Ecology of Macroinvertebrates in Seasonal Wetlands

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This thesis is presented for the honours degree of Bachelor of Science of Murdoch University 1986, being an account of my own research.

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ABSTRACT

Two seasonal lakes on the Swan Coastal Plain, Western Australia - Forrestdale Lake and Thomsons Lake - were sampled for macro-invertebrates over a period of six months. Three sites were chosen at each lake along a 500m transect from the fringing vegetation to the lake centres. The lakes were sampled when dry to determine which, if any, macroinvertbrates remained in the exposed sediments during the dry phase. The lakes began to fill in May, and sampling was carried out at flooded sites in May, June and July. Between June and August the water was sampled for nutrients (nitrogen and phosphorus), chlorophyll *a*, pH and conductivity. Organic content was measured in all samples of the sediments.

The water chemistry and organic content measurements revealed that both of the lakes were freshwater and meso-eutrophic. Altogether 78 taxa of macroinvertebrates were found, (62 species in Thomsons Lake excluding the zooplankton, and 41 in Forrestdale Lake). Thirteen species were recorded from the dry lake beds, and these and the rest of the aquatic fauna were considered to be well adapted to the seasonal cycle of drying and flooding. After flooding, species richness, density of individuals and diversity increased at most sites on each sampling occasion. Temporal differences between sites were greater than spatial differences. The class Insecta contained the largest number of species but a crustacean group, the Ostracoda, was the most abundant in terms of numbers of individuals. Sites near the fringing vegetation were found to contain the most species and have the highest density of individuals.

The two lakes appear to be very productive, in terms of species richness and density of individuals, compared to other Australian wetlands.

This is probably due to the trophic status of the lakes and their seasonal nature, both of which are thought to increase lentic production.

Chapter 1

Introduction

Since the 1960s the research effort on Western Australian wetlands has increased in intensity, so that now both government departments and tertiary institutions are involved for various reasons. Despite this concentrated effort there is still much to be learned about the aquatic invertebrate life of Western Australian wetlands. The aim of this study was to describe the changes in the invertebrate populations of two seasonal lakes, which take place between summer (when the lakes were dry) and winter (as the lakes filled). Water levels in the lakes vary as a result of changes in the seasonal water balance.

A series of management plans for wetland based reserves have been produced by the Department of Conservation and Land Management (formerly the Department of Fisheries and Wildlife). These plans for Thomsons Lake and Forrestdale Lake were the primary source of background information on the two lakes. The management plans for Thomsons Lake by Crook and Evans (1981), and Forrestdale Lake by Bartle *et al.* (1986) draw together all the information relevant to the reserves, including history, hydrology, fauna, flora and environmental threats to the reserves.

Researchers from the Department of Botany, at the University of Western Australia have studied lakes north of the Swan River. From these studies several papers and reports have been published, including that of Congdon and McComb (1975), Congdon (1979) and Gordon *et al.* (1981). Their work concentrates on nutrients and phytoplankton in the lakes. Hembree and George (1978) reported upon the invertebrate fauna of the northern Swan Coastal Plain. This study compared the invertebrate populations of several wetlands of differing physical and chemical nature, and examined the adaptations of the fauna to variations of water levels. Perth wetlands were the subject of a group honours project by University of Western Australia students (Ayre *et al* 1977). This project looked at the faunal, floral and chemical characteristics of several lakes, however they were not seasonal and did not dry out during summer. A preliminary report by Bunn (1982) looked at the invertebrate fauna of several wetlands in the Kemerton region of Western Australia. In 1983, van Alphen recorded the results of a six months study of the biota of fresh and saline lakes south of the Swan River. This study attempted to relate differences in seasonal salinity and water level changes between the lakes to community diversity and composition. A broader comparison of Perth wetlands was prepared by Beckle (1984), who compared lakes in terms of their physical, chemical and biological parameters. Arnold and Wallis (1986) considered Perth wetlands in the light of groundwater development and summarized the characteristics of local wetland ecosystems. Davis and Rolls (1986) of Murdoch University prepared a draft report for the Department of Conservation and Land Management and the Water Authority of Western Australia. Their report presented the results of a study of the invertebrate fauna of five wetlands in the Perth metro area, including how this element of the fauna changes with seasonal fluctuations of water level and water chemistry. One aim of their study is to use the data as a basis for biological monitoring of these lakes, so that the effects of groundwater draw-down might be predicted.

The paucity of knowledge on Australian aquatic invertebrates makes comparisons between lakes and lake systems difficult, also much of the information has been gathered by sampling on one occasion (Timms, 1980). The types and origins of Australian lakes are extremely varied, ranging from glacial to coastal lakes, of marine or terrestrial origin, temporary or permanent lakes, and oligotrophic to eutrophic. This diversity of water-bodies makes it hard to explain invertebrate faunal differences resulting from single physical or chemical differences between lakes. Few comprehensive studies have been conducted on most of these lake types, except perhaps the saline lakes of Eastern Australia. In particular little work appears to have been carried out on seasonal wetlands. By comparing the literature that discusses the invertebrate fauna of Perth lakes with similar studies for other Australian water-bodies, several patterns emerge.

Firstly, the invertebrates of seasonal wetlands are clearly adapted to cope with the seasonal variations in water level and the resulting chemical changes, either by means of their life-cycle or behaviour. Many species survive extremes of water level and chemical fluctuations by forming resistant stages such as eggs or embryos, e.g. Cladocera and Ostracoda (DeDekker and Geddes, 1980) and Copepoda (Williams, 1985). Others can survive as adults, e.g. chironomids (Klaster and Jacobi, 1978) and Isopoda (Williams, 1985). Maher and Carpenter (1984) also found that the life-cycle of chironomids were especially suited to the seasonality of wetland habitats; these animals took advantage of the changing water levels to complete several generations as lakes flooded. Yet other invertebrates migrate as mature flying adults and re-colonize the wetland in the next wet season. Marchant (1982) studied temporary billabongs in the Northern Territory, and found the fauna well adapted to the seasonal cycle of drying and flooding. Secondly, the drying of lakes seems to increase productivity in the flooded lake by regenerating nutrients bound up in the aquatic biota. Thirdly, other parameters that are thought to influence the invertebrate populations of lakes include salinity, depth and trophic structure, (Timms, 1980), though the effects are often subtle and much research is needed before conclusive patterns emerge.

According to Timms (1973), the invertebrate fauna of Australian lakes is low in species richness, due to combination of geographic isolation, the young age of most still water habitats and the impermanence of most lakes, leading to a trend toward generalist invertebrates. However, Fulton (1983) disputes this, arguing that the northern hemisphere lakes that were compared to the Australian lakes, were neither morphologically similar nor equally sampled.

Previous studies of the Perth wetlands have tended to concentrate on the fauna of the flooded wetland, and studies on the dry lake bed fauna are noticeably absent. Also this study is different to most in that transects were laid out across the lakes to study spatial differences in invertebrate populations. The objectives of this project were thus twofold:

1. To find out which, if any, macroinvertebrates inhabit the lake bed after drying;
2. To investigate the changes in macroinvertebrate populations as the lakes flood.

The two lakes studied were Forrestdale Lake and Thomsons Lake, both of which lie on the Swan Coastal Plain, about 14 km south of the Canning and Swan Rivers respectively (Fig. 1). Thomsons Lake lies closest to the coast (5km) whereas Forrestdale Lake lies a further 11km east. Both are shallow, (maximum depth never exceeding 4m, and usually much less), seasonal, freshwater lakes lying in interdune depressions.

The Swan Coastal Plain

The Swan Coastal Plain is the name given to the lowlands between the Darling Scarp to the east, and the coast. It is made up of parallel series of sediments of various origins (Fig. 1). These sediments are of two basic types; firstly those closest to the scarp are alluvial, and the rest are of aeolian origin (wind deposited). The Pinjarra Plain, also known as the Guildford Formation, is made up of sediments brought down from the Darling Range by streams and rivers, forming fans of alluvial deposits of Quaternary Age (Hodgkin *et al.* 1979). These fans merge with floodplain, estuarine and lake sediment deposits (Seddon, 1972). West of this lies the Bassendean Dunes; these are beach sand accumulations of Pleistocene origin, formed when the sea level was higher. Originally calcareous, all calcium has now been leached by rains, leaving grey coloured siliceous sands (Hodgkin *et al.*, 1979). Directly to the west of these dunes lie the Spearwood Dunes; these are also of Pleistocene origin but are still younger than the Bassendean system (Seddon, 1972). The sands here are a yellow colour, having lost less of their calcareous content (Hodgkin *et al.*, 1979). Drainage in this system is more suitable to agriculture than the Bassendean system, and for this reason a market garden industry flourishes on these dunes. Of recent origin are the present coastal dunes, between the Spearwood system and the ocean, known as the Quindalup dunes. The surface deposits described above lie above older Cretaceous formations (Fig. 2), (Metropolitan Water Authority, 1983).

Between the different sediment deposits lie chains of wetlands (Fig. 1). Associated with the Quindalup Dunes and the western regions of the Spearwood Dunes, (south of the Swan River) are a series of saline lakes which formed during a recession of the sea level, an example being White Lake (Fig. 1). Further east, in depressions between the Spearwood Dunes, lie many wetlands, especially north of the Swan River. Banganup Lake and saline Lake Coogee near the coast are examples south of the river. In depressions between the Spearwood Dunes and the Bassendean Dunes are a long series of freshwater lakes, including Lake Pinjar in the north and Thomsons Lake in the south, separated by a distance of 45km. Associated

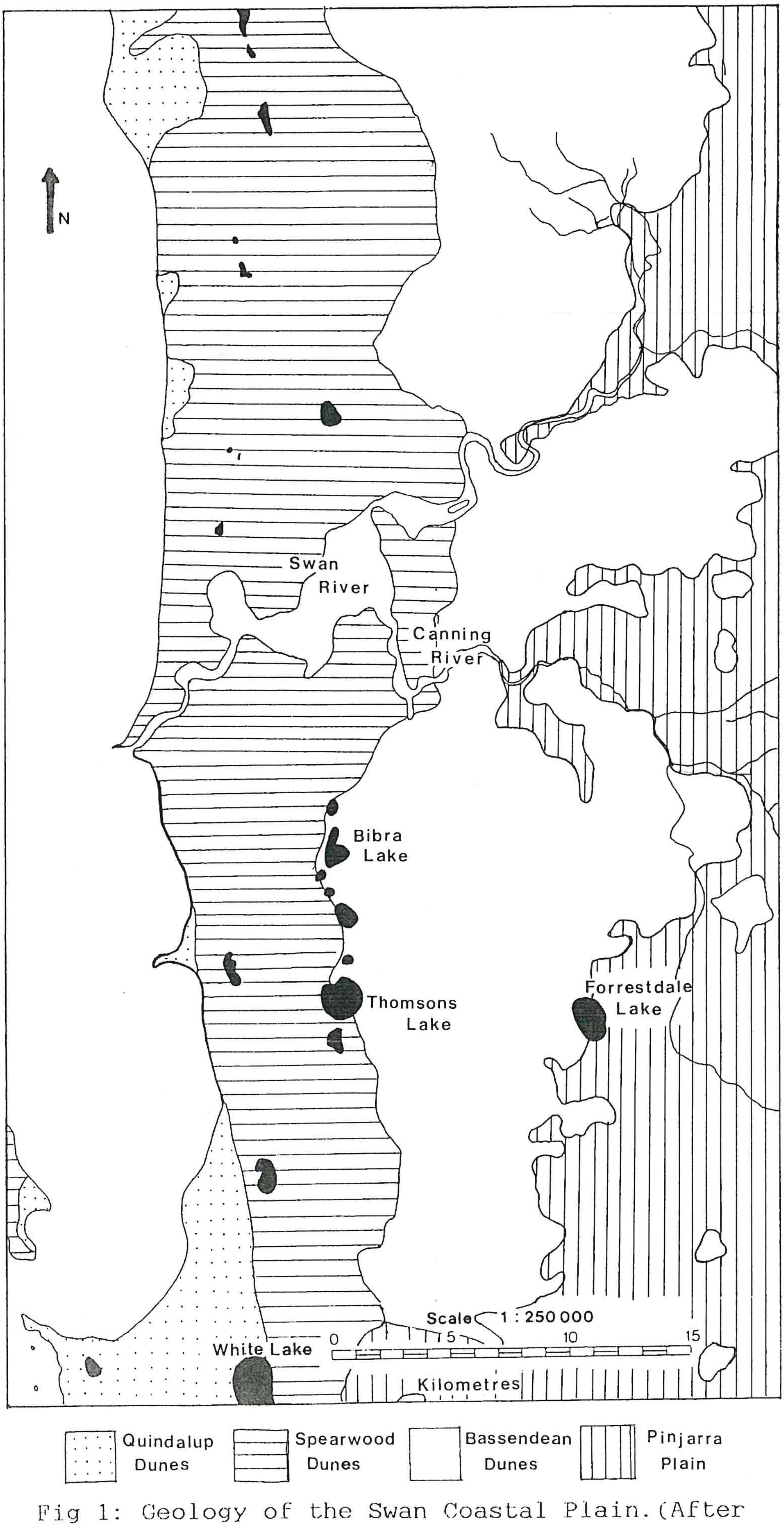


Fig 1: Geology of the Swan Coastal Plain. (After Metropolitan Water Authority, 1983).

