The Ecology of Episodic Saline Lakes of Inland Eastern Australia, as Exemplified by a Ten Year Study of the Rockwell-Wombah Lakes of the Paroo.

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Studies on salt lakes are mostly snapshots of their unique characteristics and relationships. Longer term studies provide different perspectives on variability in hydrology, salinity and biological communities. Such a study on five lakes near the Paroo River in the northwestern Murray-Darling Basin showed most hold water episodically for about 80% of the time, but each fluctuate over a characteristic salinity range : unnamed lake 0.6 – 19 gL^{-1}, Wombah 1.2 – 30 gL^{-1}, North Blue 0.3 – 31 gL^{-1}, Mid Blue 0.7 – 103 gL^{-1}, and Bulla 1.8 – 262 gL^{-1}. Generally, instantaneous biodiversity is low and not necessarily correlated with salinity, but unlike southern seasonal salt lakes, species accumulation lists are long, approaching 80 species of invertebrates, 50 bird species and a few fish species per lake. Diversity is promoted by salinity fluctuation and habitat heterogeneity. Most species reach peak abundance in any season as long as conditions are within their physiological salinity tolerances. Invertebrate fauna is of inland affinities, but with some localized substractions and additions explained by hydrology and/or salinity; waterbird numbers are influenced by events elsewhere in Australia as well as by local conditions. Like most naturally salinised lakes, production can be high, especially at low to moderate salinities and algal blooms occur naturally from time to time.

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INTRODUCTION

Over the last few decades much has been learnt about the numerous salt lakes in Australia. Limnological summaries are available for Victoria (Williams 1981) and the eastern inland (i.e. Queensland, New South Wales, adjacent South Australia) (Timms 2007) and southwestern Western Australia (Pinder et al. 2004a), Tasmania (De Deckker and Williams 1982), and southern South Australian lakes (De Deckker and Geddes 1982; Williams 1984. In essence, most Australian salt lakes are shallow, intermittent (either seasonal or episodic), chemically dominated by NaCl, markedly alkaline, and have a crustacean-dominated fauna that decreases in diversity with increasing salinity (see above references). Additionally, unlike salt lakes in the northern hemisphere, there is considerable regionalisation of the fauna (Williams 1984; Timms 2007).

Australian saline lakes are changing due to various adverse environmental pressures, as reviewed by Williams (2002) and Timms (2005), In Australia the greatest problem is secondary salinisation and it is manifest mainly in southwestern Western Australia (Davis et al. 2003; Halse et al. 2003) and to a lesser degree in some areas of southern Victoria and South Australia (e.g. Lake Baird, Pellana Lagoon, Lake Wangary on Eyre Peninsula (author, unpublished data))(Fig 1 in Timms, 2005). However in the remote inland, saline systems have remained unaffected by anthropogenic secondary salinisation.

One such inland area is the middle and lower Paroo River catchment in northwestern New South Wales and adjacent southwestern Queensland (Fig. 1 in Timms, 2006). Here there are many freshwater wetlands but a few are naturally salinised. Although surrounding terrestrial environments are degraded after 120 years of grazing, aquatic habitats are almost pristine (Timms 2001a). Study of them provides a 'control' for investigations into secondary salinised

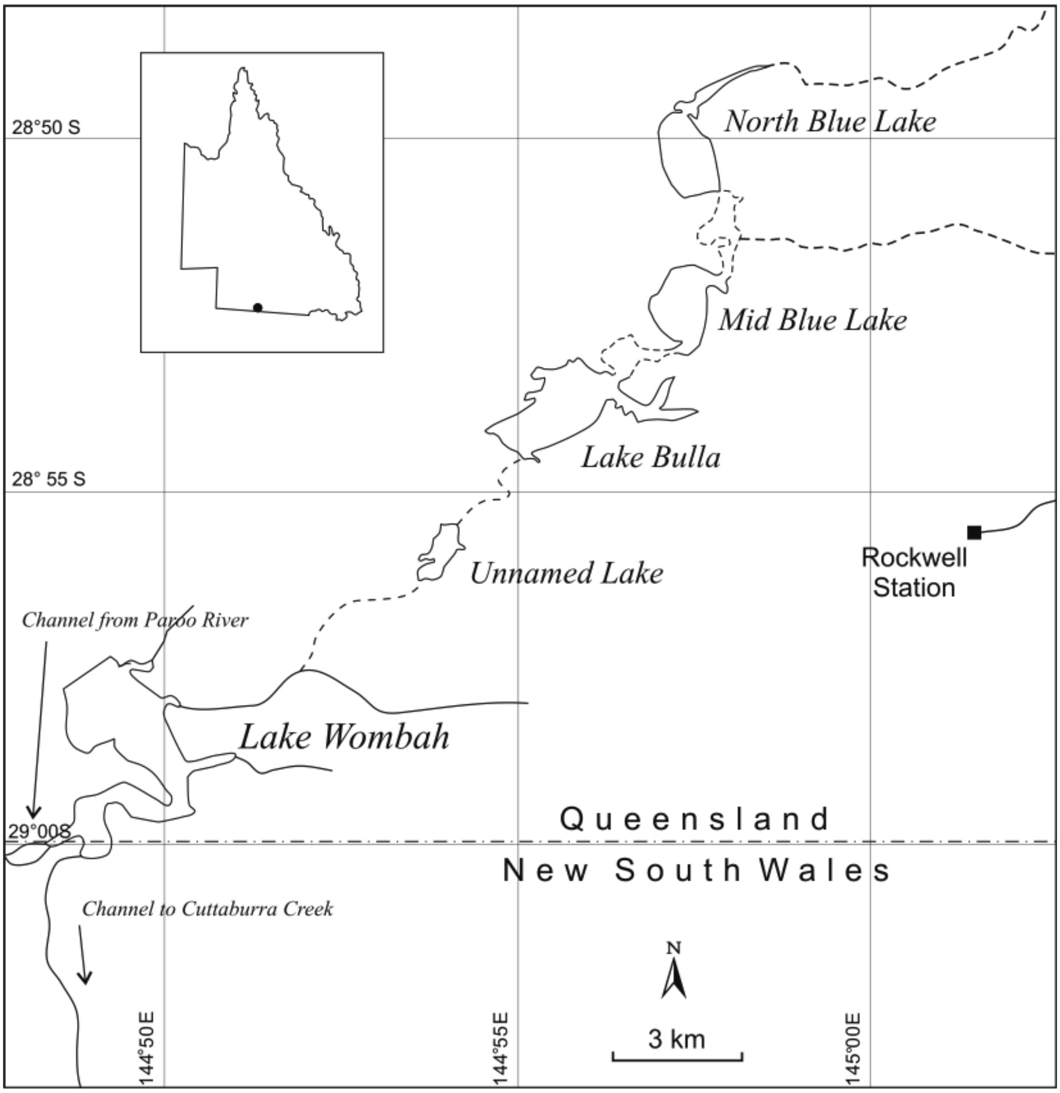

Figure 1. Map showing the five lakes on Rockwell and Wombah stations, southwest Queensland.

systems. However, they have accumulated their salt over millennia, so the rate of salinisation is different to that in anthropogenically affected systems. Also, the latter are affected by multiple degrading factors rather than just by salt increase (Davis et al. 2003).

