prominent in that area (in *A. robusta*, this area is flat and forms a small pocket). The hemipenis is similar to that of *A. robusta* except that the lateral lobe is broader at the base. The thoracopoda I ventrodistal seta is almost half the length of the claw in both sexes. The shell has also a very distinctive nacreous colour.

A. robusta and *Australocypris* sp. nov. 1 have similar salinity tolerances (see Fig. 6). The highest salinity recorded for the former species was 38‰, a value much lower than that of 83·5‰ recorded in Victoria (De Deckker 1975). The high value of 132‰ for *A. robusta* recorded by Geddes (1976) is probably invalid because it was assumed by that author that all specimens of *Australocypris* collected were *A. robusta*. At salinities above 45‰, *A. hypersalina* replaced *A. robusta* and *Australocypris* sp. nov. 1 and was among the first species to appear in most lakes and nearly always remained until temperature and salinity rose as the lake dried out. The salinity range for the species was 5–131‰. Two size groups of this species were found in some lakes: large adults were present during winter and early spring when salinity and temperature were low and smaller adults (about two-thirds the size) were found in late spring when salinity and temperature were higher. The large specimens had globules of unknown composition inside the carapace whereas none were seen in the smaller ones. Occasionally the faeces of *A. hypersalina* were seen to consist almost entirely of *Calamoecia* sp. fragments.

A. rectangularis was present only in lakes of high salinity (localities 19–21). In two localities juveniles were found in June as the lakes were filling and when the salinity was 73 and 115‰; hatching must have occurred at or above these salinities. The first record of *A. rectangularis* in lake 21 was in July at 154‰. Most records of this species lie between 50 and 160‰ but one record is at 195‰ and another at 218‰ when animals were dying.

Diacypris. The six species recorded were *Diacypris compacta* (Herbst), *Diacypris* *dietzi* (Herbst), *Diacypris fodiens* (Herbst), *Diacypris whitei* (Herbst), *Diacypris* sp. nov. 1 and *Diacypris* sp. nov. 2, the taxonomy of which has recently been revised by De Deckker (1980). Species will be discussed in order of their salinity tolerance. *Diacypris* sp. nov. 1 has already been recorded twice in the literature: as Cyprinae genus C from a lake south of Robe at 36·2‰ (Bayly 1970) and as 'that species with 2 large and a few small spines on the posterior edge of the carapace, with one small spine on the anterior edge' (De Deckker 1975). Subsequently it was recorded by McKenzie (1978) as ?*Diacypris* sp. from Western Australia. The number of small spines can vary tremendously as can the size of the two posteroventral spines. The dorsal overlap of the two valves occasionally resembles a 'keel'. This feature, when present, can either be sharp or rounded. A similar variation can occur on *Diacypris* sp. nov. 2. The salinity range of *Diacypris* sp. nov. 1 is 4–52‰; a single specimen was found in lake 5 when almost dry at 88·2‰. This species was often present with *M. praenuncia* in lakes of low salinity. *D. compacta* is pale to dark green and was ubiquitous in lakes of salinities below 130‰. It can occur in very high numbers, being dominant in localities 2, 6, 7, 11 and 13. Like other *Diacypris* species, this species is an adept swimmer, and is also commonly found creeping on the halophytes. Most records lie within the range 8–131‰ with three other records of a few specimens up to 216‰ and a record at 218‰ where the specimens were very sluggish or dying. At the time the lake was nearly dry. *D. dietzi*, which is most often pale green to occasionally orange, had a basic salinity range of 4–141‰ but a few specimens were taken at 216‰. It is a very common species as it was present, at least at some stage, in 16 of the 23 lakes studied, emphasizing therefore its tolerance to a wide range of salinities and environments. A similar remark applies to *D. compacta*. *Diacypris* sp. nov. 2 is bright orange and is characterized by a triangular shape in lateral view, a dorsal keel extending from the left valve as in *Diacypris* sp. nov. 1, an occasional row of very fine denticles along the valve margins anteriorly and posteroventrally, and a rectangular lateral lobe plus a horseshoe-shaped median lobe on the hemipenis. The extent of the dorsal keel is very variable from small to large and sometimes even pointed. The salinity range of this species was 12–143‰. This species was found at most times of the year in lakes except during the drying-up phases. *D. fodiens* is the largest *Diacypris* species and is dark brown. It was collected on only 13 occasions from 33 to 195‰ (see Fig. 6). *D. whitei* is pale orange to beige, and was collected only eight times. Its salinity range was very similar to that of *D. fodiens* except that it was recorded once at 14 and 18‰ (range: 14–195‰, see Fig. 6). It was never found in the early stages of lake filling.