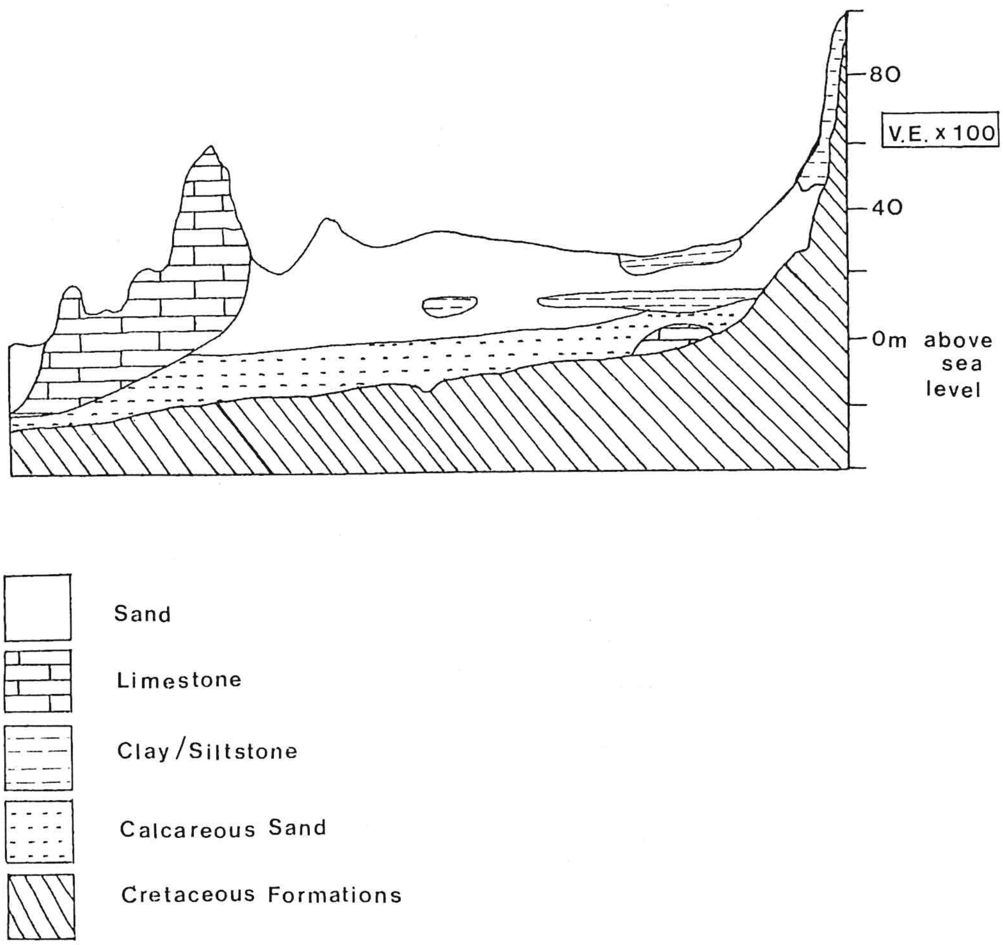


Fig 2: Cross Section Through the Swan Coastal Plain, at the Region of Thomsons and Forrestdale Lakes. (After Metropolitan Water Authority, 1983).

with Thomsons Lake are Bibra Lake, North Lake, Yangebup Lake and several smaller wetlands (Fig. 1). Interdune depressions of the Bassendean system also contain some wetlands, although fewer than the Spearwood System. These are mainly low areas which flood for a while in the wet season, although Lake Bangup is more permanent. Where the Pinjarra Plain meets the Bassendean sands, swampy areas occur (Seddon, 1972). Forrestdale Lake is a more defined wetland in this region, and represents one of the oldest wetlands on the plain (Arnold and Wallis, 1986).

Water running down the impermeable formations of the Darling Scarp seeps below the permeable sediments of the Swan Coastal Plain. Hence some streams peter out, for example Wungong and Cardup Brooks. The average monthly rainfall at two sites on the Swan Coastal Plain is plotted in Fig. 3. The first of these sites is the nearest monitoring site to Thomsons Lake; the second (Jandakot) is close to Forrestdale Lake. This graph shows that rainfall is higher, in most months, near Forrestdale Lake than it is near Thomsons Lake.

The stream and river water and rainfall which seep below the surface sediments form an unconfined groundwater aquifer. The depth of the aquifer varies, but averages 50m north of Perth, and 20m to the south, with a maximum depth of 100m (Allen, 1981). The aquifer is recharged by rainfall and as rainfall is very seasonally variable (Fig. 3), so is the water table level. The water table is deeper in the Spearwood Dunes, and a net seaward flow of groundwater occurs. The groundwater is closer to the surface in two areas, known as mounds, one to the north (Gnangara mound), and one to the south (Jandakot mound), (Fig. 4), of the Swan River. The northern mound is the larger in area and height, rising to 70m above sea level (Beckle, 1984). Jandakot mound, while being smaller, rising to only 20m above sea level (Beckle, 1984), is important in the hydrology of

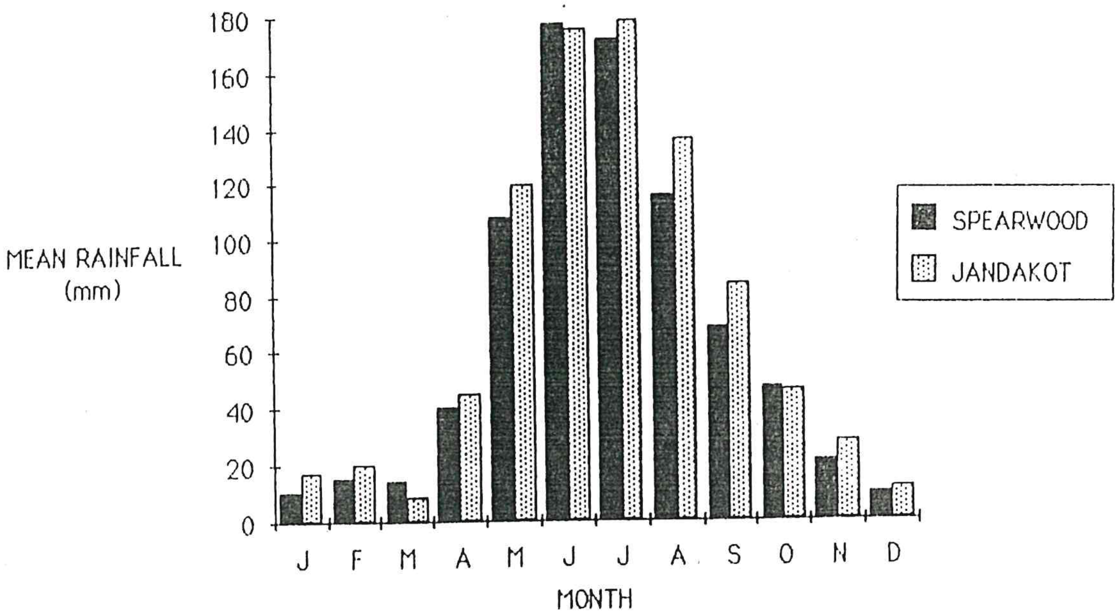


Fig 3 : MEAN MONTHLY RAINFALL FOR SPEARWOOD AND JANDAKOT FOR THE PERIOD 1958-1985

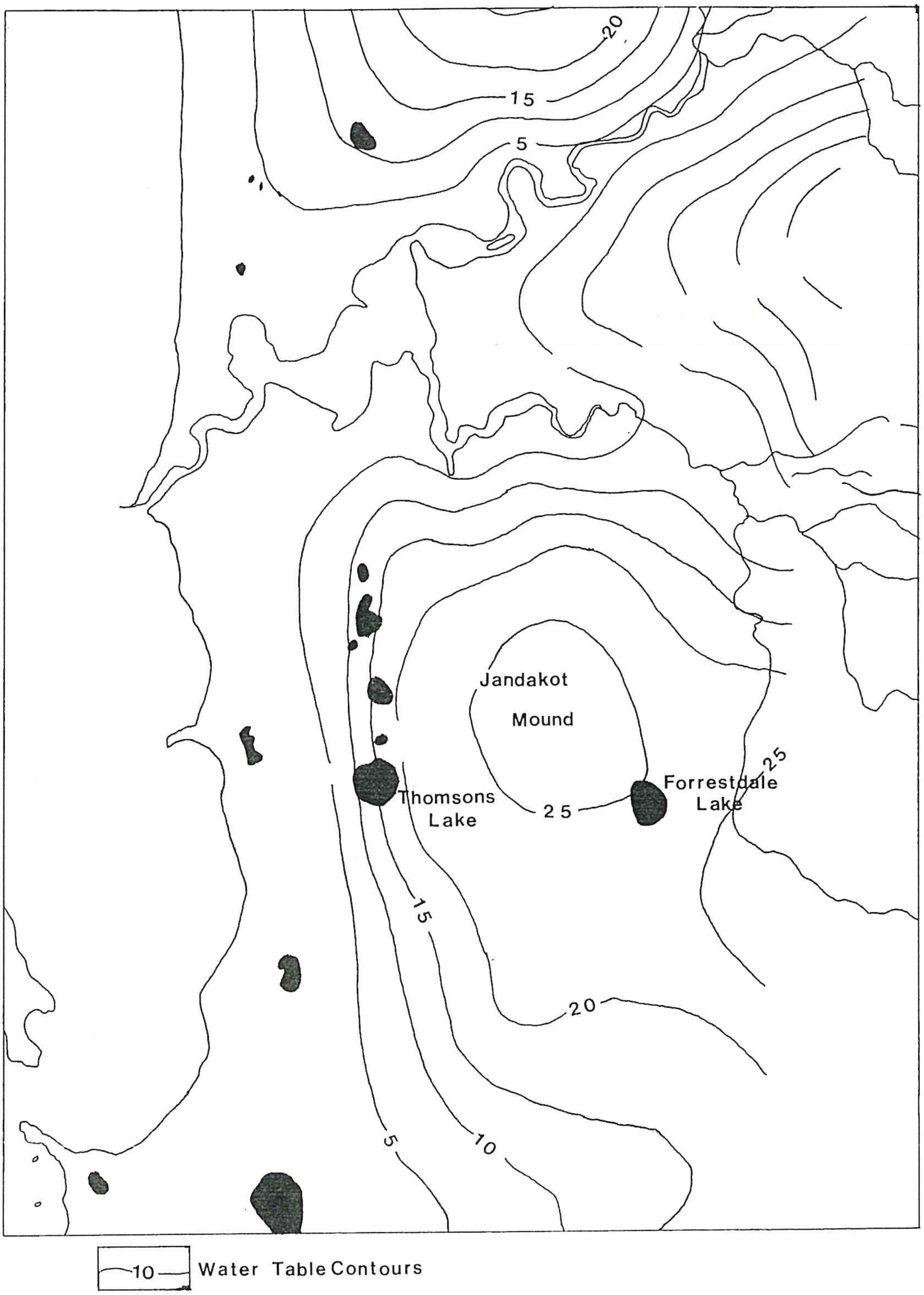


Fig.4: Position of Lakes in Relation to the Jandakot Groundwater Mound.(After Metropolitan Water Authority,1983).

the two lakes under consideration. Water within these mounds drains outwards at right angles to the water table contours (Metropolitan Water Authority, 1983) and drains into the ocean and rivers. Where the water table intercepts dune depressions, wetlands occur; Thomsons Lake and Forrestdale Lake are two such wetlands. As well as drainage to the coast and rivers, evapotranspiration from these wetlands represents a significant water loss from the aquifer. Pumping of water by public and private bores also depletes the water levels.