Much of the existing data on saline lakes were collected on single field trips, or perhaps at best, a few over a year, so that long-term fluctuations associated with variable weather patterns have gone unrecognised. Yet these fluctuations could be a major difference between primary and secondary salinised lakes (Hudson et al. 2003). So understanding of inland lakes over a longer time frame than provided by most studies will provide better understanding of some of the impacts in secondary salinised systems. The present study aims to do this in a context of other saline lakes in the Paroo and of Australia in general.

THE LAKES

The five lakes lie on a creek line (called Number 10 creek upstream of North Blue Lake) that flows southwestward to join an anabranch of the Paroo River on the New South Wales – Queensland border 40-50 km east of Hungerford (Fig. 1). The creek is channelled between the upper three lakes (North Blue, Mid Blue and Bulla) which coalesce when full, but is obliterated by dunes downstream of Lake Bulla. It reappears as a small stream near Lake Wombah (Fig. 1). Paroo floodwater often enters Lake Wombah and leaves by the same route, but rarely reaches upstream to Lake Bulla. The last times this occurred were in 1974 and 1990 (P. Tuite, pers com.). The upper three lakes fill from Number 10 Creek, together with local streams from the east. The unnamed lake fills entirely

Table 1. Geomorphic and physicochemical features of the five lakes

Parameter	Lake Wombah	Unnamed Lake	Lake Bulla	Mid Blue Lake	Nth Blue Lake
Area (ha)	740	70	420	210	205
Depth (m)*	2.3 (3.2)	0.2 (1.8)	4.4 (4.9)	3.3 (3.9)	2.3 (3.6)
% of years with water	80	15	82	82	75
TDS range mgL^{-1}	1.2 - 30	0.6 - 19	1.8 - 262	0.7 - 103	0.3- 31
Mean TDS (gL^{-1})	7.6	5.6	34	9.1	6.8
Median TDS (gL^{-1})	4.9	3.3	9.8	4.1	4.2
Mean water Temperature (^{0} C)	22	19.5	19.4	23.6	23.8
Mean Turbidity ± SE (FTU)	34 ± 10.9	12 ± 2.7	7 ± 1.7	14 ± 3.5	13 ± 5.1
Mean pH ± SE	9 ± 0.21	8.7 ± 0.16	8.8 ± 0.19	8.9 ± 0.12	8.8 ± 0.23

* Figures in brackets are heights of highest water marks, but were not recorded during study.

from local streams and Lake Wombah receives most of its water from the Paroo River.

METHODS

Areas of the lakes were established from aerial photographs and depths from gauges in the lakes and the height of stranded beaches/wave cut notches determined with a dumpy level (Table 1). The later relate to intense local rainfall and large Paroo floods such as occurred in 1974 and 1990 (P. Tuite, pers. com.).

The lakes were visited at approximately three-monthly intervals from July 1995 to June 2004 for the purposes of determining some physicochemical parameters and sampling zooplankton and littoral organisms On each visit a surface water sample from about 50m offshore was taken for the immediate measurement of temperature with a mercury thermometer, pH with a HANNA HI8924 meter and later measurement of total dissolved solids (TDS) by gravimetry, with turbid waters being allowed to settle for many months in a sealed container. Turbidity was measured spectrophotometrically in the laboratory at 450 nm with the results recorded in Fittou's Turbidity Units. Five times during 1997 and 1998 nitrate and phosphate was determined in the field on the water samples from Wombah, Bulla, Mid Blue and North Blue using a HACH DR/2000 spectrophotometer and method 8171 for dissolved nitrate and 8048 for dissolved phosphate. These measurements were made during a hyposaline and a meso/hypersaline stage. Nutrients were measured once only (July 1998) in the unnamed lake.

Zooplankton and littoral organisms were collected with nets of mesh size 159 µm and 1mm respectively, identified and counted as outlined in Timms and McDougall (2004). Benthos was sampled with a Birge-Ekman grab just once in the four larger lakes─ Wombah in April 2004 and Bulla, Mid Blue and North Blue in December 2001. Five grabs were taken from each lake near the deepest part, sieved onshore through a 0.4 mm mesh and sorted while organisms were alive. Fish were caught sometimes in the littoral net and often in yabbie traps set for an hour or two to catch *Cherax* crayfish. These traps were not employed regularly or in any pattern.

Waterbirds were counted from January 1998 onwards. Shore based total counts were made with binoculars and/or a spotting scope on each visit. Counts were always made from the same vantage points each time, and covered the full surface area of all lakes except Lake Wombah. In this lake only the northern half was surveyed, for if the southern part was included it would take several hours to count the birds and impossible to account for bird movements because of the terrain. Small waders were underestimated in Lakes Wombah and Bulla when full as distances were too great for accurate determination.

RESULTS

Physicochemical Conditions

Average annual rainfall for the 10-year period was 366 mm, but yearly totals varied widely and included unusually wet years of 1998 (618 mm) and 2000 (622 mm) and the particularly dry year of 2002 (92 mm)(Fig. 2). Major local inflows to the top three lakes from intense local rain occurred in April 1998 and March-May 2000, and Paroo floods filled Lake Wombah in July 1998, March 2000 and February 2004. Between major fillings lake levels fell slowly with evaporation or rose slightly with minor inputs, so that four of the lakes held water for ca 80% of the time (Table 1). High salinities were experienced only briefly during March to December 1997 (to April 1998 in Bulla) and again variously during much of 2001-2002 in Wombah, Bulla, Mid Blue and North Blue (Fig. 3). The small unnamed lake held water for a few months in 1998-99 and again in 2000, both as a consequence of unusually heavy rainfall in those years (see above).

All five lakes varied widely in salinity, from fresh in all cases to hyposaline (i.e. to ca 20gL^{-1}) in the unnamed lake, to mesosaline (i.e. 20-50 gL^{-1}) in Wombah and North Blue, to hypersaline (i.e. >50 gL^{-1}) in Mid Blue and very hypersaline (> 200 gL^{-1} in Bulla (Table 1). Mean salinities are deceptive due to the short time the lakes spend at higher salinities (Fig 3) so that median salinities are more representative than mean salinities of typical conditions in the lakes (Table 1); in this respect all lakes are often hyposaline, with Bulla the most saline and the unnamed lake the least.

