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A study of the Werewilka Inlet of the saline Lake Wyara, Australia – a harbour of biodiversity for a sea of simplicity

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Abstract

Lake Wyara receives most of its water from Werewilka Creek, with the area between the two forming Werewilka Inlet which is highly variable in area, and salinity and has high habitat heterogeneity. Over 12 years, 84 species of macroinvertebrate were found in the inlet, but only 34 in the lake. Halobiont and halophilic species were the same in each, but there were many fewer salt-tolerant species in the lake and no freshwater species. The latter were excluded by salinity, but habitat homogeneity due to strong wave action in the lake seems to limit many salt-tolerant species to the inlet. Species richness in large saline lakes in inland Australia is limited by salinity, poor speciation opportunities engendered by their episodic nature, and habitat homogeneity.

Introduction

Large episodically-filled temporary saline lakes support fewer species than equivalent lakes which are filled regularly (Williams, 1984; Timms, 1998a; Williams et al., 1998). Because of habitat unreliability, they are thought to be poor evolutionary loci, a hypothesis supported by presence of widely dispersed species and few endemics in large lakes in inland South Australia (Williams & Kokkinn, 1988). However, habitat homogeneity is also believed to contribute to their relatively depauperate fauna, as shown for Lake Wyara in southwest Queensland (Timms, 1998a). This lake is less speciose than nearby smaller lakes, which are otherwise reasonably similar in their salinity fluctuations and intensity of study (see Table 5 in Timms, 1998a).

Shallow saline lakes are usually well mixed and generally of the same salinity throughout the lake basin (Hammer, 1986), but it is possible in semi-isolated bays and in inlets receiving river inflows, for salinities to be different from those in the main lake. Given the inverse relationship between species richness and salinity (e.g. Timms, 1998b; Williams, 1998), lake inlets receiving fresh waters may support more species than the lake itself. Furthermore in large lakes, shores are generally wave washed and in those confined to old soft sediments, shorelines are often homogeneous as they are in Lake Wyara (Timms, 1998a). By contrast, in inlets the habitat is likely to be heterogenous due to uneven and unsorted sediments and chance accumulation of organic detritus, large and small. Therefore, if the fauna is restricted by habitat homogeneity, the inlets would be expected to be much more speciose than the main lake. On the other hand, if the depauperate fauna observed in large inland lakes is due solely to their being poor evolutionary loci, then biodiversity in the inlet would be no greater than that associated with its lower salinity.

Wyara and its associated inlets at 144° 14′ E, 28° 42′ S in south-western Queensland provides a site for exploring these relationships. The lake body is 34 km^2 in area and is subject to irregular wind action, particularly from the south-west and north-west, while there are four main inlets receiving freshwater inflows (Timms, 1998a). Werewilka Inlet at the northern end (Fig. 1) provides about 76% of the inflows received by the lake, and is 7.5 km long and 6.4 km^2 in area when flooded (Timms, 1997). Although previously referred to as an 'estuary', it has few similarities with marine estuaries (e.g. no tidal flushing, no regular changes in salinity or water-levels) so the use of this term is discouraged and the neutral term 'inlet' is preferred.