Reticypris. *Reticypris herbsti* McKenzie, 1978 and a new species were recorded. The carapace of *Reticypris* sp. nov. 1 is very similar to that of *R. herbsti*, but it can easily be distinguished from the latter species by the shape of the hemipenis: the outline of the lateral lobe is boot-shaped in *R. herbsti* whereas it is larger, crescent-shaped and broadest at the base where two lumps are visible on the inner side of *Reticypris* sp. nov. 1. For both species, the ornamentation of the carapace varies extensively from nearly smooth, partly smooth, to coarsely reticulated. The outline of the shell is also variable with a dorsal lap of the left valve over the right being very obvious or nearly non-existent. A ventral ridge can be seen in some specimens, especially in juveniles. *R. dedeckkeri* is considered here to be synonymous with *R. herbsti* (*R. herbsti* has priority as it was designated as the type species) as the soft anatomy, especially the taxonomically important hemipenis, of both species is very similar.

The earliest record of *Reticypris* sp. nov. 1 was in July some time after the lakes filled. The highest salinity where it was initially collected was 49‰ at locality 18;

generally initial collections were from salinities between 12 and 27‰. The average salinity tolerance for *Reticypris* sp. nov. 1 ranged between 5 and 131‰. The salinity range of *R. herbsti*, 12–141‰, extended higher than that of *Reticypris* sp. nov. 1 (with three supplementary records at 195, 216 and 218‰ where animals were scarce or dying). On Fig. 5 it is possible to see that *Reticypris* sp. nov. 1 was never dominant or subdominant in the collections at salinities above 68‰ whereas *R. herbsti* was dominant between salinities 104 and 124‰. Only in one locality (locality 7) were the two species found together and this co-existence persisted throughout the year.

Platycypris. *Platycypris baueri* Herbst was commonly encountered over the salinity range 5–130‰ with two other records at 143 and 195‰ and a third at 218‰ where the animal was found dying. It was never recorded as dominant or subdominant at salinities above 30‰ and generally only appeared later in the season. Geddes (1976), who gave a salinity range for this species of 9·3–176‰, stated that it was the first ostracod to hatch in many of the lakes he studied and that it became the dominant zooplankter in the more saline of the localities. The present series of lakes are not as saline, with high salinities being recorded only as lakes dry out, which may explain the differences between the present study and that of Geddes (1976). In localities 20 and 21, *P. baueri* appeared when the salinity was above 100‰; this value is comparable to the high hatching salinity of 125‰ reported by Geddes (1976).

Amphipoda

The amphipod *Austrochiltonia australis* (Sayce) was collected from localities 1, 5, 8, 13 and 15. Its congener *Austrochiltonia subtenuis* (Sayce) was not recorded although both species occur in South Australia and were sympatric in Lake St Clair (Bayly and Williams 1966). In locality 15, specimens were collected only once, but in the others several collections were made from June until November. The field salinity range was 6·3–62·2‰ with several records considerably exceeding the previous upper record of 25·3‰ (Bayly and Williams 1966) for *A. australis* and 37·0‰ (Lim 1964) for *A. subtenuis*. They also exceed records for the North American salt-tolerant amphipod *Hyalella azteca* which occurs in Saskatchewan at salinities up to 30‰ (Rawson and Moore 1944). In locality 1, where the population of *A. australis* was large, observations on population structure were made. In June most individuals were small; by August many individuals were adult, 9 mm in length, and breeding. In all localities the amphipods were generally found on the aquatic macrophytes. It appears that *A. australis* is able to persist in lake basins in the absence of open water. Locality 1, a very small pool, had a large population in October 1975 (Geddes and Brock 1978) and throughout 1978 and it seems unlikely that these represent successive introductions. Amphipods do not have a special resistant stage in their life cycle and Bayly and Williams (1966) considered it likely that *A. australis* had behavioural adaptations which allowed persistence in Lake St Clair and small lakes near Lake Eliza, South Australia. Some other amphipod genera are known to be semiterrestrial (Hurley 1959). The ephemeral saline lakes of south-eastern South Australia, with their thick macrophyte beds and open groundwater aquifers, may represent favourable environments for the survival of *A. australis* in the absence of free water. Minor differences in conditions within lake beds may help explain the occurrence of *A. australis* among the present series of lakes.