Mean water temperature for the ten years was 21.6 ^{o}C, with a minimum of 8 ^{o}C and maximum of 36 ^{o}C. Lake waters were generally clear, except following major inflows, or when shallow and wind-stirred, or in Lake Wombah's river-derived water (Table 1). Variability was greatest in the two lakes (Wombah and North Blue) receiving mostly flood water and least in Bulla where abundant salt helped to settle colloidal clay (Table 1). All five lakes had well buffered, markedly alkaline water, except again for some variation in the two lakes receiving most floodwater (Table 1).

Nutrients were high, around 1-2 mgL^{-1} nitrate and 0.2-0.4 mgL^{-1} phosphate, with highest values in Lake Bulla (Table 1).

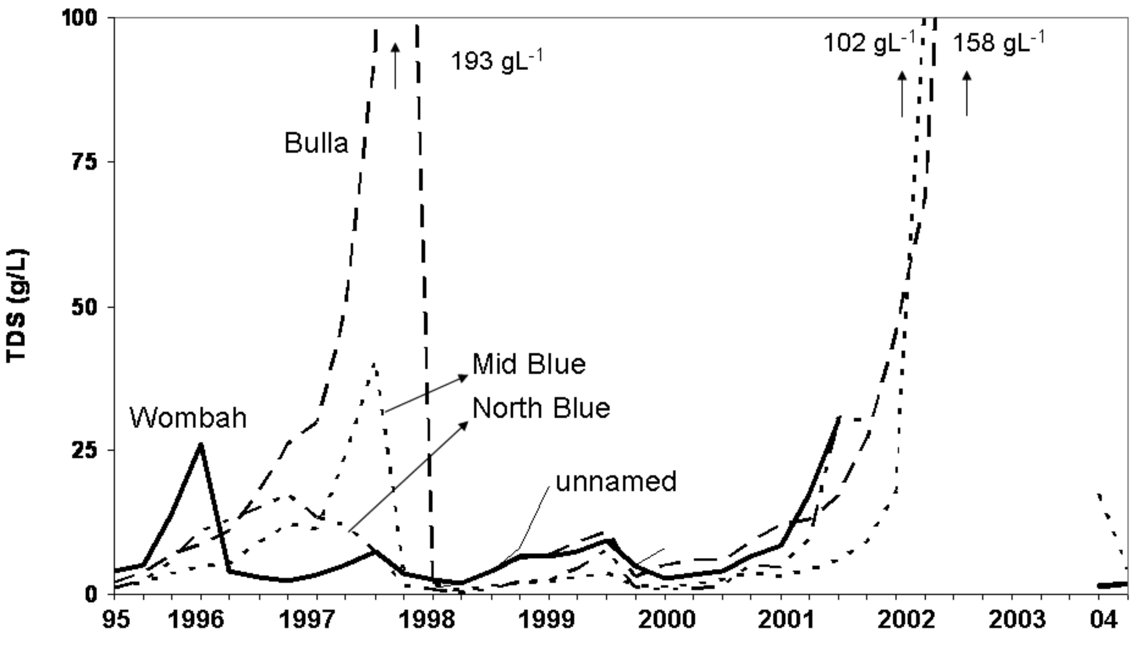

Figure 3. Fluctuations in TDS in the five lakes.

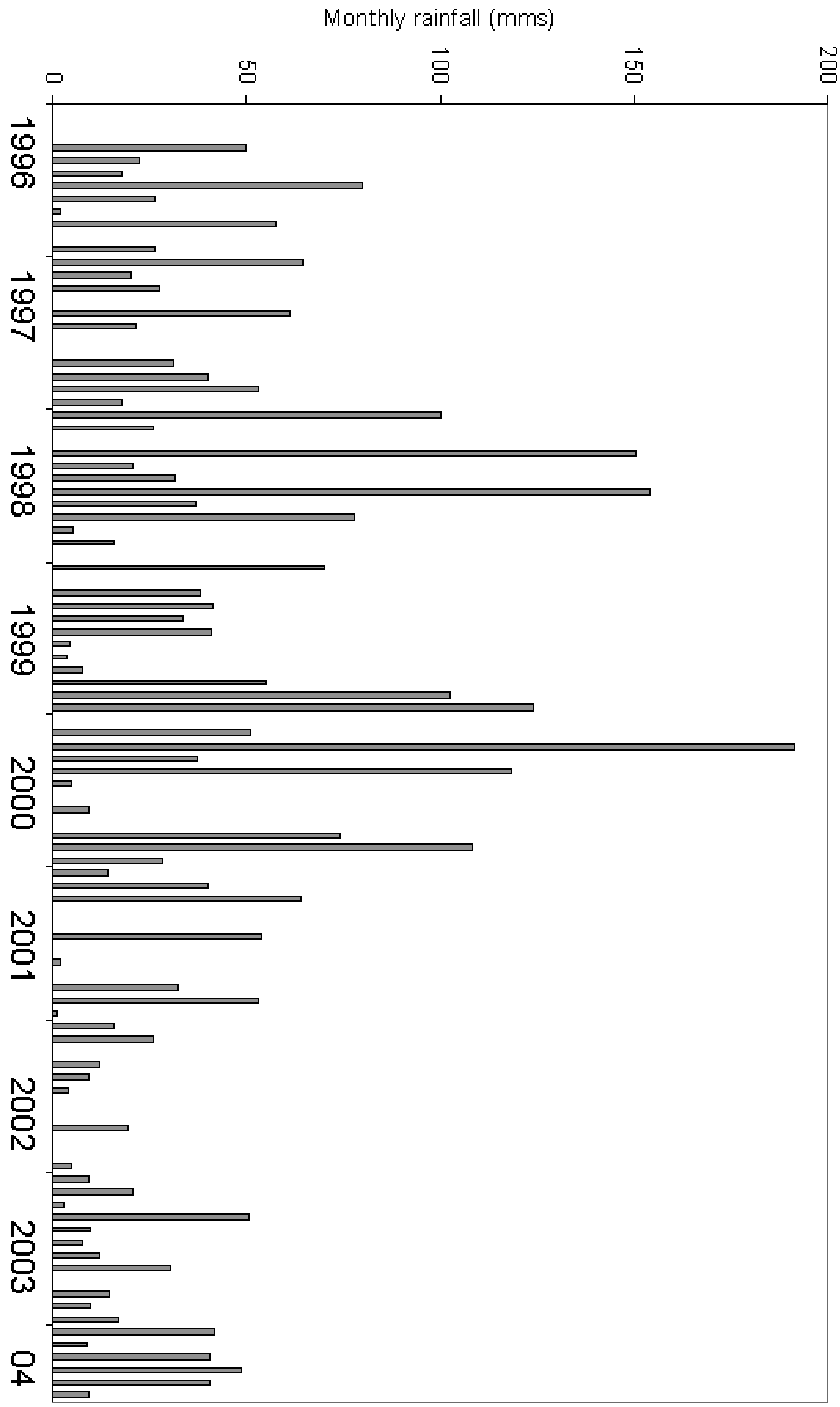

Figure 2. Monthly rainfall at Rockwell station homestead 1996-2004.