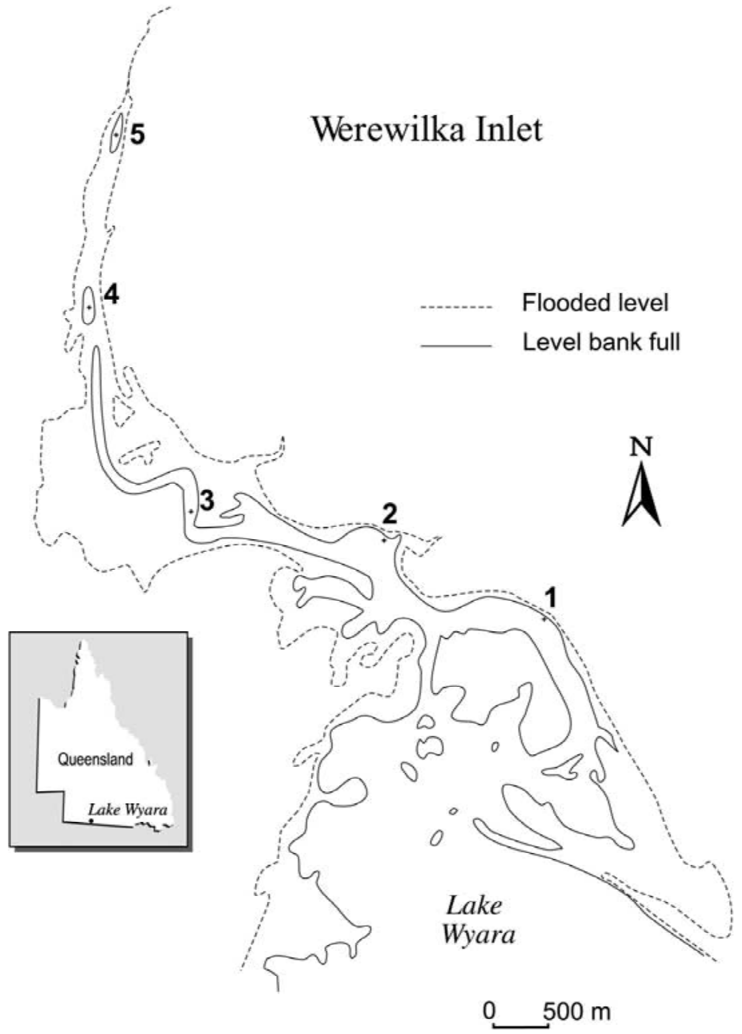

Figure 1. Map of Werewilka Inlet at the northern end of Lake Wyai in south-western Queensland. Collecting stations within the inlet are numbered 1–5.

Methods

The lake and Werewilka Inlet were visited 26 times over 12 years, from August 1987 to June 1999. The lake was sampled on the north-eastern shore, though initially samples were taken from four other sites along the eastern shore. Vehicular access to these sites damaged the shoreline (the lake is in a National Park) and samples from them hardly increased species richness for the lake as a whole, so they were discontinued. In the inlet, five stations were used, each 1–1.5 km apart (Fig. 1); the most remote site, station 5, was sampled regularly only after December 1997. This long study period encompassed a variety of situations in the lake-inlet system, including dryness in July 1995, overflow and aimost fresh conditions in May 1990, and many times when the lake level was within 'normal' limits but with differing hydrological conditions in the inlet (e.g. during long dry periods in summer, after recent rains in both summer and winter).

At each site, a water sample was collected and pH was determined with a Hanna HI 8924 meter. In the laboratory, turbidity was measured on a freshly agitated sample on a spectrophotometer at 450 nm, and the concentration of total dissolved solids (hereafter TDS) determined on duplicate filtered samples by gravimetry. In order to assess the degree of habitat heterogeneity, a standard Birge–Ekman grab was used to obtain duplicate sediment samples in December 1999 from 5 stations along the shore the lake and

Table 1. Variation in TDS (in g l^{-1}) in Lake Wyara and Werewilka Inlet, 1987–1999

Site	Mean	Median	Range
Lake Wyara	36.5	26.4	5.1–226
Werewilka 1	24.3	22.0	2.2– 67.4
Werewilka 2	21.6	21.5	0.3– 59.6
Werewilka 3	13.4	6.1	0.6– 47.0
Werewilka 4	5.9	3.7	0.1– 22.1
Werewilka 5	3.5	2.1	0.1– 10.4

Location of the Werewilka sites are shown in Figure 1.

Table 2. Variation in pH and turbidity in Lake Wyara and Werewilka Inlet, 1987–1999

Site	pH		Turbidity (in FTU)	
	Mean	Range	Mean	Range
Lake Wyara	8.6	8.1–10.3	10	0–40
Werewilka 1	9.2	8.4–10.1	22	0–60
Werewilka 2	9.2	8.4–10.4	101	0–600
Werewilka 3	8.7	7.5– 9.7	68	0–550
Werewilka 4	8.3	7.2– 9.8	376	15–1200
Werewilka 5	7.9	7.0– 8.6	352	25–1340

Location of the Werewilka sites are shown in Figure 1.

from the 5 stations in Werewilka Inlet. Coarse particulate organic matter (CPOM) was strained out, dried and weighed, and the remainder wet sieved into size classes and weighed dry.