Forrestdale Lake

Forrestdale Lake (Figs. 5 and 6), an oval lake (with an area of 198.7ha), may be considered to be important for several reasons. Firstly it is in a relatively natural state and is a good example of a Swan Coastal Plain wetland, and it is the largest wetland within the geological area. The lake has considerable value as a waterbird habitat, providing breeding grounds for a large number of Australian species, and overwintering habitat for a variety of northern hemisphere species. For this reason it is under consideration for nomination as a wetland of international significance, by the Royal Australian Ornithological Union (Arnold and Wallis, 1986). Management of the invertebrate fauna is essential in both lakes in light of their capacity as waterbird refuges. The purpose of the Forrestdale Lake Nature Reserve (A class, No. 24781), protection of fauna and flora, and recreation, recognizes the lake's ecological importance.

In 1885 the first settlement by the lake was established and by 1948, 50% of the area surrounding the lake had been cleared for residential or small agricultural subdivisions. During this period some of the surrounding swamps were drained. Up until this time the southern and eastern regions of the lake surrounds had been relatively little interfered with; however

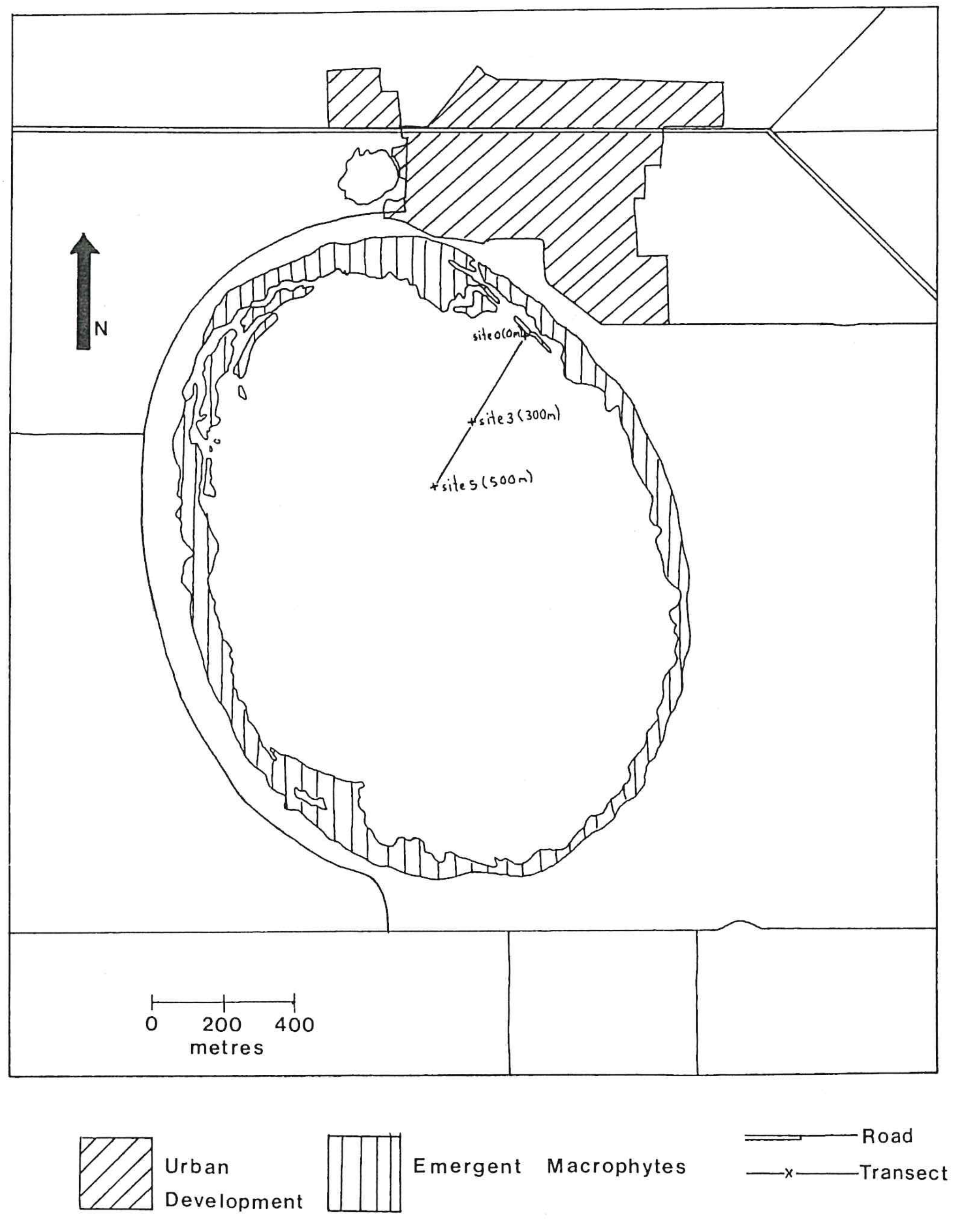


Figure 5: Forrestdale Lake, Showing Position of Transect.

a

b

Fig. 6: Forrestdale Lake. (a); dry lake, March 1986.
(b); flooded lake, July 1986.

between 1948 and 1963 these areas were also partially cleared. By the 1970s the town of Forrestdale had become established around the northern fringes of the reserve.

Water seeps into this lake from the Jandakot mound to the west, and also from the Armadale drainage system to the east (Metropolitan Water Authority, 1983). No natural surface drainage to the lake occurs, although man-made drains now enter and, during periods of high water levels, leave the lake. Drainage from agricultural and urban land to the north, west and south occur from drains dating from 1916 onwards (Bartle *et al.*, 1986). Water flowing downward from the Jandakot mound rises above the lake bed to flood the lake, although rainfall is also a major source of water. The average yearly rainfall for the years 1958-85 was 867mm (Fig. 3) (Bureau of Meteorology Data, measured at nearby Jandakot on the same longitude). High summer temperatures and low summer rainfall result in a net evaporation rate of 228 mm per month for Perth wetlands in summer (Seddon, 1972). Over the last 13-15 years the rainfall in Perth has been below average, and this has resulted in low water levels over the last 10-15 years (Bartle *et al.*, 1986). However, pumping of water from the public and private bores is likely to have also affected water table levels around the mound. The lake has dried out completely in summer since at least 1980, but this was not always the case (Arnold and Wallis, 1986). According to Bartle *et al.*, (1986) the annual evaporation for Forrestdale Lake is twice the average annual rainfall, so the extra water must come from the drains and groundwater seepage, no doubt similar processes occur in nearby wetlands, including Thomsons Lake.

Normally in seasonal wetlands, nutrient concentrations peak as the water levels fall in summer, but according to Figures 14-16 of Bartle *et al.* (1986), this pattern has been disrupted since around 1980. Since this time total phosphorus concentration has been significantly low, yet still above

Vollenweider's standard eutrophic level (Vollenweider, 1971). While no studies have confirmed that the low phosphorus levels are due to increased growth of *Typha*, it seems a likely explanation. At the same time a large increase in inorganic nitrogen concentration since 1983 has been accompanied by a fall in organic nitrogen concentration. Perhaps this increase in nitrates has been due to drainage of urban land and leaching of domestic and agricultural fertilizers. Other factors affecting the nutrient status of the lake includes pesticide spraying for midges and septic tank leakage.

Forrestdale Lake lies at a change from siliceous sand of the Bassendean dunes to the clay-textured soils of the Guildford Formation (Pinjarra Plain), and this is reflected in its sediments. Overlying dune sand on the lake bed is peaty material with a high clay content.

Growing around the edge of Forrestdale Lake is a complex of eight vegetation types, listed in Bartle *et al.* (1986). Probably most important as far as the macroinvertebrates are concerned are the dense stands of *Typha* that have colonized the littoral fringe (Fig. 5). Prior to 1968 few reeds grew around the edges of the lake, at this time *T. orientalis* was first observed. Since then it, and less common reeds, have come to dominate the entire surrounds of the lake. The dominant aquatic species is *Ruppia polycarpa* (van Alphen 1983), which occurs over the whole lake during spring; *Chara* is also very common (Bartle *et al.*, 1986).

Forrestdale Lake is a very productive wetland with most of its foreshores remaining undeveloped. For this reason it is used by a great many water birds, 63 species being recorded by Bartle *et al.*, 1986, from various sources. At the present time the major stresses on the wetland are:

- possible lowering of the water levels due to pumping from the public water supply area; and,

- nutrient enrichment from surrounding urban and agricultural areas.

Thomsons Lake

Thomsons Lake (Figs. 7 and 8) is situated in a depression between the limestone of the Spearwood Dunes, and siliceous material of the Bassendean System (Fig. 1). The lake is a similar shape to Forrestdale Lake, but slightly smaller (172 ha.). It is in the centre of a 509ha Class 'A' nature reserve (No. 15556). Surrounding the lake and its littoral area is a variety of vegetation associations, dominated by *Eucalyptus*, *Melaleuca* and *Banksia* species and their associated understoreys. A thick band of *Baumea articulata* surrounds this lake, with some *Typha* scattered through the *Baumea*. The aquatic vegetation is dominated by *Myriophyllum salsugineum* after flooding, which becomes established over the entire lake bottom (well before the annual aquatic vegetation of Forrestdale Lake does). In both lakes the dry lake bed is colonized by terrestrial plant species, moving inwards from the edge of the lake, as can be seen in Fig. 6a.