Aquatic Plants

Aquatic macrophytes were most common and persistent in the clear waters of Lake Bulla, where *Myriophyllum verrucosum* Lindl, *Lepilaena bilocularis* Kirk, and *Chara* spp. were common at lower salinities (<30 g/L). At higher salinities (30-60 g/L) the dominants were *Chara* sp. and *Ruppia* sp. These species occurred in the other lakes, but were less abundant, except occasionally in North Blue. A new species of *Chara* occurs in Bulla and Mid Blue (A. Garcia, pers. comm..) In summer and autumn, filamentous algae often shrouded plants, and appeared to be associated with their demise for the season.

Zooplankton

At least 37 taxa occur in the five lakes, with 12-28 species per lake (Table 2). The dominant freshwater species were *Boeckella triarticulata*, *Daphnia angulata* and *D. lumholtzi,* while the most common saline species were *Apocyclops dengizicus*, *Daphniopsis queenslandensis*, *Cyprinotus* sp. and *Diacypris* spp. (Table 2). There are broad similarities between average percentage composition between the lakes (Table 2), though the most intermittently filled unnamed lake had the highest percentage of clam shrimps (14.3%) and the most saline lake (Bulla) had the highest percentage of saline species (69.9%), followed in order by Mid Blue (56.0%), North Blue (44.4%) and Wombah (14.7%). Freshwater eulimnetic species with limited salinity tolerance (e.g. *Calamoecia lucasi, Daphnia lumholtzi, Daphnia angulata, Ceriodaphnia* spp., *Diaphanosoma* spp., *Moina australiensis*) comprised <22% in all lakes and were lowest in Bulla (10.2%) and the unnamed lake (1.1%). While salinity influenced a few species, momentary species richness was not related significantly to salinity in any of the lakes (Wombah r = -0.2148, n=27; unnamed lake r = 0.0832, n=7; Bulla r=-0.4885, n=31; Mid Blue r = -0.1425, n=35; North Blue r = -0.2505, n=29).

Typically, composition and dominance varied markedly between sampling dates in each lake and there was little seasonal repeatability over the ten years. Exceptions to this were *Daphnia lumholtzi* which often peaked in autumn in the fresher lakes, and *Daphniopsis queenslandensis* which was most common in winter-spring and *Moina baylyi* in summer-autumn, when lakes were saline. The most predictable occurrences were of saline species when lake salinity was elevated (e.g. *Daphnia* n.sp, *Cyprinotus* sp. at lower salinities, and *Apocyclops dengizicus* and *Diacypris* spp. at higher salinities).

Table 2 (RIGHT) . Zooplankton of the five lakes, showing mean percentage composition and maximum salinity for each species.

The amount of zooplankton in each sample varied greatly, with means ranging from 22.2 (Bulla) to 4.1 (North Blue) mls per minute of standardised collecting (Table 3). Variablility was greatest in the more saline lakes (Table 3). Dense populations were relatively uncommon but sometimes occurred in winter, soon after filling, or when the lakes increased in salinity as they dried rapidly (as a consequence of long periods of warm dry weather), but this was not significant statistically.

Table 3. Measure of standing crops

Lake	Zooplankton	Birds*	Benthos
	volume ± SE (mls)	no./ha ± SE	g m-2 ± SE
Wombah	19.4 ± 5.4	7.3 ± 2.3	9.1 ± 1.1
unnamed	16.6 ± 2.6		
Bulla	22.2 ± 8.1	15.5 ± 5.5	33.5 ± 0.9
Mid Blue	9.4 ± 2.9	13.2 ± 4.3	4.5 ± 0.7
Nth Blue	4.1 ± 0.8	18.6 ± 3.6	4.9 ± 0.4

*densities based on lakes being on average half full

Littoral Invertebrates

At least 78 species occur in the five lakes, with an accumulated species richness in each lake between 36-58 species (Table 4). Mean momentary species richness in each lake ranged from 6.4 to 10.9 (Table 4). The dominant species in all lakes was *Micronecta* sp., with the two ostracods *Mytilocypris splendida* and *Trigonocypris globulosus* and *Anisops gratus* and other backswimmers and boatmen common in most lakes, except in the unnamed lake. All common species had wide salinity tolerances (Table 4). Though *Tanytarsus barbitarsus* had by far the highest salinity tolerance, it was common only in mesosaline waters and above.

Beetles, although diverse, were not common in the lakes, and larvae were uncommon too. Odonatans were most abundant in lakes with extensive macrophytes (Bulla, Mid Blue). Ephemeropterans were most abundant in the lower salinity lakes (unnamed, Mid Blue and North Blue). River dominants such as large crustaceans *Macrobrachium australiense* and *Cherax destructor* were hardly encountered and then only in