Zooplankton was collected with a net of mesh size 159 μm mounted on a pole and with a aperture 30 × 15 cm. It was trawled for 1 min (sometimes longer when zooplankton were sparse) and the sample preserved in formalin. Species present were identified in the laboratory and their relative abundance was determined by counting the first 200 organisms seen in a representative subsample and then by scanning the whole collection looking for rare species.

A similarly constructed net, but of mesh size 1 mm was used to catch littoral invertebrates. At each site, 15 min was spent collecting invertebrates on each visit; the collections were then sorted and identified and for each species an estimate was made of abundance using the following notation and criteria: x = 1–10 individiuals, xx = 11–100 individuals, xxx = 101–1000 individuals, xxxx = 1001–10 000, and rarely, xxxxx = 10 000–100 000. Representative specimens were preserved in alcohol for later identification.

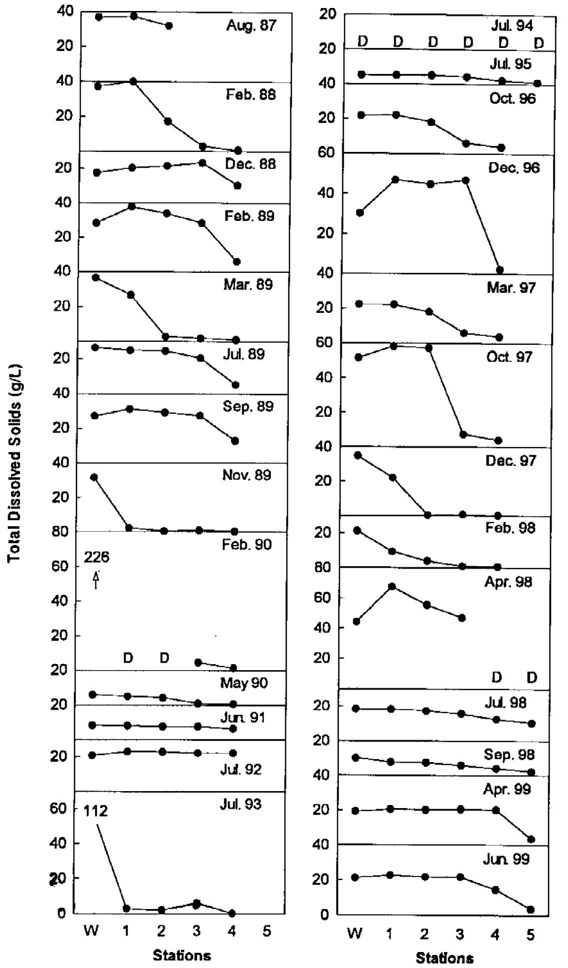

Figure 2. TDS in Lake Wyara and five stations in Werewilka Inlet on 26 occasions between August 1987 and June 1999. D indicates the site was dry, and blank that it was not sampled.

Results

Typically Werewilka Inlet contained water when the lake did and dried when the lake dried. Occasionally when the lake-level was low, some parts of the lower or upper inlet dried (Fig. 2). During the study, salinity fluctuated greatly due to episodic major inflows (see Timms, 1998a for rainfall and lake-levels during 1987–96) – major inflows occurred in May 1990. January 1995 and moderate inflows in December 1987, May 1989, February 1991 and April, July and September 1998. Drought conditions prevailed through much of 1991–94. Generally the lake and lower inlet had similar salinities, while values were lower in the upper inlet (Table 1). In this context, the median salinity for any station was a more representative of the 'average' condition than the mean salinity. Four major patterns in instantaneous salinity profiles along the inlet were apparent (Fig. 2): (a) a decrease steadily away from the lake – most common in cooler seasons and after recent rain (within the previous two weeks), (b) little change throughout the inlet except perhaps at the most remote station – most common in cooler seasons with little preceding rainfall, (c) sharp declines at any point along the inlet – associated with significant rainfall (>20 mm) within the previous 2 weeks and occurring in any season, and (d) salinity markedly higher in most of the inlet than in the lake – associated with dry conditions in summer when evaporation is highest.