Isopoda

The endemic oniscid isopod, *Haloniscus searlei* Chilton, occurred in localities 1, 5, 7, 8, 10, 13 and 14. In locality 1, the species was collected from June to November, but in most other localities only one or two records were made. The sampling technique was not efficient for benthic forms such as *H. searlei* and generally only one or a few individuals were collected. The salinity range was 6·3–123·5‰ which is within the range the species is known to tolerate (Bayly and Ellis 1969; Ellis and Williams 1970).

The present collections are the first of *H. searlei* from waters known to be ephemeral. The species was collected from localities 1, 5, 8 and 10 by Geddes and Brock (1978) in 1975 (localities 7, 13 and 14 were not sampled) and so it may be concluded that the species persists in dry lake basins. Bayly and Williams (1966), considering the generally terrestrial nature of the Oniscidae, suggested that *H. searlei* may have behavioural adaptations allowing survival in lakes with no surface water. Direct proof of this was obtained in the experiments where water was added to lake muds. In one sample, seven *H. searlei* individuals of various sizes became active within a few hours. The patchy distribution of *H. searlei* among the present series of lakes may be explained by differences in the suitability of lake basins for survival in summer. *H. searlei* occurred in four of the five lakes in which *A. australis* was found.

Gastropoda

There has been controversy as to the identification of gastropods from Australian salt lakes. It is considered that all specimens collected in the present study belong to *Coxiella striata* (Reeve). Doubt is cast on the value of the diagnostic features of the shell and operculum recognized by McPherson (1957) for her eight species of *Coxiella* and for *Coxiellada gilesi* (Angas), as single populations in the present study developed several of these features at different times of the year and at different salinities. It appears that size and shape of the animals depend on various ecological factors such as temperature, salinity, eustacy and food availability, and the features of the shell and ornamentation of the operculum [which McPherson (1957) considers to be of diagnostic importance in the taxonomy of the various species] vary tremendously within one population.

Coxiella striata was present in all lakes except localities 3, 4, 6 and the three most saline lakes. Localities 3 and 4 were small, isolated and short lived, while locality 6 was the most turbid lake. *C. striata* were not generally recorded in early collections, probably because they were burrowing under the lake surface feeding on algal mats (Walter *et al.* 1973). Later in the season juveniles were commonly found attached to *Ruppia* and/or *Lepilaena* spp. stems. Numbers were often very high with as many as 5000 m^{-2} in locality 18. At times orange eggs were seen attached to the outside of the shell in the collar area; these were probably eggs of *C. striata*. The range of salinity over which *C. striata* were active was 6–124‰. Kirton (1971) showed that with acclimation *C. striata* from Lake Corongamite, Victoria, survived over the range 0·5–74·3‰. When the lakes were dry, specimens of *C. striata* with intact opercula were seen lying on the lake floor. 'Dormant' specimens brought back to the laboratory and placed in slightly saline water became active within a few minutes. Some of these specimens had been in dry lakes for up to 3 months. These results are inconsistent with those of Kirton (1971) who was unable to have *Coxiella* spp. survive desiccation.

Polychaeta

Benthic polychaetes were recorded from localities 5, 8, 9, 12 and 16, and represent a new species of *Manayunkia* (Hutchings, De Deckker and Geddes, unpublished data). This is the first record of the genus in Australia. It belongs to the Fabriciinae, and is estuarine in affinity. The polychaetes *Ceratonereis erythraeensis* Fauvel and *Capitella capitata* (Fabricius) collected by Bayly and Williams (1966) and Bayly (1970) near Lake Eliza were not encountered in this study. Specimens of *Manayunkia* sp. nov. 1 were kept alive in the laboratory at 20°C and 82‰ for 3 months, and also emerged from dried lake muds after the addition of distilled water in the laboratory.