SPECIES	max. salinity	Lake Wombah	unnamed Lake	Bulla Lake	Mid Blue Lake	Nth Blue Lake
	gL^{-1}	n=27	n =7	n=31	n=35	n=29
Spinicaudata						
Caenestheria n.sp.	3.3		13.6			
Caenestheriella packardi Spencer & Hall	0.7				<0.1	<0.1
Eocyzicus parooensis Richter & Timms	3.3	<0.1	0.7			
Copepoda						
Boeckella triarticulata Thomson	19	48.0	54.5	18.5	12.8	16.9
Calamoecia lucasi Brady	6.7	4.0		1.5	0.3	2.1
Thermocyclops decipiens Kiefer	7.7	7.8	15.7		1.2	8.0
Mesocyclops kieferi Van de Velde	4.2	4.9			4.2	5.3
Apocyclops dengizicus (Lepeschkin)	94	4.4		30.2	24.3	13.9
Cletocamptus deitersi (Richard)	13	0.1		0.5	0.9	0.1
Cladocera						
Daphnia lumholtzi Sars	6.7	0.1		2.8	9.4	6.9
Daphnia angulata Hebert	5.4	7.9	0.9	2.4	7.9	9.4
Daphnia cephalata King	2.1			0.1		
Daphnia n. sp.	16			3.4	0.5	2.3
Daphniopsis queenslandensis Sergeev	59	1.9		9.5	9.5	8.8
Ceriodaphnia cornuta Sars	2.1				<0.1	
Ceriodaphnia n.sp.	1.9	<0.1	0.2	1.6	2.6	2.8
Simocephalus vetulus (King)	0.7					<0.1
Diaphanosoma excisum	3.1	1.8		<0.1		
Diaphanosoma unguiculatum Gurney	1.7					1.2
Moina australiensis Sars	4.9	4.9				
Moina baylyi Forro	59	0.1		3.1	0.7	0.3
Macrothrix carinata (Smirnov)	8.5	0.1	0.6	0.2	1.3	0.2
Latonopsis australis Sars	4.2				0.2	
Alona spp.	11	4.6		0.2	1.1	2.0
Celsinotum spp.	19	0.2	2.4	0.4	0.7	0.2
Dunhevedia sp.	11			0.3	0.4	<0.1
Leydigia sp.	5.9					0.4
Ostracoda						
Bennelongia sp.	6.2	0.9	1.9		1.7	
Cyprinotus sp.	16	3.0	8.4	9.0	9.1	9.1
Diacypris spp.	157	2.1		14.1	8.3	2.5
Heterocypris sp.	41	0.3		0.9	0.5	4.5
Ilyocypris sp.	2.2				<0.1	<0.1
Newnhamia sp.	2.2				<0.1	<0.1
Reticypris sp.	35	0.7		0.2	1.7	2.5
Mytilocypris splendida (Chapman)	40	1.8		0.7	0.3	0.2
Trigonocypris globulosa De Deckker	46	0.2	1.0	0.4	0.4	0.1
number of species		24	12	23	28	28

Table 4. Littoral invertebrates in the five lakes. All numbers expressed as mean log abundance (Log 1 = 10) individuals per 15 minute collection).

	max.	Lake	unnamed	Bulla	Mid Blue	Nth Blue
Species	salinity	Wombah	Lake	Lake	Lake	Lake
	gL-1	n=23	n=7	n=28	n=34	n=26
Anostraca						
Branchinella australiensis (Richters)	1					<0.01
Branchinella buchananensis Geddes	3		0.14			
Spinicaudata						
Caenestheria sp.	3		0.71			
Caenestheriella packardi Spencer & Hall	1	0.04	0.57	<0.01	0.03	0.05
Eocyzicus parooensis Richter & Timms	3		0.86	<0.01		
Eocyzicus n sp	1	0.06				
Limnadopsis birchii (Baird)	3	<0.01	0.14			
Ostracoda						
Mytilocypris splendida (Chapman)	68	1.15		1.36	0.74	0.62
Trigonocypris globulosa De Deckker	68	0.52	0.01	1.68	0.92	1.16
Decaopda						
Cherax destructor Clark	4	<0.01				
Macrobranchium australiense Riek	6	<0.01				
Ephemeroptera						
Cloeon sp.	5	0.09	0.31	0.07	0.30	0.35
Tasmanocoenis tillyardi (Lestage)	5				0.30	0.16
Odonata						
Austrolestes annulosus (Selys)	4			0.03	<0.01	
Ischnura heterostricta (Burmeister)	30	0.05		0.22	0.15	0.28
Xanthoagrion erythroneurum Selys	12	0.04	0.14	0.28	0.21	0.06
Diplacoides bipunctata (Brauer)	12			0.11	0.06	<0.01
Hemicordulia tau (Selys)	12		0.16	0.22	0.30	0.06
Hemianax papuensis (Burmeister)	3	0.04		0.18	0.06	
Trapezostigma loweii (Kaup)	4			0.03		
Hemiptera						
Anisops calcaratus Hale	8	0.18	<0.01	0.14	0.09	<0.01
Anisops gratus Hale	26	1.2	1.01	0.53	0.71	0.35
Anisops stahi Kirkaldy	13				0.03	
Anisops thienemanni Lundbald	12	0.35	0.59	0.18	0.43	0.36
Micronecta sp.	94	1.93	2.71	1.26	2.16	2.26
Agraptocorixa eurynome Kirkaldy	17	0.48	1.44	0.22	0.33	0.23
Agraptocorixa hirtifrons Hale	17	0.32	0.59	0.14	0.11	0.24
Agraptocorixa parvipunctata Hale	17	0.31		0.07	<0.01	0.04
Sigara sp.	3				0.06	
Trichoptera						
Notolina sp.	5				0.06	<0.01
Oecetis sp. a	5	<0.01	0.14	0.04	0.03	0.05
Oecetis sp. b	5			0.03	0.06	0.04
Triplectides australicus Banks	11	0.17	0.44	0.11	0.33	0.20

Coleoptera						
Allodessus bistrigatus (Clark)	12	0.05	0.16	0.19	0.25	0.20
Antiporus gilberti Clark	8	0.08	0.43	0.18	0.21	<0.01
Bidessoides sp.	8				0.06	
Cybister tripuncatus Olivier	68	0.08		<0.01	0.04	<0.01
Eretes australis (Erichson)	8	0.05		<0.01		
Hydroglyphus leai (Guignot)	4				<0.01	<0.01
Hyphydrus elegans (Montrouzier)	1	<0.01		<0.01		<0.01
Megaporus howitti (Clark)	2				0.03	
Platynectes decempunctatus (Fabricus)	2	<0.01			0.03	
Rhantus suturalis (MacLeay)	8		<0.01	<0.01	0.03	
Sternopriscus multimaculatus (Sharp)	12	<0.01		<0.01	0.04	
Haliplus sp.	3		<0.01		0.04	0.04
Hydraena sp.	3		0.14			
Hydrochus sp.	1	<0.01				
Berosus approximans Fairmaire	1				0.03	0.08
Berosus australiae Mulsant	2		0.14		0.06	
Berosus debillipennis Blackburn	3				<0.01	
Berosus macumbensis Blackburn	2		0.29	0.04	0.03	0.04
Berosus munitipennis Blackburn	26	0.14	0.57	0.04	0.12	<0.01
Berosus nutans MacLeay	12		0.3		<0.01	
Enochrus andersoni Blackburn	7	0.06	0.29	0.11	0.12	
Enochrus maculiceps (MacLeay)	2				0.03	
Hydrophilus brevispina Fairmaire	7		<0.01	<0.01		<0.01
Limnoxenus zealandicus (Broun)	8		<0.01	0.04	0.06	
Beetle larvae *Antiporus* sp.		<0.01		0.08	<0.01	
Beetle larvae *Eretes* sp.			<0.01			
Beetla larvae *Rhantus* sp.			0.43		0.03	
Beetla larvae *Berosus* sp.		0.09		0.04	0.04	<0.01
Beetla larvae *Hydrophuilus* sp.			0.14			<0.01
Diptera						
Chironomus spp.	11	0.18	1.14	0.33	0.46	0.58
Coelopynia sp.	8	0.02				0.01
Cryptochironomus sp.	8	0.21		<0.01	0.09	0.15
Dicrotendipes sp.	30	0.17	0.44	0.11	0.09	0.12
Polypedilum nubifer Skuse	17	0.26		0.25	0.41	0.35
Procladius sp.	68	0.17		<0.01		0.15
Tanytarsus barbitarsus Freeman	193		0.04	0.54		0.12
unidentified ceratopogonid larvae	34	0.04		0.18	0.12	0.08
Aedes sp.	3		0.43			
Anopheles sp.	12		0.43		0.06	0.04
unidentified syrphid larvae	1	<0.01				<0.01
unidentified tabanid larvae	7		0.29	0.22	<0.01	
Lepidoptera						
unidentified pyralidae larvae	4	<0.01		0.04	0.12	0.04