On some occasions a drift of lake water into the inlet was noticed at Stations 1 and 2 when strong south-easterly or south-westerly winds were blowing, and on other occasions there was a drift outwards associated with strong north-westerly winds. No seiches or macrotides were observed nor river currents except at the two upper stations. However, significant river currents occur at times of major inflows as evidenced by points and bars in the sediments of the channel from station 5 down to station 2.

The shoreline of the lake generally consists of a uniform muddy clay (Fig. 3) with little variation horizontally along the shore. At higher water levels, there are beaches of well sorted sand. Unlike the main lake, inlet stations had variable sediments of larger particle size and higher amounts of CPOM (Fig. 3). On a mesoscale, the bottom and shoreline of the inlet are uneven, with deeper pools, shallow bars, minor inlets and braided channels. Deposits of coarse organic detritus (leaves, sticks, small logs) and beds of pebbles are increasingly common upstream. Aquatic plants are rare in the inlet, though occasionally some grow at the lower stations. Overall, station I has similar topography and sediments to the shores of the main lake, station 2 is otherwise similar but with sandy deposits, stations 3 and 4 have very uneven topography and mainly sediments of pebble, while station 5 is also uneven topographically but with sediments of various grades of sand.

There were also trends in pH and turbidity along the length of the inlet (Table 2). Mostly at lower stations, pH was similar or higher than the lake, but upstream values were lower, particularly after inflows. Turbidity increased up the inlet, particularly at stations 4 and 5 associated with turbid fresh inflows. Occasionally these inflows were observed further down the inlet and caused mean values there to be much higher and unrepresentative of normal conditions. Almost certainly during major inflows, this turbid water flowed into the lake, but this was not observed due difficulty of access during major rainfall events.

Eighty-four species of invertebrates were found in the Werewilka Inlet over the 12 years (Table 3). Momentary species richness ranged from 8 to 34 and averaged 18.9; it was not correlated with mean salinity of the estuary (r = 0.328, P = 0.1, n = 25) or with season for the whole estuary (r = 0.102, P>0.1, n = 25). The most common species were *Moina baylyi, Apocyclops dengizicus* and *Mytilocypris splendida* in the plankton, and *Anisops gratus, Micronecta* spp., *Paratanytarsus* sp. and *Antiporus gilberti* in the littoral. Forty species occurred three or fewer times and 17 were encountered only once; most of these were freshwater species with low salinity tolerance (e.g. the conchostracan *Eulimnadia* sp., the crab *Hoithuisiana transversa*), or freshwater species with limited tolerance to salinity (e.g. cladoceran *Dunhevedia crassa*, mayfly *Tasmanocoenis tillyardi*). Also, many of these 40 species are more common in other habitats such as freshwater riverine waterholes (e.g. the shrimp *Macrobrachium australiae*, copepod *Calamoecia lucasi* or in claypans (e.g. fairy shrimp *Branchinella australiensis*, clam shrimp *Caenestheria lutraria*) (Timms, 1997). The most abundant group in the inlet are salt-tolerant freshwater species (Table 4), though many of the dominant species are halophilic or halobiont (Tables 3 and 4). Most species occurred within known salinity ranges (see Tables 6, 7 and 8 in Timms, 1993), but for many, particularly beetles, salinity limits were extended upwards (see Table 3).

The number of species in Lake Wyara is less than half that in the inlet (Table 5 and Timms, 1998a) but dominant species are similar. The number of species of plankton for the two is almost identical, though there are some differences in abundance with the cladoceran *Daphniopsis queenslandensis* and the ostracod *Diacypris* spp. more important in the lake than the inlet. It is among littoral species that there are large differences between the lake and inlet: all groups, particularly beetles and odonates, are more speciose in the inlet than in the lake, and where species are shared (e.g. *Aniosops gratus* and *Antiporus gilberti*) they are typically more common in the inlet.