As with Forrestdale Lake, Thomsons Lake is important both scientifically and aesthetically as a relatively intact coastal wetland, and as an important water bird habitat, 47 species being listed by Crook and Evans (1981). Originally the reserve was set aside for drainage purposes (Crook and Evans, 1981) after it was formally brought to the attention of the Department of Fisheries and Wildlife in 1954. In 1955 its purpose was changed to 'drainage and conservation of fauna'. Due to illegal grazing and woodcutting in the reserve, it was vested in the Fauna Protection Advisory Committee, (now the Western Australian Wildlife Authority), which has the power to control these activities. In 1969 its purpose was changed

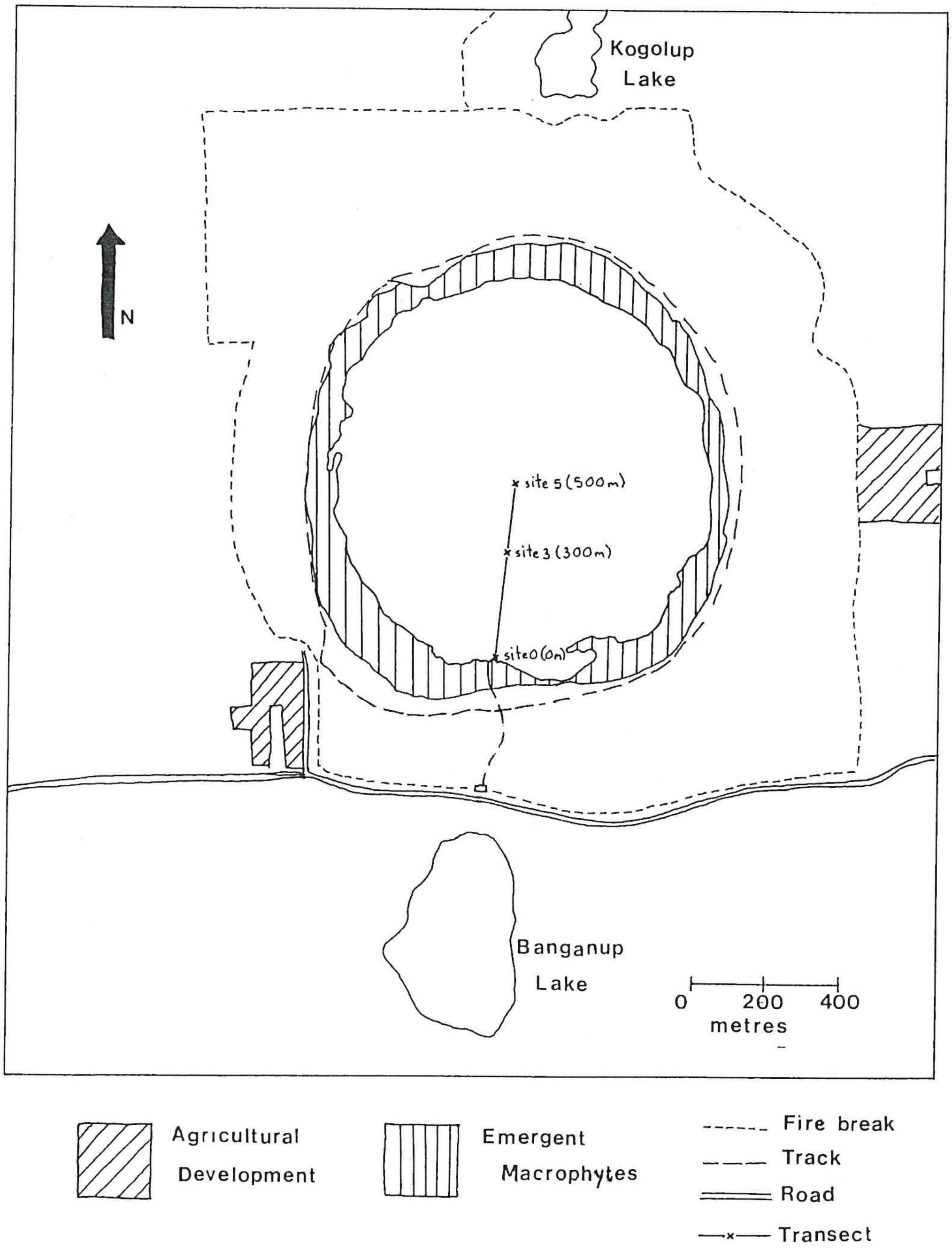


Figure 7: Thomsons Lake, Showing Position of Transect.

a

b

Fig. 8: Thomsons Lake.(a); dry lake, March 1986.
(b); flooded lake, July 1986.

to 'fauna conservation, research and drainage', and in the following year it was given the status of an 'A' class reserve. The buffer zone around the lake is quite wide; however, clearing of land outside the reserve to the east and south-west have occurred, mainly for small scale agriculture. To the east of the lake this development has occurred around neighbouring swamps. Man made drains enter Thomsons Lake from the north, bringing water from Kogolup Swamp, and from the east. The eastern drain comes from agricultural land, and this source enriches the lake with nitrogen and phosphorus (O'Connor *et al.*, 1976), causing intermittent blooms of the cyanobacteria *Microcystis aeruginosa* (Crook and Evans, 1981). Significant decreases in oxygen concentrations have been recorded by O'Connor *et al.* (1976), presumably due to these blooms. Natural drainage to the lake is from the Jandakot groundwater mound to the east and from the limestone ridge to the west (Beckle, 1984). Seasonal variation in water level in parallel with the water table is normal, and complete drying of the lake common, while the maximum recorded depth is 3.6m. Average yearly rainfall is slightly less than that for Forrestdale Lake, for the period 1958-85 it was 797mm (Bureau of Meteorology data, recorded at the nearby Spearwood monitoring station). As with all seasonal wetlands, nutrient concentrations vary with water level and the data for 1986 are presented in this study.

The sediments are very peaty, and appear to contain less clay material, data on sediment analyses are also presented in this study.

Stressors of this lake appear to be nutrient enrichment from artifical drains and possibly draw-down effects of the public water supply scheme. It should be noted, however, that slightly enriched waters may be beneficial to the water birds being protected, as overall production of the waters may be increased, as Bartle *et al.* (1986) pointed out.

Chapter 2

Methods and Materials

Sampling Sites

At each lake a 500m transect was measured out from the littoral vegetation to the lake centre (Figs. 5 and 7). Stakes placed at 0, 300 and 500 metres along this transect were used as markers for sampling sites. These sites were thus named site 0, site 3 and site 5. Stratified random sampling was used; this involved the use of random numbers to determine the precise site for each replicate, around the fixed transect site. All sampling was carried out during daylight hours.

Fauna Sampling of 'Dry' Sediments

In late February/early March the lake sediments were sampled to determine which, if any, invertebrates inhabited the dry lake bed. Two replicate samples were taken at each site using a cylindrical corer of 9.4cm diameter and 15.6cm depth. The samples were placed in plastic bags without preservative. In the laboratory approximately $^1/_4$ of the core was placed in glass jars and flooded with aerated water. This was done so that any eggs or dormant stages might hatch or become active. The remainder of the core was preserved with 70% ethanol until sorting.

Fauna Sampling of the Flooded Lakes

The lakes both began to fill towards the end of May, and the first pump samples were taken in the last week of this month, subsequent sampling dates are set out in Table 1.

Ten replicate samples were taken during the May sampling. The diversity, species richness, abundance and variation in species richness were plotted against the number of replicates, to determine how many replicates needed to be taken at each site to sample the fauna adequately. Upon the basis of these analyses it was decided that six replicates would be appropriate.

A bilge pump was used to remove a known volume of water, (18.63 x depth(cm) ml), from within a 15.4cm diameter PVC cylinder, the upper few centimetres of sediment were also pumped out. The material pumped out was passed through a 250μm net before bagging and preservation in 70% ethanol. This net was also used to take semi-qualitative samples, the net being pushed along the surface of the sediment for one minute.

Sorting and Identification of Fauna

The samples of dry lake bed were hand sorted after passing through 2mm and 600μm sieves. The <600μm material was made up to 400ml with water and 100ml was sorted in 10ml samples. This method proved to be very time consuming, and for this reason a sorting device was constructed (an elutriator, Fig. 9). This device is a modification of the design in Magdych (1981). It consists of a section of PVC piping, joined to air and water supplies at its base, and an output hole at the top. A coverable opening allows the sample to be poured into the rising water where uprushing air and water carries the more buoyant organic matter to the outlet, the heavier sediments sink to the bottom and come to rest on the sieve plate. Before putting the sample through the elutriator a 2mm sieve is used to remove large particles and invertebrates. The elutriate is passed through a 180μm sieve as it pours from the elutriator. Material in this sieve was then split into two size classes with the aid of a 600μm sieve. One

SITE / DATE	SITES (for both lakes)		
	SITE 0	SITE 3	SITE 5
February / March	C	C	C,S*
May			P,S
June		P,S	P,S
July	P,S	P,S	P,S

Table 1: Sampling Regime. C = core sample, P = pump sample, S = sweep sample

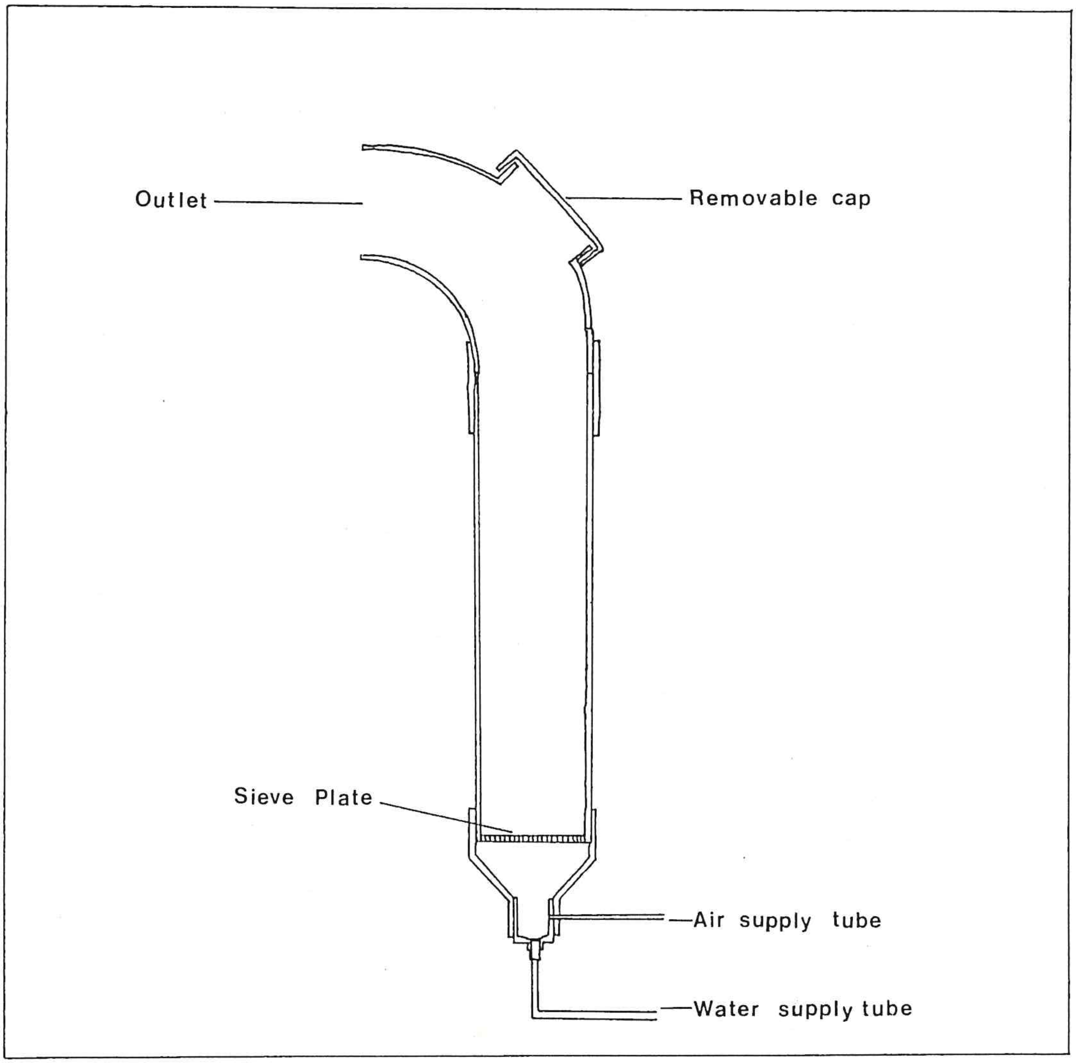


Figure 9: Elutriaor.(Modification of Design by Magdych, 1981).

eighth of each size class was sorted under the microscope. Subsampling was carried out initially by making the volume of sediment water mixture up to 400ml in a beaker, and vigorously stirring prior to pouring out a known volume of this in 10ml lots. Later a subsampler was constructed which allowed the sample to be evenly halved.