Table 4 continued						
Species	max. salinity	Lake Wombah	unnamed lake	Bulla Lake	Mid Blue Lake	Nth Blue Lake
Hydrocarina						
Arrenurus sp.	7	<0.01		0.18	0.13	0.12
Eylais sp.	5	0.22	0.31	0.04	0.18	0.04
Hydrachna sp.	8	0.13			0.06	0.16
Limnesia sp.	7	0.17		0.14	0.21	0.42
Poina sp.	1			<0.01		0.04
unidentified water mite	2				0.03	0.12
Gastropoda						
Coxiella gilesi (Angas)	34			0.79	0.30	
Glyptophysa sp.	3			0.04	0.09	0.04
momentary species richness (MSR)		6.4	10.9	7.1	9.5	8.0
MSR SE		0.6	2.1	0.8	0.8	0.7
number of species		45	36	49	58	51

Lake Wombah. *Coxiella gilesi* was abundant only in Lake Bulla and Mid Blue Lake. Chironomids were present in most lakes and were no doubt more diverse than indicated in Table 4. The unnamed lake was the most distinctive of the five lakes, with a fauna dominated by large branchiopods.

Momentary species richness correlated negatively with salinity in three of the five lakes: Wombah r = -0.3700, n=27, ns; unnamed lake r = -0.6135, n=7 ns; Bulla r = -0.6245, n=31 significant at P< 0.01; Mid Blue r = -0.5072, n=35, significant at P < 0.01; North Blue r = -0.4853, n=29, significant at P< 0.01.

Benthos

Based on limited sampling, benthos of unvegetated offshore zone of the lakes was abundant but communities were simply structured (Table 5). Chironomids dominated, with ceratopogonids and large ostracods present, and an oligochaete in one lake. Biomass was by far the greatest in Lake Bulla.

Table 5. Benthic invertebrates of four of the lakes (numbers per m²).

Lake	Wombah	Bulla	Mid Blue	Nth Blue
TDS(gL^{-1})	1.5	17.1	6	30.9
Depth (m)	1.5	2 – 2.4	1 – 1.55	0.2
Dero digitata (Muller)			22 ± 22	
Mytilocypris splendida (Chapman)		2177 ± 166		
Trigonocypris globulosa De Deckker		1320 ± 219		
Chironomus sp.	6600 ± 895		100 ± 62	
Procladius sp.	310 ± 92	1364 ± 182	3250 ± 723	3720 ± 267
Tanytarsus sp.		25655 ± 944		
Ceratopogonid larva		280 ± 55	250 ± 108	324 ± 83
Total numbers (m^2)	6910 ± 768	30796 ± 712	3622 ± 544	4044 ± 248
Biomass (gm^2)	9.1 ± 1.1	33.5 ± 0.9	4.5 ± 0.7	4.9 ± 0.4

Fish

A variety of fish occurred intermittently in the lakes. Bony Herring (*Nematalosa erebi*) and Spangled Perch (*Leiopotherapon unicolor*) were present in Lakes Bulla, Mid Blue and North Blue from at least mid 1998 to 2001 and Mosquito fish (*Gambusia holbrooki*) and Carp (*Cyprinus carpio*) were common in Lake Wombah over the same period. Other fish could have been present in these four lakes as the sampling technique was not designed to catch all species. No fish were seen in the unnamed lake.

There was a major fish kill in Lake Bulla in March 2001 at the same time as there was a bluegreen algal bloom. Carp in Lake Wombah died en masse in December 2001 as the salinity reached 30 gL^{-1}. Fish in the Blue lakes seemed to disappear slowly over 2001, after which piscivorous birds were rarely seen on these lakes.

Waterbirds

Forty-eight species of waterbirds were seen on the lakes; Wombah had 34 species, the unnamed lake 15, Bulla 43, Mid Blue 41 and North Blue 38. The most common species were Grey Teal (*Anas gracilis*)(particularly in Wombah), Pink-eared Duck (*Malacorhynchus membranaceus*)(particularly in Bulla) and Eurasian Coot (*Fulica atra*)(mainly in Bulla and North Blue). Other species present in appreciable numbers included: Hardhead (*Aythya australis*), the Australasian (*Tachybaptus novaehollandiae*) and Hoary- headed (*Poliocephalus poliocephalus*) grebes, Black Swan (*Cygnus atratus*), Australasian Pelican (*Pelecanus conspicillatus*), Little Black Cormorant (*Phalacrocorax sulcirostris*), Little Pied Cormorant (*Phalacrocorax melanoleucos)*, Silver Gull (*Larus novaehollandiae*), Black-winged Stilt (*Himantopus himantopus*) and Red necked Avocet (*Recurvirostra novaehollandiae*). Only Black Swans bred on the lakes during 1995-2004, mainly on the islands in Bulla.

Numbers fluctuated greatly between lakes and observations (Fig. 4 and Table 3). Mean numbers of birds on the lakes varied between 18.6 ha^{-1} (North Blue) and 7.3 ha^{-1} (Wombah) (assuming the lakes were on average three-quarters full)(Table 3). Variability was greatest in Bulla which had the greatest salinity range, and there was no correlation between species richness or bird numbers with salinity ($r = 0.1364$ and $r = -0.0839$ respectively).

DISCUSSION

Naturally salinised lakes in the eastern inland of Australia have many distinctive features as itemised below, and with particular reference to the Rockwell-Wombah lakes.