Notwithstanding the greater number of species in the inlet, the number of species there is less than half that known to be living in wetlands of the area (Timms, 1997; Timms and Bouton, unpublished data). Notably, phyllopods (which live mainly in claypans and

Table 3. List of macroinvertebrates found in Werewilka Inlet

Species	Times recorded	Times common	Times dominant	Salinity range g l^{-1}
CRUSTACEA: Anostraca				
Branchinella australiensis (Richters)	2			3.7–5.9
Spinicaudata				
Eulimnadia sp.	1	1		0.3
Eocyzicus n. sp.	3	1		0.6–4.2
Caenestheria lutraria Brady	4	2		0.9–1.8
Caenestheriella n. sp.	6	1		0.3–9.3
Cladocera				
Daphnia carinata King	8		1	0.3–6.1
Daphnia n. sp.	1			7.9
Daphniopsis queenslandensis Sergeev	28	3	3	2.1–55.5
Ceniodaphnia coruta Sars	2			0.2–0.3
Moina baylyi Forro	47	7	7	2.9–59.6*
Moina micrura Kurz	4	3		0.2–0.9*
Alona rigidicaudis Smirnov	2			4.1–9.6
Celsinotum spp.	2			7.5–8.1
Dunhevedia crassa King	3			2.0–6.5
Pleuroxus jugosus (Henry)	2	1		0.3–2.1
Macrothrix carinata (Smironov)	3			0.2–1.1
Copepoda				
Boeckella triarticulata Thomson	20	4		0.1–9.3
Calamoecia lucasi Brady	3	2		0.1–1.3
Apocyclops dengizicus (Lepeschkin)	46	7	4	3.5–67.4
Macrocyclops sp.	1			2
Metacyclops platypus Kiefer	6	1	1	14.8–22.8
Microcyclops spp.	20	8	1	0.1–5.9
Schizopera spp.	6			3.5–34.1
Ostracoda				
Cyprinotus sp.	14	4	1	0.6–14.8
Diacypris spp.	20	5	1	7.3–59.6
Heterocypris sp.	2			1.8–15.6
Newnhamia sp.	1			5.2
Mytilocypris splendida (Chapman)	43	13	3	2.1–55.5
Trigonocypris globulosa De Deckker	5	2		2.9–39.9
Macrobrachium australiae (Ortmann)	2			0.3–3.7
Cherax destructor Clark	1			2.2*
Holthuisiana transversa von Martens	1			0.1
INSECTA: Ephemeroptera				
Cloeon sp.	3			0.1–3.8
Tasmanocoenis tillyardi (Lestage)	2			0.1–0.3
Odonata				
Diplacodes sp.	2			0.6–7.5
Hemicordulia tau Selys	12			0.6–12.8*
Hemianax papuensis (Burmeister)	1			7.5
Orthetrum caledonicum (Brauer)	1			20.2
Austrolestes annulosus (Selys)	14	2		0.9–15.6
Xanthoagrion erythroneurum Selys	8			0.3–20.4*
Hemiptera				
Anisops calcaratus Hale	17	2		0.1–17.2
Anisops gratus Hale	43	11	4	0.1–27.3