Foraminifera

Benthic Foraminifera were found in 13 of the 23 lakes (localities 1, 5, 7–11, 13–15, 17–19). These forams were pigmented but, as Boltovskoy and Lena (1970) demonstrated that pigmentation of the protoplasm remains in forams for up to 3 months after death, it is uncertain whether all were alive at the time of collection. The specimens with pigmented protoplasm were considered to have been alive at some stage during 1978. The most common species was *Elphidium* sp., generally bright orange but occasionally pale green. *Trochammina* sp., which is chitinous brown in colour, was rarer and found only in the low salinity lakes. It was the most common in locality 1. Large specimens of the orange *Elphidium* sp. became active after water was added to lake muds in the laboratory. In the dry lake sediments temperatures can reach 40°C or more. Mats of dead macrophytes could form a semimoist cover over the lacustrine sediments, which are sometimes wet because of the presence of hygroscopic salt crystals, and help survival of Foraminifera. Further investigations have been carried out by Cann and De Deckker (1981).

Other fauna

Nematodes and ciliates were common in the lakes and were abundant in the early stages of lake filling. In the laboratory, these organisms emerged within a day from samples of lake mud after distilled water was added (Table 2).

Small numbers of dipteran larvae including mosquitoes and ephydrids were occasionally collected.

The rotifer *Branchionis plicatilis* Müller was recorded once in locality 2 in December at 18·2‰.

Tests of unidentified diatoms were noticed on many ostracod shells from quite a number of localities when these shells were examined by scanning electron micrography.

Discussion

The following localities in this study were studied in 1975 by Geddes and Brock (1978) and the numbers they assigned to the lakes are given in parentheses: 1(3), 5(4), 8(9), 9(5), 10(7), 11(8), 15(1), and 16(2). In 1978 (this study) the lakes were relatively less saline, due to higher rainfall. The fauna was similar in the two years except that *Boeckella triarticulata* was absent from locality 1 and *Daphniopsis pusilla* from localities 8, 11 and 15 in 1975, and *Australocypris robusta* was absent from locality 8 and replaced by *A. hypersalina* in 1978; this was probably because salinities did not fall sufficiently to allow hatching of these species. The occurrence of *Parartemia cylindrifera* is erratic as it was present in locality 16 in 1975 only and in several other localities in 1978. These differences between 1975 and 1978 show that not all of the fauna present as resistant stages in lake basins will hatch in any one year.

All of the fauna recorded by Geddes (1976) in ephemeral saline lakes in western Victoria, except for the halophilic anostraca *Branchinella compacta*, has been recorded in the present study. Several additional species were found including a second species of *Parartemia*, three further species of *Microcyclops*, the harpacticoid *Schizopera* sp. nov. 1, ostracods in *Limnocythere*, *Mytilocypris* and *Reticypris*, several more species of *Australocypris* and *Diacypris*, an isopod, an amphipod, a gastropod, and a polychaete. This list includes considerably more species, especially of ostracods, than were in the review of studies on western Victorian lakes by Williams (1978). One reason for this expanded species list is that the taxonomy of the groups is now better known. Other reasons may be that the present series of lakes is less saline, and that the lakes are near the Coorong lagoon and the sea and most have a dense cover of aquatic grasses. In comparing the present fauna with that from other studies, distinction should be made between temporary and permanent salt lakes. The latter may have quite different faunas, including fishes and other species of marine affinity, that do not have resistant stages in their life cycles. Thus some of the lakes quite near the present ones contained atherinid fish and other marine forms such as *Ceratonereis erythraeensis*, *Acartia clausii* and the harpacticoids *Onychocamptus propinqua*, *Robertsonia bengalensis* and *Heterolaophonte wellsi* (Bayly 1970).