1. Hydrological regime and geomorphic factors determine the presence of salt lakes and their salinity fluctuations (Hammer 1986; Williams 1998a; Timms 2006). When hydrologically closed, i.e. without overflow, bodies of water tend to accumulate salt. This explains the different salinity regimes in the Rockwell-Wombah lakes. Lake Wombah is the only one to be flushed by river flood water and then evaporation concentrates the isolated waters. Turbidity is greatest in Lake Wombah, due to the colloidal clays of Paroo River water (Timms 1999). Lake Bulla is generally the evaporative terminus of a blocked stream system flowing onto the Paroo floodplain, so it has accumulated the most salt and, associated with this, its waters are the clearest. Every few decades it overflows and presumedly salt is lost so that it is only hypersaline as it nears dryness (similar to Lake Wyara on the other side of the Paroo floodplain – Timms 1998). Mid Blue and North Blue Lakes are intermediate settling basins; differences between them largely reflect the relative shallowness of North Blue Lake. The unnamed lake is the most intermittent of the five due to its relatively small catchment; salt accumulation consequently is quite modest.

2. For episodic saline lakes even 10 years is not long enough to encounter all the variations in environmental conditions. Judged from comparative rainfall averages at Rockwell during 1995-04 (366mm) compared to long term averages for the area (325 mm over 105 years at Boorara nearby – A. McGarth, pers. com; 302 mm over 75 years at Warroo nearby – M. Dunk, pers. com.), the Rockwell-Wombah lakes were probably full for longer than a long-term average during 1995-2004. On the other hand, if the lakes had been studied during the much drier 1910s to 1930s they would have held only a little water occasionally and would have been more saline on average. An even longer time frame would encompass climate change and quite different hydrological conditions (Bowler 1983; Pearson et al. 2003).

3. While there is a classic negative relationship between diversity and salinity in salt lakes (Hammer 1986; Timms 1993), other factors may mask it (Williams 1998b); in the case of these lakes only the littoral assemblage in Lake Bulla and the two Blue Lakes were significantly correlated with salinity. None of the other influencing factors considered by Williams (1998b) seems be important in these lakes.

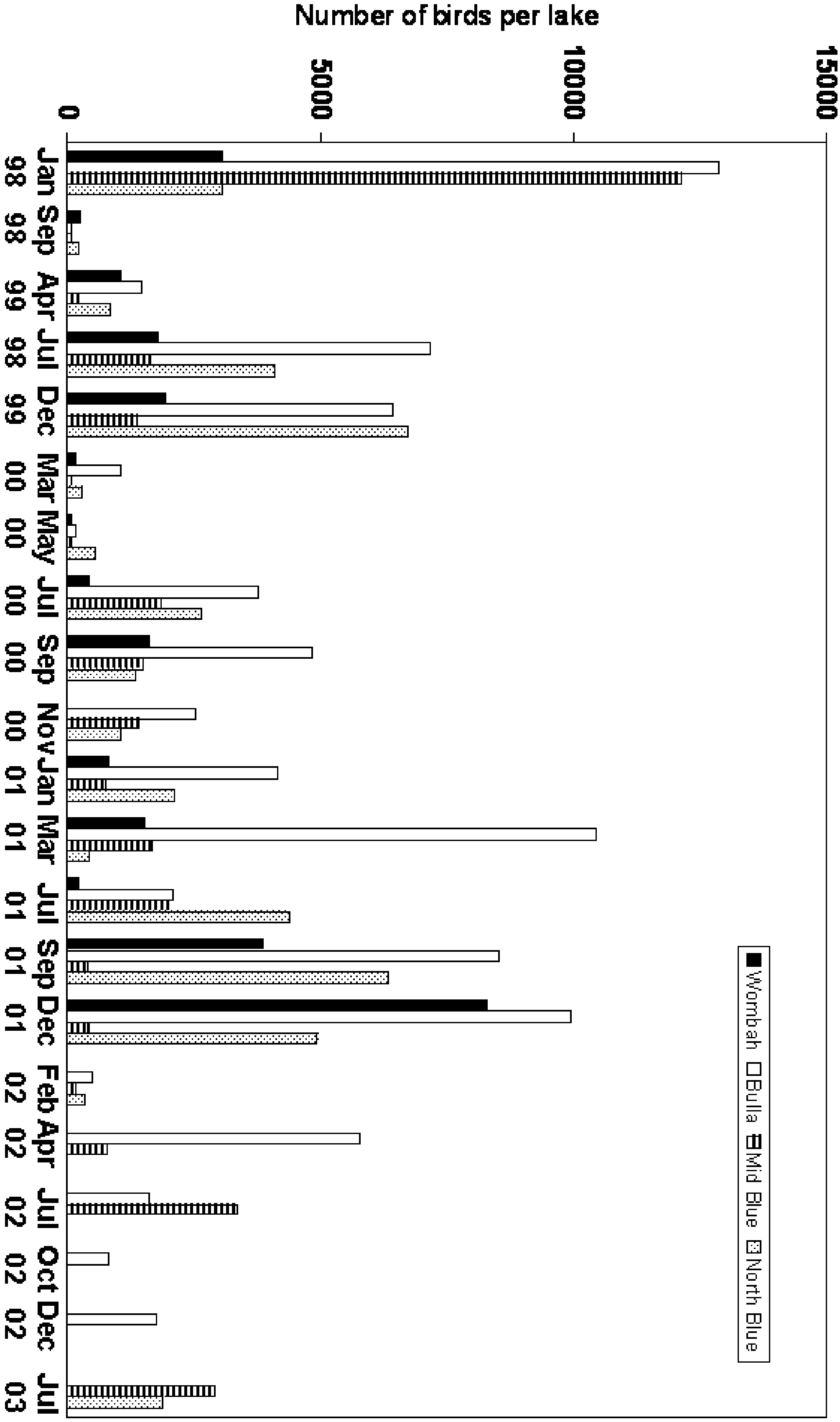

Figure 4. Variations in bird numbers in four of the lakes 1998-2003.

Indeed, the wide salinity tolerance of many species is in accord with that in the remainder of Australia so that it is only where lakes exceed 50 gL^{-1} that salinity has a significant impact as a determinant of community structure (Williams et al. 1990; Williams 1998b).