Continued on p. 250

Table 3. Continued

Species	Times recorded	Times common	Times dominant	Salinity range g l^{-1}
Anisops stahli Kirkaldy	5			0.1–7.3*
Anisops thienemanni lundbald	21			0.3–28.6*
Agraptocorixa eurynome Kirkaldy	31	9		0.3–28.5*
Agraptocorixa hirtifrons Hale	12	1		0.3–17.2
Micronecta spp.	49	9	5	0.1–29.1
Sigara truncatipala Hale	2			2.0–12.6
Trichoptera				
Oecetis sp.	5			2.1–10.4*
Triplectides australicus Banks	7	1		2.1–7.6
Lepidoptera				
Pyralidae (Nymphulinae)	1			37.1
Diptera				
Chironomus spp.	7			2.2–12.8
Cryptochironomus griseidorsum Kieffer	3			0.1–1.8
Dicrotendipes sp.	5	1		0.1–3.2*
Polypedilum nubifer Skuse	4			0.1–3.2*
Procladius sp.	8	1		3.5–22.6
Paratanytarsus sp.	32	7	3	2.1–55.5
Anopheles spp.	6			0.9–5.9
Ceratopogonidae	14	2		1.3–55*
Tabanidae	2			22.1–47*
Coleoptera				
Haliplus fuscatus Clark	5			0.3–7.3*
Allodessus bistrigatus (Clark)	7			3.7–21.6
Antiporus gilberti Clark	34	11		0.1–31.2
Eretes australis (Erichson)	9	1		0.3–34.1*
Hydaticus variagatus Watts	2			12.8–20.4
Megaporus howitti Clark	1			0.3
Necterosoma penicillatum (Clark)	8			3.5–47*
Rhantus suturalis MacLeay	1			3.5
Sternopriscus multimaculatus (Clark)	9			0.3–20.4
Berosus approximans Fairmaire	4			7.6–21.6
Berosus australiae Mulsant	3			3.7–20.4*
Berosus macumbensis Blackburn	1			14.7*
Berosus munitipennis Blackburn	16	3		0.3–27.3
Berosus nutans MacLeay	5			20.3–47*
Enochrus eyrensis (Blackburn)	4			0.8–14.6*
Limnoxenus zealandicus (Brown)	2			3.5–20.4*
Chrysomelidae	1			3.5
Larval *Antiporus*	24			0.3–31.2
Larval *Berosus*	11			1.8–29.1
Larval *Hydrophilus*	1			4
Larval *Necterosoma*	1			47
Larval *Rhantus*	2			3.7–4.0
ROTIFERA				
Asplanchna sp.	5			0.2–1.1
Brachionus plicatilis Muller	26	2	3	3.7–55.5
Hexarthra sp.	12		1	5.9–59.6
Filinia sp.	1			0.3

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Table 3. Continued

Species	Times recorded	Times common	Times dominant	Salinity range $g\,l^{-1}$
ARACHNIDA				
Arrenurus spp.	1			4.0–9.3
Eylais spp.	6			4.0–9.3
Hydrachna spp.	3			4.0–16.7
MOLLUSCA				
Isidorella newcombi (Adams & Angas)	3			0.8–1.8
Glyptophysa gibbosa (Gould)	2			0.2–1.1

Table 4. Species richness among sites as influenced by salinity tolerance

Site	Freshwater species with no salinity tolerance	Salt-tolerant freshwater species	Halophilic and halobiont species
Lake Wyara	0	20	14
Werewilka Inlet	22	47	15
Paroo 1993 study[a]	50	52	22
Paroo Wetlands[b]	120	54	22

[a] See Timms (1993) – a study of saline lakes and a few freshwater lakes over 3 years. [b] See Table 5 and Timms & Boulton (unpublished data) – a study of many types of wetlands over 12 years.

temporary pools) are poorly represented in Werewilka Inlet, as are cladocerans (most common in vegetated localities), ostracods (most common in temporary pools and small salme lakes with wide fluctuations in salinity), dipterans (mainly in freshwater temporary pools), beetles (most common in freshwater pools) and snails (mostly in non-saline habitats (Timms, 1997).

When Lake Wyara is hypersaline (>50 $g\,l^{-1}$), then there is no overlap of species between the lake and inlet – indeed the lake is then devoid of macroinvertebrates (Timms, 1998a) but the fresh to mesosaline waters of the inlet contain a few species (Fig. 4). Conversely when the lake and inlet are hyposaline ($<$10 $g\,l^{-1}$), most species are common to the lake and inlet (Fig. 4). At such times, the lake has greatest proportion of species momentarily confined to it. There is a sequence of changes from these extremes as the lake becomes more saline and the difference in TDS between the lake and inlet becomes greater (Fig. 4). No species was confined to the lake but many species were restricted to the inlet. These included the freshwater species and a large group of species that could tolerate the prevailing salinity in the lake, as judged from field salinites recorded elsewhere in the Paroo (Timms, 1993, 1998), but were not recorded there. The former includes all the decapods, *Moina micrura, Tasmanocoenis tillyardi, Cryptochironomus griseidorsum, Asplanchna* sp. and *Isidorella newcombi*. Among the latter group are *Eocyzicus* n. sp., *Alona rigidicaudis, Metacyclops playtpus, Heterocypris* sp., *Xanthoagrion eryothroneurum, Anisops thienemanni, Allodessus bistrigatus, Necterosoma penicillatum, Sternopriscus multimaculatus* and *Limnoxenus macer*.