All copepods and cladocerans were grouped as zooplankton and treated separately as they are not strictly macroinvertebrates. Identification usually began with Williams (1980), and the following general texts: Bayly, Bishop and Hiscock (1967); C.S.I.R.O. (1970) and Merrit and Cummins (1984), then more specialized keys were used as follows: Crustacea; Morrissy (1977) and Williams (1962), Hemiptera; Knowles, (1974), Lansbury (1970) and Wroblewski, A. (1970), Coleoptera; Charpentier (1967), Mathews (1982a, b), Watson (1962) and Watts (1963), (1978), Diptera; Edwards (1964), Mollusca; Smith and Kershaw (1979). Details of these keys are given in the Bibliography.

Statistical Analysis of the Fauna Data

Numbers of animals per sample were converted to numbers per square metre of lake bed. From these data total abundance, mean and standard error of the abundance, of each species was calculated. The diversity of each sample was found using the Shannon-Weiner index:

$$H^1 = \sum_{i=1}^{s} \left(\frac{Xi}{N} . \log(e) \frac{Xi}{N} \right)$$

where: H^1 = diversity

s = number of species in sample

Xi = number of individuals in species i

N = total numbers of individuals in the sample

The Jaccard coefficient of similarity was calculated to compare sites over space and time. The formula is as follows:

$$J = \frac{b + c}{a + b + c}$$

where: J = similarity

a = number of species occurring in both samples

b = number of species occurring in sample 1 but not sample 2

c = number of species occurring in sample 2 but not sample 1

This index of similarity is based on presence/absence data and thus compares species composition only.

One-way analysis of variance was carried out using abundance, species richness and diversity to compare sites at each lake over space and time. The same analyses were carried out to compare species richness, abundance, diversity and similarity between the lakes.

Water Chemistry

Once every month for three months, (June to August), chemical and physical parameters of the lakes were measured. Similar measurements taken by S. Rolls of Murdoch University were used in conjunction with my own data. Water temperature, (using a standard alcohol thermometer), depth and pH (with an Activon digital pH/mV meter), were measured in the field. Samples of water were taken in 'Nasco Whirlpaks' for analysis of nitrogen and phosphorus compounds. The analyses were carried out by the Centre for Water Research at the University of Western Australia. Total nitrogen and phosphorus were measured using the Technicon Industrial Method No. 329-74 W/D B (Technicon Industrial Systems 1977). Nitrite/Nitrate measurements were carried out using the copper-cadmium reduction technique, as described in Tehnicon Industrial Systems (1977). Ammonia analysis was carried out by the cyanurate method, also described in Technicon Industrial Systems (1977). Ortho phosphate was measured by a method derived from the CSIRO Standard Methods for Marine Chemistry, Major (1972). A 500ml bottle of water was also taken for laboratory conductivity measurements (using the Activon Digital Conductivity Meter PTI-58) and chlorophyll *a* determination. Chlorophyll *a* was measured using the fluorometer technique which measures chlorophyll *a* and its breakdown products (phaeophytins).

CHAPTER 3

RESULTS

Lake Sediments

The sediments of the lake bed of Thomsons Lake had a higher organic content, ranging from 27% to 50%, than Forrestdale Lake, which ranged from 2% to 33% (Fig. 10). In both lakes the littoral site had the lowest organic content. This difference was especially evident in Forrestdale Lake. Unlike Forrestdale Lake, Thomsons Lake organic content differed significantly between the 300m and 500m sites. Within each site organic content differed very little over the study period, although some sites showed an increase in July. It should be noted, however, that the organic content was assumed to remain constant over the dry period; after February and March only flooded sites were sampled (Table 1).

The distribution of sediment particle sizes in the lakes is given in Figs. 11 and 12 which reveal that there is large variability between sites and sampling dates. Fig. 11 shows that a slight trend towards smaller particle sizes occurs at each of the Thomsons Lake sites over time. Forrestdale Lake shows no such trend, and appears to be more constant, except for relatively less fine gravel at site 0.

Water Chemistry

Similar concentrations of nitrogen were present in both lakes although concentrations in Thomsons Lake appeared to be more variable (Figs. 13 and 14). In both lakes there is an overall drop in total nitrogen levels, the net change being almost identical (Figs. 13a and 14a), from 3150 to 2300 $\mu g.l^{-1}$ in Thomsons Lake, and 3230 to 2394 $\mu g.l^{-1}$ in Forrestdale Lake, between June and August. Almost all the nitrogen is in

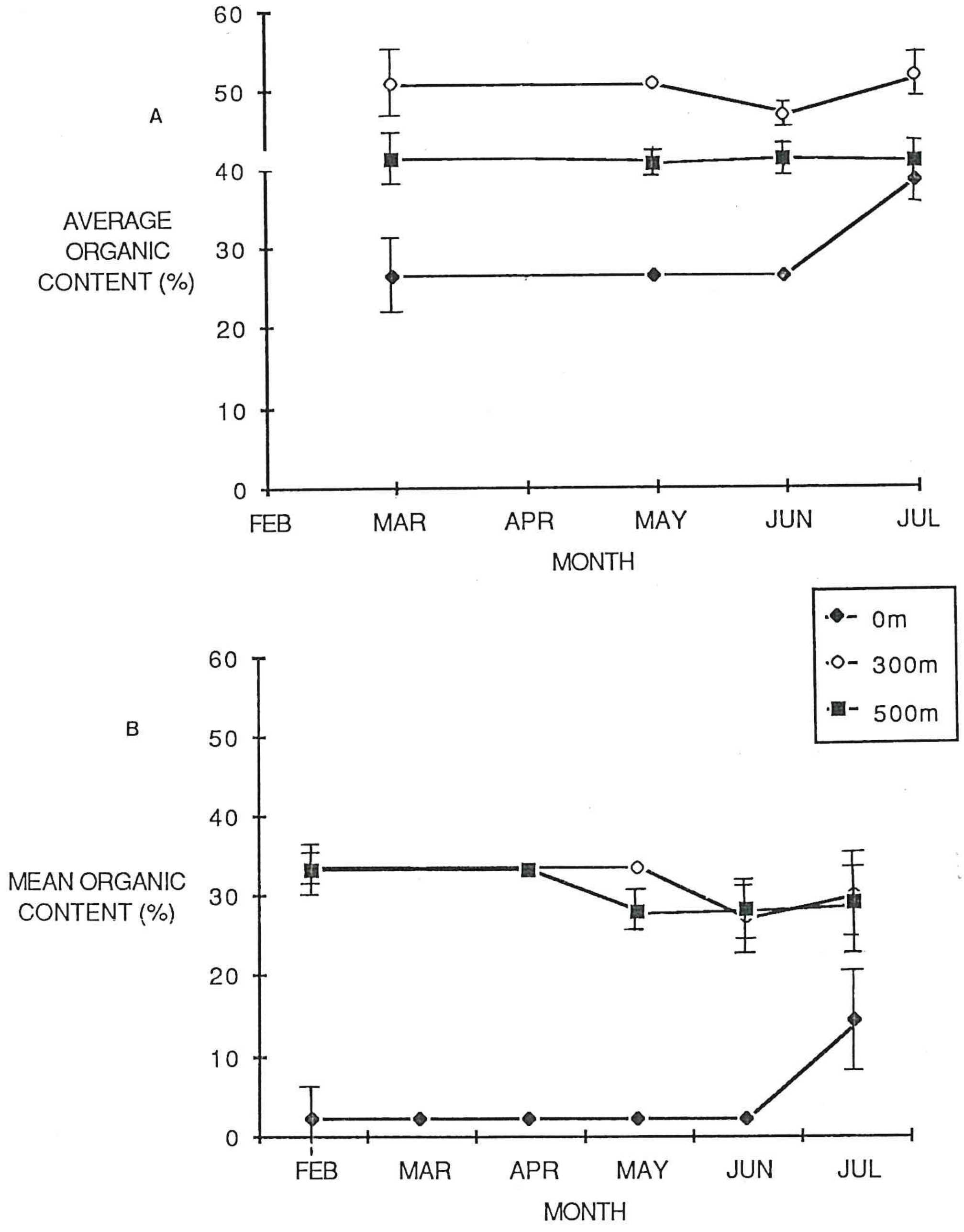


Fig. 10: Organic Content of Lake Sediments.
(a); Thomsons Lake, (b); Forrestdale Lake.

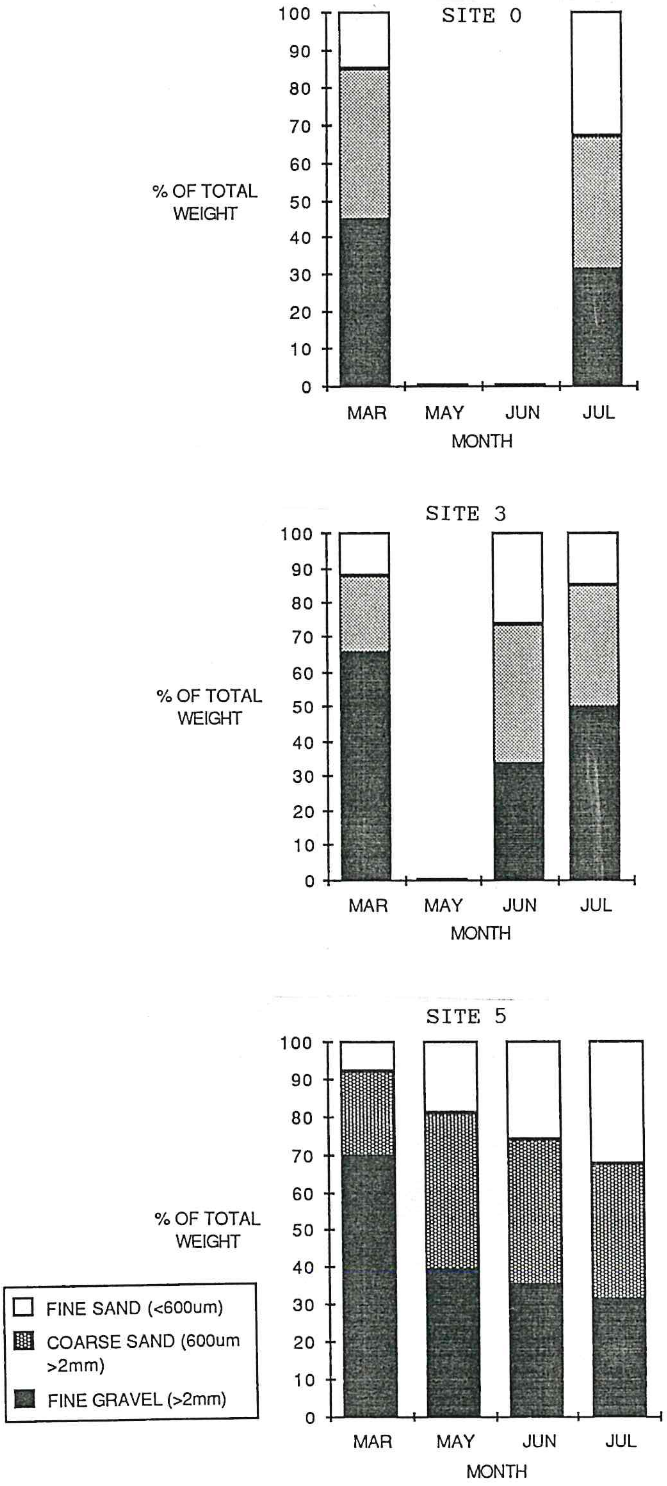


Fig. 11: Sediment Particle Size Distribution of Thomsons Lake Sediments.