4. Salt lake fauna is regionalised in Australia (Williams 1984; Timms 2007), though all areas share a dominance of crustaceans, particularly *Parartemia* spp., *Apocyclops dengizicus*, *Daphniopsis* spp., and a host of ostracods (*Diacypris, Heterocypris, Reticypris, Platycypris*) including a few mytilicyprinid genera (*Australocypris, Mytilocypris, Trigonocypris*) (Williams 1981; Pinder et al. 2002, 2004a, 2004b; Halse & McRae 2004; Timms 2007;). Lakes in more propititious climates have higher crustaceans such as amphipods (*Austrochiltonia* spp) and the isopod *Haloniscus searlei* which have no resistant stage and need at least dampness to survive dry periods, and calanoid copepods (*Calamoecia* spp.) and more ostracod genera (Williams 1984; Pinder et al. 2002). The eastern inland has a distinct regionalised fauna, though as more is being learnt about inland Western Australian fauna (Pinder et al. 2002, 2004a; Timms et al. 2006) many of the distinctive species of the east are being found in the west as well. Examples include recent discoveries of *Eocyzicus parooensis*., *Daphniopsis queenslandensis*, *Moina baylyi*, *Celsinotum* spp., and *Trigonocypris globulosa* in inland Western Australia (Halse et al. 2000; Pinder et al. 2002, 2004; Timms et al. 2006). The eastern inland is still characterised by the unique presence of *Parartemia minuta*, a new *Daphnia* sp. in hyposaline waters, many halotolerant insects, and many monotypic genera whereas there has been multiple speciation in other areas, particularly in Western Australia (Geddes et al. 1981; Pinder et al. 2002, 2004a), and a greater relative importance of a variety of insects (mainly odonatans, corixids, notonectids, and coleopterans).

5. Not all lakes have a full complement of the regional fauna probably due to a mixture of local environmental factors, stochastic events and inadequate sampling. In the case of the Rockwell-Wombah lakes, species composition is typical for lakes in the middle Paroo with fluctuating salinity (Timms, 1993; 1999; Timms and Boulton, 2001). Notable absences include *Calamoecia canberra* (because waters are not turbid enough when fresh – Timms 2001b), and *Parartemia minuta* (because the lakes often have fish). Notable unusual occurrences include the snail *Coxiella gilesi* (absent in most other Paroo lakes investigated), *Daphnia lumholtzi* (more common in these lakes than elsewhere in Paroo), and *Branchinella buchananensis* (this is the only known site in southwest Queensland). Some differences between the lakes can be explained in terms of various environmental factors. The presence of shrimps and yabbies in Lake Wombah when it is fresh-subsaline is explained by its episodic river connection. The importance of large branchiopods in the unnamed lake can be associated with the permanent absence of fish in it. Finally the longer species list of coleopterans in Mid Blue Lake (23 species cf 13 -17 in the other lakes) could be a reflection of this lake's greater littoral heterogeneity, among other factors.

6. Lakes that fill predictably each season have a shorter list of species than those fill episodically (areas being of the same magnitude). The Rockwell-Wombah lakes, together with other Paroo lakes and Lake Gregory in northwest Western Australia with episodically fluctuating salinities, have relatively long species lists (ca 70-100 species) (Table 2 and 3; Timms 1998; Halse et al. 1998; Timms & Boulton, 2001; Timms & McDougall 2004). By contrast, seasonally-filled salinas in southern Victoria (Geddes 1976) and southeast South Australia (Geddes & Brock 1978; De Deckker & Geddes 1980) have less than half this number (ca 25 -40 species). The explanation lies mainly in the significant periods of hypsosaline conditions (these lakes have lower median salinities than most southern seasonally filled lakes), and also in the unpredictable and fluctuating conditions in the episodic lakes suiting various species at different times, compared with predictable and generally muted environmental conditions of the seasonal lakes allowing just one suite of tolerant species to persist throughout much of the season. Lack of salinity variation to maintain diversity may well be a major factor contributing to low species richness in secondarily salinised lakes (Hudson et al. 2003).

7. Habitat heterogeneity is another major factor influencing biodiversity in saline lakes (Timms 1998, 2001c; Williams1998b), and needs to be considered in conjunction with salinity variation. Large salinas such as Lake Eyre are far more homogeneous than small salt lakes and have fewer species (Timms 1998). A Paroo example is a comparison of Lake Wyara (3400 ha) and nearby Lake Bulla (420 ha), both studied for 10 years, both exhibiting similar salinity fluctuations over this time and both studied by similar methods – with 34 species recorded in Lake Wyara, but 73 in Bulla (Timms 1998). This role for environmental heterogeneity as a species richness driver is confirmed

by the presence of 84 species in the Werewilka Inlet of Lake Wyara (Timms 2001c).

8. Distinctions between descrete zooplankton, littoral and benthic communities are blurred in most saline lakes, because most are shallow and many have rich macrophyte growth throughout the lake. The situation is not helped by the giant ostracods (*Australocypris, Mytilocypris, Trigonocypris* species) and the large branchiopods (*Parartemia* spp., *Eocyzicus parooensis*., *Triops 'australiensis'* and halobiont species of *Branchinella*) which live and fed variously in all three habitats (Marchant and Williams 1977 on *Parartemia zietziana*; Timms 1981 on giant ostracods in L.Gnotuk; others from unpublished data, author). Many studies (e.g. Geddes 1976; Geddes & De Deckker 1980) therefore make little distinction between habitats, while others try, but with overlapping species lists (e.g. present work). Most undersample the benthos either by failing to dig the littoral net sufficiently into the sediments, or no or few specialised studies with quanitative devices such as Birge-Ekman grabs, or both. Thus while many benthic species seem to be recorded in so called littoral samples, indications of abundance are far too low (cf chironomids in Tables 4 and 5).

9. Hyposaline and mesosaline lakes attract waterbirds because of their rich resources (Kingsford et al. 1994; Kingsford & Porter 1994; Timms 1997). Even hypersaline lakes can support vast numbers of a limited diversity of birds, mainly large waders (Chapman & Lane 1997) and can be important breeding sites for some species (e.g. Banded Stilts– Burbridge & Fuller 1982). The Rockwell-Wombah lakes supported many thousands of birds belonging to 48 species. Numbers fluctuated widely (Fig. 4) due in part to varying food resources (Kingsford & Potter 1994; McDougall & Timms 2002), but these were not studied in these lakes. Mobile waterbirds are also influenced by events elsewhere in the inland. For example, the low numbers in the Rockwell-Wombah Lakes and also in nearby Lake Yumberarra during 2000 (Timms & McDougall 2004) probably marks their movement to the Lake Eyre Basin in response to even better conditions there (Roshier et al. 2002).

10. Saline lakes are usually productive, especially when hyposaline or mesosaline, but not when euhypersaline (Williams 1972; Hammer 1981a, 1981b; Timms 1983). In the Rockwell-Wombah lakes there are indications that Lake Bulla, the most saline lake is also the most productive (Table 3). However at any instant, some of the present lakes are unproductive due to either the aftermath of a bluegreen algal bloom (as at Lake Bulla) or by filamentous algae overgrowing and killing macrophytes as seen in many summers at the Blue lakes.

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