Discussion

Werewilka Inlet has a higher biodiversity than the saline lake to which it connects. This is expected given the dominant role of salinity in determining species richness, but few authors have documented it. Two relatively well studied situations are the Caspian and Aral Seas, in which inlets of inflowing rivers have proved important in recent decades and over the centuries as harbours of biodiversity when lake salinities have been high (Latypov et al., 1991; Aladin et al., 1998; Malinovskaya et al., 1998). Shivoga (2001) reports the adverse effect on biodiversity of increased

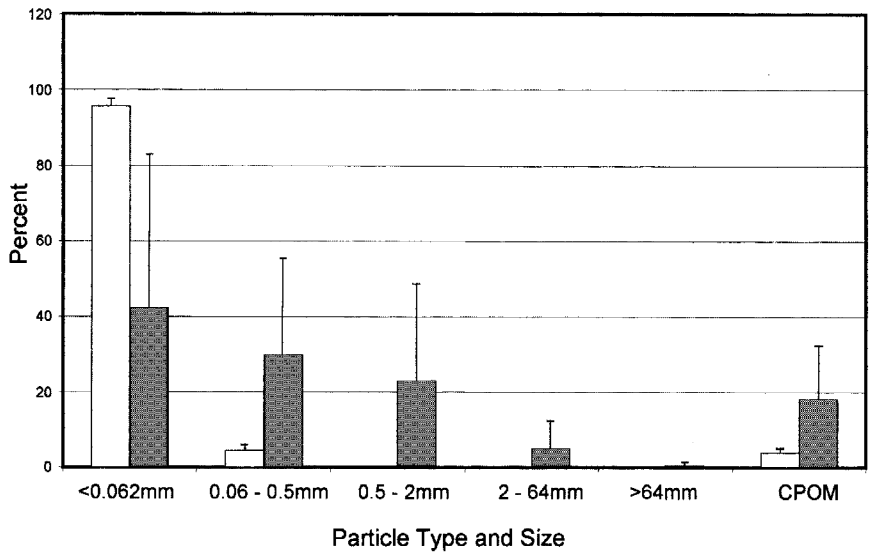

Figure 3. Differences in the nature of the substrate and its variability (indicated by error bars of one SD) at littoral stations in Lake Wyara (blank bars) and Werewilka Inlet (solid bars). CPOM = Coarse particulate organic matter.

Table 5. Comparative species richness in Lake Wyara, Werewilka Inlet and Paroo wetlands

Taxon	Lake Wyara	Werewilka Inlet	Paroo Wetlands
Platyhelminthes	0	0	1
Annelida	0	3	
Crustacea			
Anostraca	0	1	18
Notostraca	0	0	1
Conchostraca	0	4	10
Cladocera	5	11	28
Copepoda	2	7	14
Ostracoda	5	6	14
Decapoda	0	3	3
Insecta			
Ephemeroptera	0	2	2
Odonata	2	6	8
Hemiptera	5	8	17
Trichoptera	1	2	5
Diptera	4	9	28
Coleoptera	5	17	40
Lepidoptera	1	1	1
Arachnida	1	3	7
Mollusca	1	2	6
Rotifera	2	4	?
Total	34	84	196

stream conductivities as they flow into saline Lake Nakuru in Africa. None of these studies is pertinent to the present situation, since the Caspian and Aral Seas are permanent lakes and some of the species of marine origin and the Nakuru study was on streams, rather than on the ponded waters of an inlet. Situations like that pertaining for Lake Wyara–Werewilka Inlet are probably common enough in large saline lakes, but do not seemed to have been studied, possibly because of field difficulties and/or focus on the homogeneous lake rather than the heterogeneous backwaters.

Werewilka Inlet provides a greater range of environmental conditions, including a greater variety of habitats than the main water body of Lake Wyara. Besides variation in salinity along its length at any time, salinities are highly variable over time, so that at any particular site within the inlet salinity fluctuates widely. Importantly, these changes are only partly linked to changes in the main lake, thereby providing a much greater variety of habitat conditions than in the lake. These variations in salinity are quite unlike those in marine estuaries for there are no tidal rhythms and associated rapid changes in salinity or water level. Like estuaries however, there is a greater variety of habitats in the inlet, though this is very difficult to quantify.