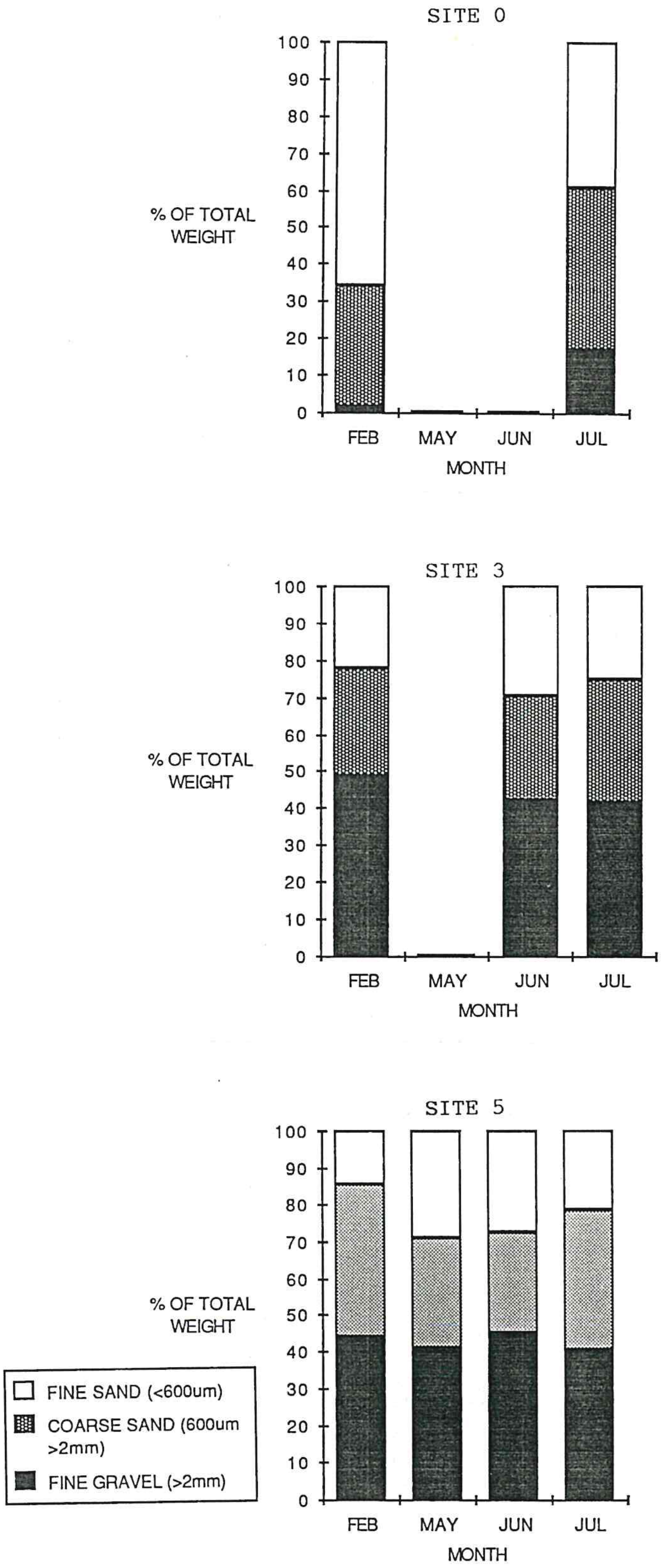


Fig. 12: Sediment Particle Size Distribution of Forrestdale Lake Sediments.

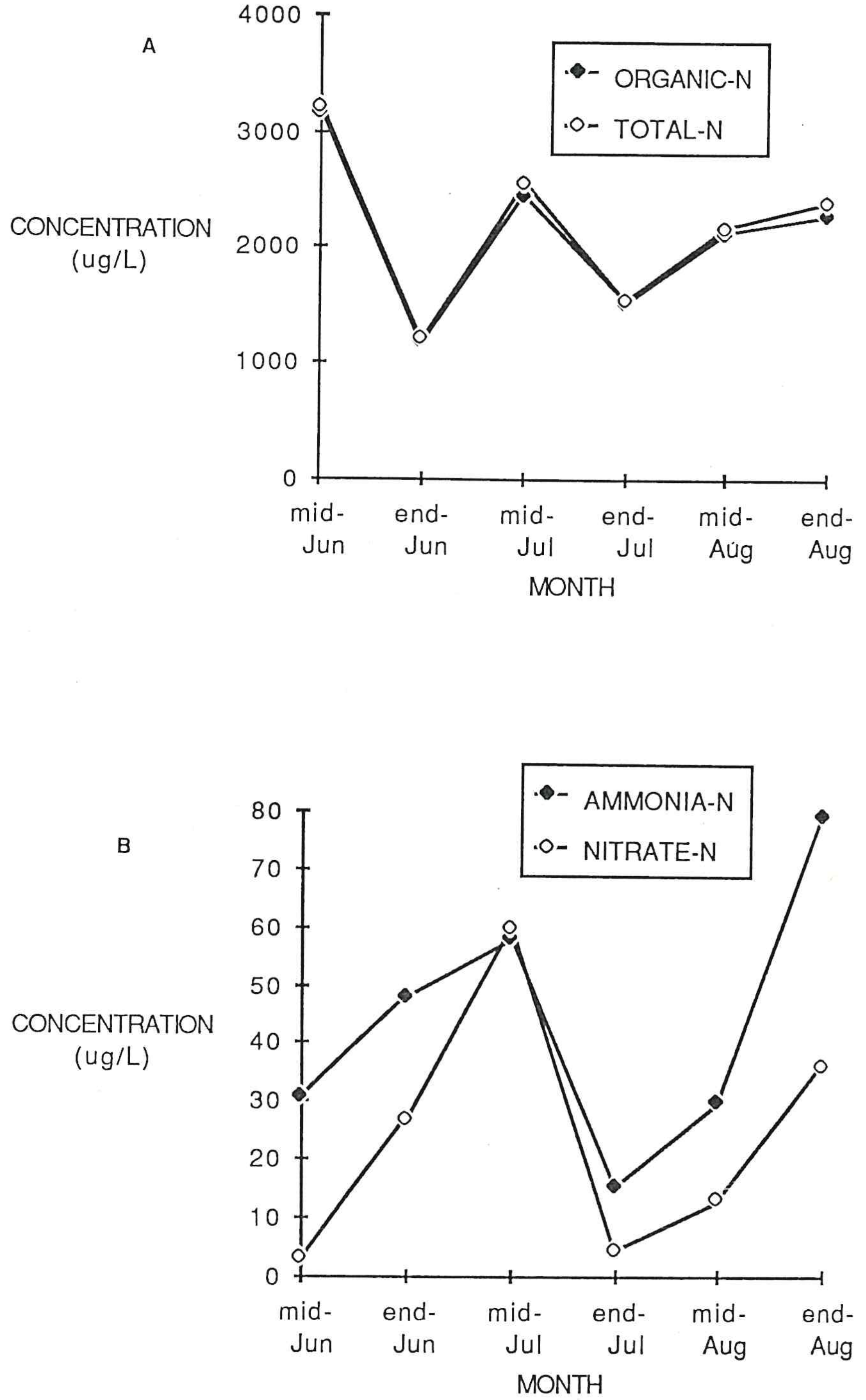
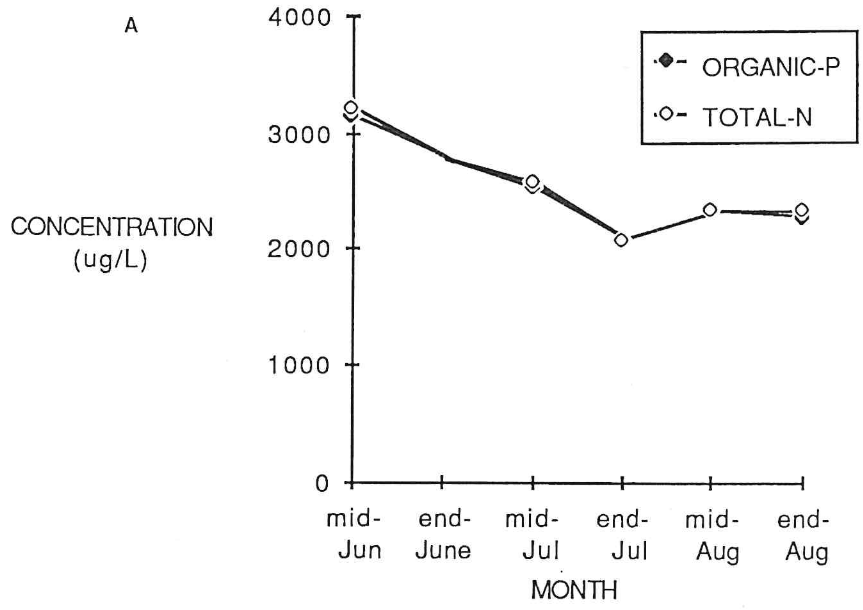


Fig 13: Thomsons Lake Nitrogen Concentrations.

(a); Total and Organic Nitrogen

(b); Ammonia and Nitrate Nitrogen.



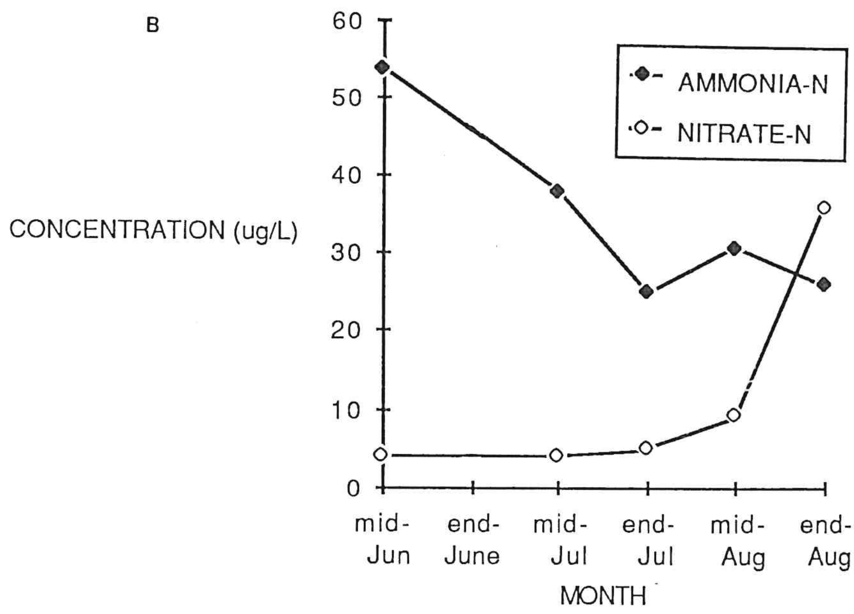


Fig.14: Forrestdale Lake Nitrogen Concentrations.

(a); Total and Organic Nitrogen.