The fauna in the present lakes is more extensive than that found in non-Australian studies. In high salinity lakes in British Columbia (conductivities 5–60 mS cm^{-1}) Scudder (1969) lists two anostracans, one *Diaptomus* sp., four corixids and three dipteran larvae, and Hammer *et al.* (1975) state that the zooplankton of salt lakes in Saskatchewan consists of the anostracans *Artemia* and *Branchinecta* spp., the cladoceran *Moina hutchinsonii*, copepods including *Diaptomus connexus* and harpacticoids and several rotifers. Thus the fauna is less diverse and different groups, especially corixids and rotifers, predominate. No ostracods are listed. Some of these differences may be because the lakes are more permanent than those in the present study. The list of fauna from ephemeral saline lakes in the northern Algerian desert includes rotifers (3), phyllopods (1), copepods (5) and dipteran larvae (2) (Beadle 1974). This is more like the Australian assemblage but again ostracods were not mentioned even though Gauthier (1928) mentioned their presence in saline waters in Algeria and Tunisia. Baird (1968) studied Sambhar Salt Lake in India and found that many species of insects, some anostracans and copepod species survived up to 72·6‰. Bayly and Williams (1966), although they compiled a somewhat different list from the one here, also emphasized the difference between the fauna of salt lakes in Australia and other areas. None of these studies is over as wide a range of salinities and seasons as the Australian studies and so comparisons are difficult.

It is of interest to consider the derivation of the fauna in the present series of lakes. Bayly and Williams (1966) emphasized that most of the fauna of salt lakes was of freshwater origin with some species, *Haloniscus searlei* and *Coxiella* spp., of terrestrial origin. Bayly (1970) studied temporary and permanent coastal salt lakes and collected many species of marine affinity. He considered that most were probably transplants and not capable of persisting in saline lakes. In the present study although the lakes are near the sea and have rich growths of estuarine grasses, the fauna is predominantly of freshwater origin. This probably relates to the fact that all lakes are ephemeral. The ancestry of most of the Crustacea has been discussed by Bayly and Williams (1966), however they did not consider all of the ostracods. The latter are not marine in affinity and belong to a family which comprises a high percentage of the freshwater ostracods although the various Australian genera studied here (except for *Limnocythere* sp.) have no direct, known freshwater ancestors (De Deckker 1981). In the present study one harpacticoid, the polychaete and the foraminiferans are of marine affinity.

Most of the crustaceans, the anostracans, the cladocerans, the calanoid copepods and the ostracods are known to survive the dry phase of lakes as eggs (Belk and Cole 1975; De Deckker 1977). However, some others survive as immature or adult stages. The cyclopoids and harpacticoids in the present study encyst as adults (or near-adults) and although encystment and diapause at this stage is well known (Elgmork 1967), there are few records of them surviving in dry lakes (Belk and Cole 1975). Perhaps the most interesting of the Crustacea are the amphipods and isopods that do not have resistant stages in their life cycles and presumably survive in suitable refuges in the lake bed. The presence of a dense covering of aquatic grass and hygroscopic crystals render the mud somewhat damp and this is probably important to survival of these crustaceans and of the polychaetes and foraminiferans. Other marine organisms such as the marine ostracods *Cyprideis* sp. and *Leptocythere* sp. have been recorded only in permanent saline lakes in Australia and presumably are unable to survive in damp muds.

The number of species co-occurring in the zooplankton and epibenthos is particularly high. Even at salinities in excess of 100‰ eight species co-occurred (Fig. 7). This would seem to contradict the statement of Williams (1972) that species diversity is greatly decreased in salt lakes. However these species are in lakes where salinities fell to <50‰ during the winter and the high number of species at 100‰ is the result of persistence at higher salinity of species that hatched then. It would not be expected that eight species would be found in lakes that are permanently above 100‰. It does seem that the effect of salinity on species diversity in the present study is not as dramatic as in the lakes analysed by Williams (1972). Factors other than salinity also affect species diversity. Diversity and standing crop were very low in locality 18, the southern end of the Coorong lagoon, and the reason for this is not apparent. Discussion of species diversity or species richness in salt lakes should not be confused with comparisons of the number of species physiologically capable of surviving at a given salinity. The number of species that can survive does decrease as salinity rises but the number of species that can co-exist in a given lake need not.

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