Lake Wyara has about 25% fewer macroinvertebrate species than would be expected from knowledge of other saline lakes in the area (Timms, 1998a). In a comparsion between the main lake and Werewilka In-

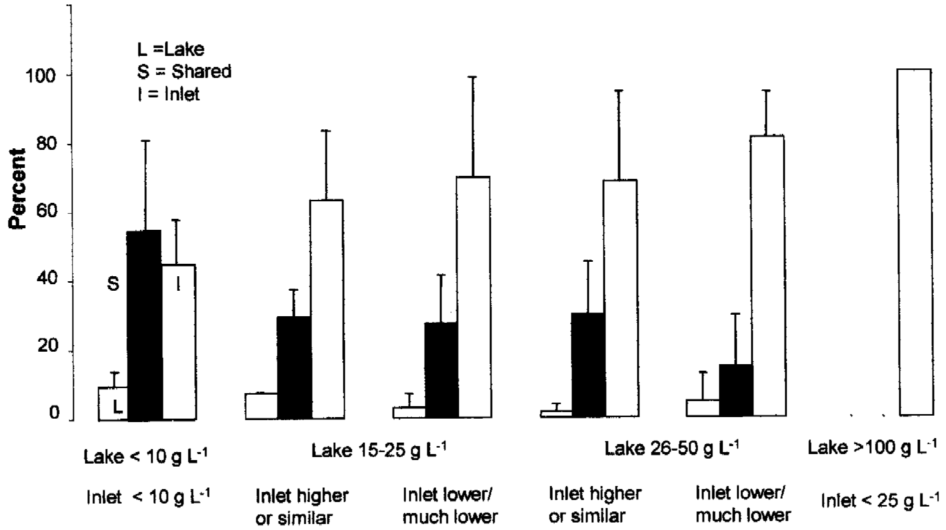

Figure 4. The influence of differences in TDS between the lake and inlet on the proportion of species found in the lake and the inlet and shared between the two. (Each set of proportions is based on 2–6 data sets (mean = 3.8), with variability indicated by error bars.)

let, the lake has 60% fewer species, but many of these (ca. 25%) are freshwater species so the difference is ca. 35%. The two sets of figures from different lines of evidence indicate the invertebrate fauna of Lake Wyara is depauperate. Almost all of the reduction is due to a lack of littoral species, strongly suggesting that the relatively homogeneous substrata in the main lake compared to those in the inlet is the reason (see also Timms, 1998a). Homogeneity of substrata needs to be added to the list of factors considered by Williams (1998) to influence the structure of biological communities in saline lakes. As Williams (1998) models in his Figure 2, the influence of such a factor is greatest at lower salinities, and is also most noticeable in larger saline lakes with wave-washed shores (Timms, 1998a).

Superimposed on reduced species richness due to habitat homogeneity is a further minimization (ca. 25% – Timms, 1998a), probably associated with these unpredictable episodic lakes being poor sites for speciation (Williams & Kokkinn, 1988). This factor is more important in lakes which rarely hold water than in the relatively benign Lake Wyara. Thus, lakes in Salinaland in Western Australia that fill very irregularly have a more restricted macroinvertebrate fauna compared to that in Lake Wyara (J. John, pers.com.).

These observations would not have been possible in a short-term study of the lake and associated inlet. This is because in fluctuating environments like saline lakes, numerous collections are needed to characterize the fauna; even then, species are added with additional collections. In this sense, mean cumulative species richness curves (*sensu* Timms, 1998b) approached an asymptote after 20 collections over 10 years, but that for the inlet was still rising, albeit slowly, after 25 sampling visits, each with 3–5 stations.

It is likely that the areas near the inlets of major streams in other large inland saline lakes in Australia, and the world, will prove to support many more species than the main lake. These inlets may provide refugia, or at least staging posts, for the colonization of the main lake when conditions in the latter are suitable (c.f. Aral and Caspain Seas – Latypov et al., 1991; Aladin et al., 1998; Malinovskaya et al., 1998). This is particularly so for insects which typically have no resistant stage in their life cycle.

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