(b); Ammonia and Nitrate Nitrogen

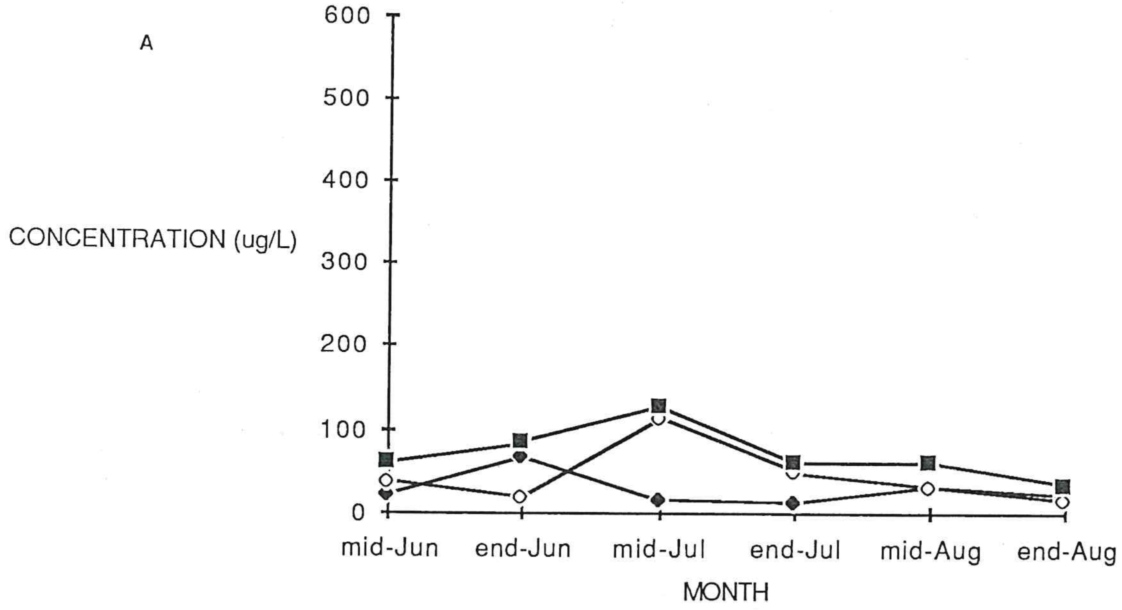
organic form, with a small percentage as ammonia and inorganic nitrogen (nitrate/nitrite). In Thomsons Lake both ammonia and the NO_3^-/NO_2^-, peaked in mid-July and fell again by the end of this month. A rise in both of these was then recorded. Forrestdale Lake showed less variation, with no significant change in inorganic nitrogen (NO_3^-/NO_2^-) until late August. Ammonia concentration in Forrestdale Lake decreased by approximately 50% between mid-June and late July, then remained at around 25-30 $\mu g.l^{-1}$ (Fig. 14).

The concentration of phosphorus differed greatly between the two lakes (Figs 15a, b). Forrestdale Lake total phosphorus rose throughout the study period, reaching 580 $\mu g.l^{-1}$. Initially most of this phosphorus was organic, but this form peaked in July and then decreased steadily (Fig. 15b). Inorganic phosphorus rose throughout the same period to become the dominant form by the end of August. The total phosphorus concentration in Thomsons Lake was much lower and constant, peaking at 132 $\mu g.l^{-1}$ in mid-July. Organic phosphorus also peaked at this time and was the dominant phosphorus form until the end of July. Usually organic and inorganic phosphorus varied inversely, except in Forrestdale Lake before mid-July (Fig. 15).

Chlorophyll *a* concentration was measured as an indicator of algal growth. In Forrestdale Lake maximum chlorophyll *a* concentrations were recorded in mid-July, at 14.5 $mg.m^{-3}$ (Fig. 16a). Thomsons Lake chlorophyll *a* rose to peak at the end of June, reaching 22.5 $mg.m^{-3}$, before falling to a figure of less than 3 $mg.m^{-3}$ by late August (Fig. 16b).

Conductivity, measured as milliSiemens per centimetre, is used as a measure of ionic concentration. An overall drop in conductivity occurred over the study period in both lakes (Fig. 17). Thomsons Lake had the highest conductivity initially, (3.61mS) compared to Forrestdale Lake

A



B

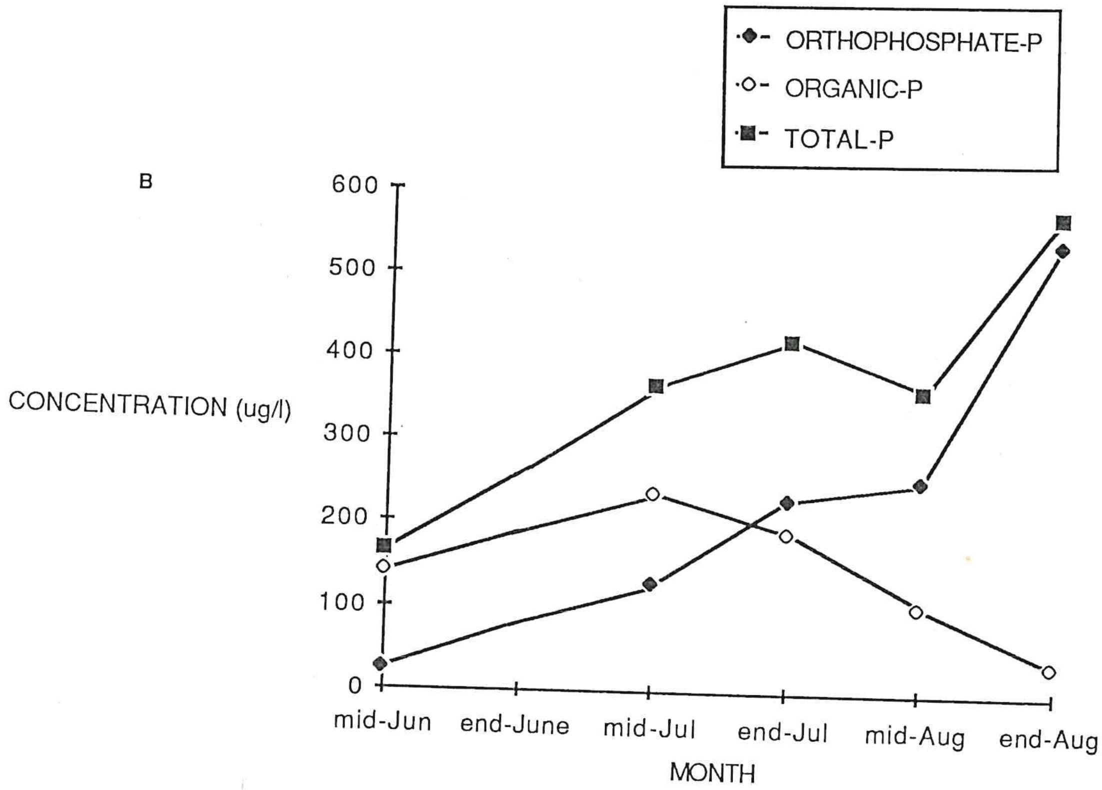


Fig 15: Concentration of Phosphorus Compounds.
(a); Thomsons Lake, (b); Forrestdale Lake.

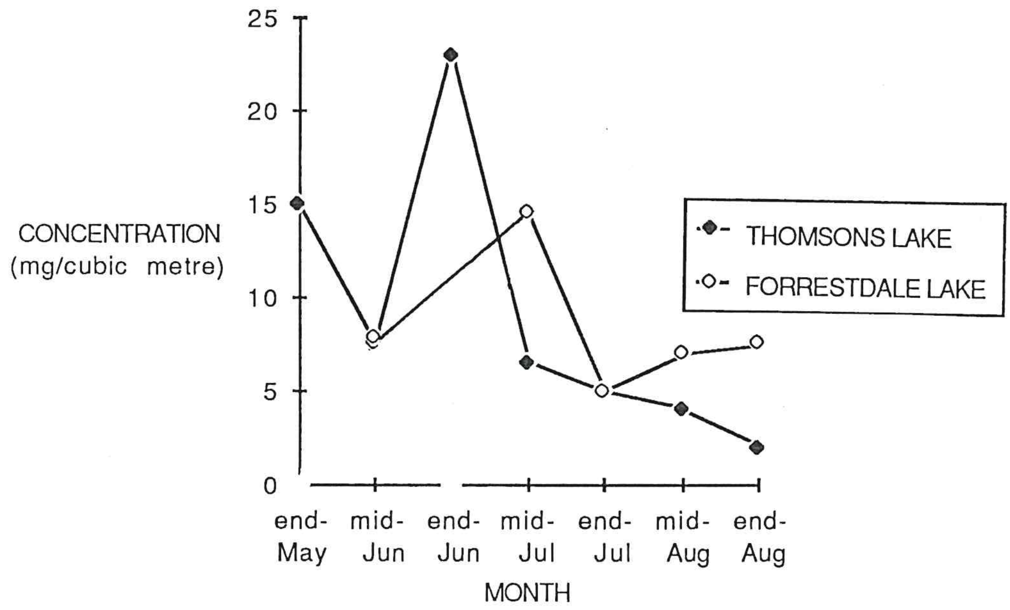


Fig. 16: Changes in Chloropyll a Concentration.

(2.27mS); however by the end of August the lakes had almost equal conductivities (1.57 and 1.52 for Thomsons and Forrestdale Lakes respectively).

The pH of Thomsons Lake varied between 7.4 and 10.1 while increasing slightly from 8.0 to 9.3 between June and August (Fig. 18b). Forrestdale Lake remained close to a pH of 8.0 throughout the sampling period. Thus both lakes are alkaline, Thomsons Lake more so than Forrestdale Lake.

Water regimes

All the sampling sites at Thomsons Lake were dry in March but the bed of the lake at the site nearest the centre (site 5) was very moist. To the north-west of the transect an area of flooded sediment persisted for a while but subsequently it too dried up. The littoral site, (site 0), was dry at the surface but moist below the first few centimetres in mid-March. By the end of March site 0 was dry and cracked down to at least five or six centimetres, and the surface of site 5 was dry. Towards the end of May sufficient rainfall occurred to cause the flooding of the deeper parts of the lake (Fig. 19b), including site 5. Site 3 only became deep enough for pump sampling in June, and site 0 by July. In the latter half of July the greatest increse in depth occurred, site 5 at this time was 70cm deep.

The water regime of Forrestdale Lake (Fig. 19a), was similar to that of Thomsons Lake, the main difference being that site 5 of the former was under one to two centimetres of water (mainly in pools) at the end of February. The littoral site (site 0) was dry at the surface in February but was moist below the upper few centimetres, as was site 3. By the end of March site 5 was also dry. The May rains flooded sites 3 and 5 (Fig. 19a), however, only site 5 was deep enough to pump sample in this month. Site

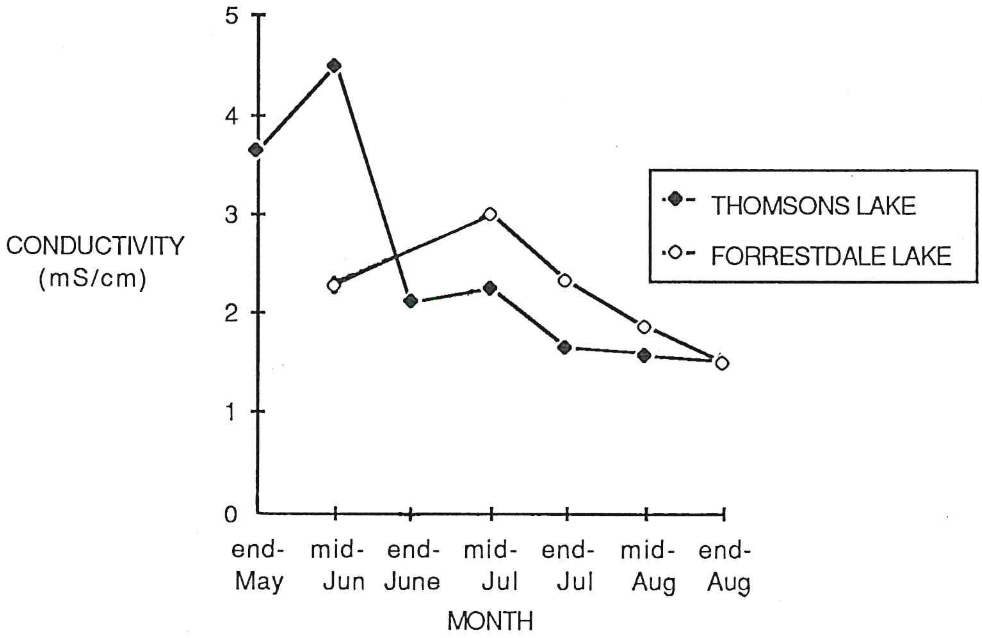


Fig. 17: Changes in Conductivity.

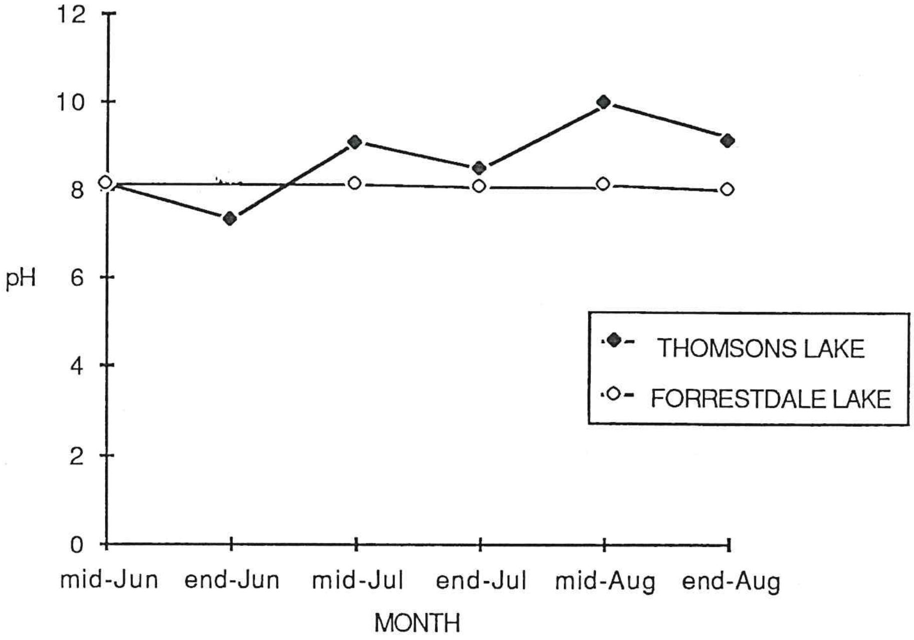


Fig. 18: Changes in pH.

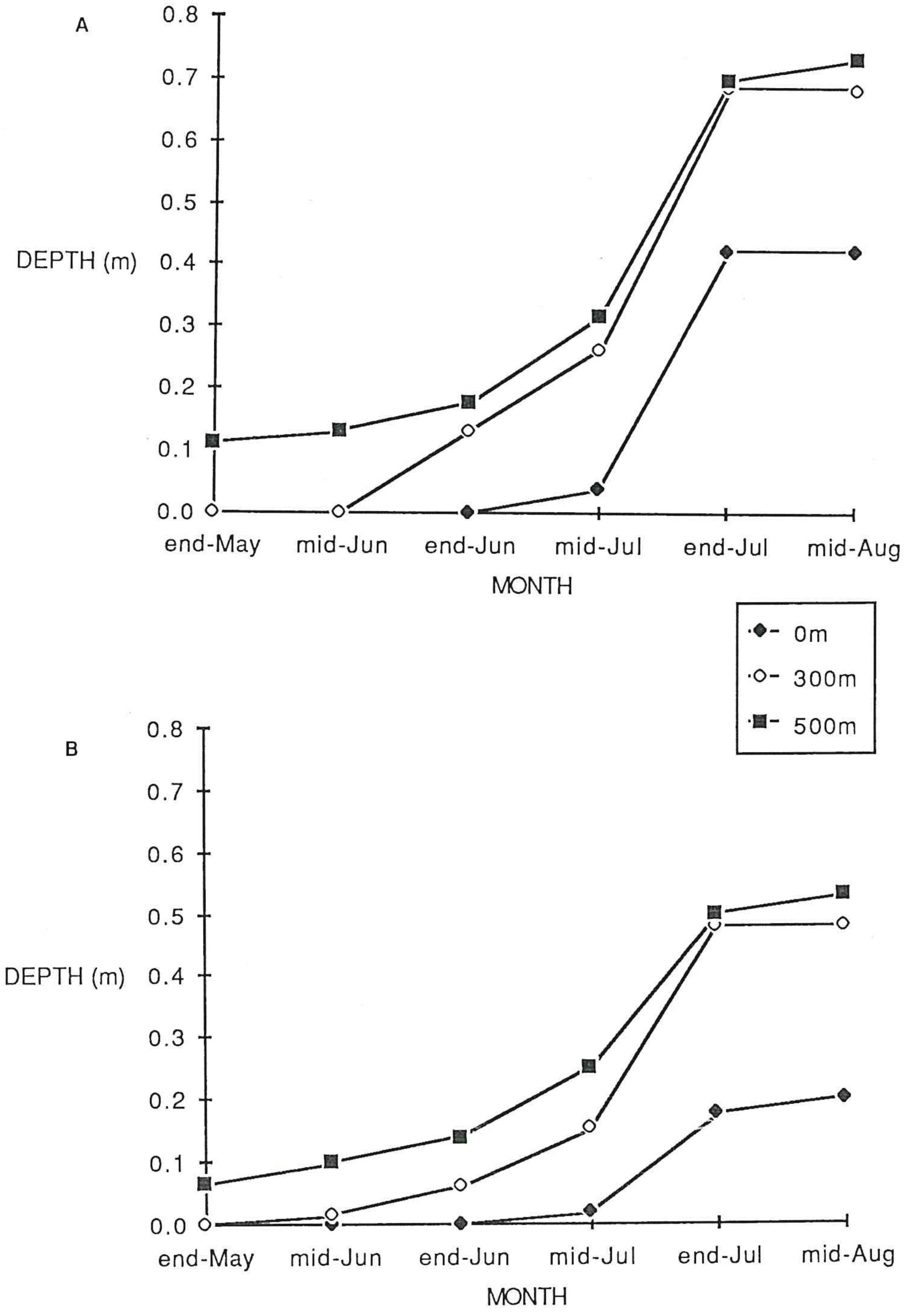


Fig. 19: Water Depths.(a); Thomsons Lake,

(b); Forrestdale Lake.

0 became deep enough for pump sampling in July, and water levels remained constant on the last two measurement occasions (mid-July and August).

Composition of the Invertebrate Fauna

Turbellaria: At least three species of flatworm were found, in Thomsons Lake only. Species found in pump samples were all classified as one taxa, as a result of changes in colour and morphology upon preservation in alcohol. The dry cores were not preserved in the field as some of each core was to be kept in jars with water. Examination of these jars yielded three distinct species. Turbellarians seem to prefer the moist conditions as they were found only in site 5 of the dry lake, and then only after artificial inundation. After flooding they were found in all three sites (Table 2).

Nematoda: Nematodes appear to inhabit the dry soil, but in both lakes they were only observed after dry cores were artificially inundated for several days. Nematodes were only found at the littoral site in both lakes (Tables 2 and 3).

Gastrotricha: These microinvertebrates were observed only in July in both lakes, and appeared to be more widely distributed in Thomsons Lake. They were not counted as macroinvertebrates.

Oligochaeta: Two species of oligochaetes were found, only one of which occurred in Forrestdale Lake. Oligochaete sp. 1 was the more abundant and widely distributed, sp. 2 being found only at site 3. No oligochaetes were found before flooding.

Mollusca: *Physastra* sp. and *Physa acuta* were observed only in Thomsons Lake at site 0, near the rushes. *P. acuta* is an introduced species, Smith and Kershaw (1979). Live specimens of both species were found only after flooding. Shells of *Coxiella* sp. and *Isidorella* sp. were found in Forrestdale Lake near the Typha stands; however no live specimens were observed.

Arachnida: In all, seven species of mites were recorded, three of which were found to be of terrestrial origin. *Limnesia* sp. (Limnesiidae), was found in both lakes, but only after flooding. Of the remaining three species *Limnochares australica* and a species of the suborder Mesostigmata were restricted to the edge of Thomsons Lake. An oribatid mite species was also collected 300m into this lake at site 3. Parasitic mites were observed on a beetle specimen but not identified or counted.

Zooplankton: All Copepoda and Cladocera were grouped as zooplankton, and were found at all sites after flooding. Harpacticoid, Cyclopoid and Calanoid copepods were found in both lakes. When dry lake sediments were artificially flooded, Harpacticoid copepods emerged after about one week. Cyclopoid copepods were found in most pump samples; however Calanoid copepods were uncommon until July in both lakes.

Ostracoda: This group was usually the most abundant in terms of numbers of individuals (Fig. 22a and b). In July this subclass accounted for 89% of the Forrestdale Lake fauna, and 75% of Thomsons Lake fauna. In Forrestdale Lake 80% of the macroinvertebrates were ostracods; in Thomsons Lake they made up 73%. Eleven species were found, seven in Thomsons Lake and nine in Forrestdale Lake. Of these, four were unique to Forrestdale Lake, and two unique to Thomsons Lake (Tables 2 and 3). After flooding *Mytilocypris ambiguosa* was found in both lakes in May (in site 5) (Fig. 21), accounting for 97 and 55% of the fauna of Thomsons and Forrestdale Lakes respectively (Fig. 22a and b). In June *M. ambiguosa* increased in numbers and remained the most abundant species in both lakes in most sites, reaching the highest density at the sites near the lake centres (Fig. 21), *Eucypris virens* was also abundant in June. In Thomsons Lake in July *Sarscrypridosa aculeata* became the dominant ostracod at all sites, reaching a maximum of 24 732 at site 0 (near the Baumea zone) (Fig. 21). In Forrestdale Lake *S. aculeata* dominated only at the lake edge (88 155/m^{-3}), the density at the centre of the lake being only 769/m^{-3}. At the other two sites (at 300 and 500m along the transect), *Diacypris spinosa* was the most abundant (Fig. 21).

Amphipoda: Only one species, *Austrochiltonia subtenuis* was found in both lakes. It appears to survive in the moist layers of the 'dry' lake bed as it was found close to the *Baumea* stands in March at Thomsons Lake, and immediately after flooding in almost all sites in both lakes.

Isopoda: *Paramphisopus palustris* was the only isopod, being found in small numbers in July only. In Forrestdale Lake it was found only at site 0, in contrast to Thomsons Lake where it was found at all sites.

Decapoda: A single specimen of *Cherax quinquecarinatus* was collected in a sweep sample by the *Baumea* stands at Thomsons Lake.

Collembola: At Thomsons Lake these invertebrates were restricted to site 0; however in Forrestdale Lake they were only found at sites 3 and 5. Being very small and inhabiting the water's surface they would be at the mercy of water currents (CSIRO, 1970). They are also easily windborne so wind patterns may also determine their distribution.

Odonata: In general the Odonata appeared to be restricted to the dry lake bed, both species in Thomsons Lake being found only in March. In Forrestdale Lake a single specimen was found in May at the lake centre.

Hemiptera: All identified species belonged to the family Corixidae. *Micronecta robusta* was found in small pools of water at the centre of Forrestdale Lake but was not recorded thereafter at either lake. A single speciment of *Agraptoconxa hirtifrons* was found at the edge of Forrestdale Lake in July, and in May a specimen of *Sigara mullaka* was found at the centre of Thomsons Lake. Three types of unidentified nymphs were found (two in Thomsons Lake), which were counted separately from the identified adults; however, they may have been the same species. Since *M. robusta* adults were only found at the end of the last wet season it would seem that one of the nymph species found after flooding may have been *M. robusta*.

Diptera: Of the Diptera species, most (67% in Thomsons Lake and 69% in Forrestdale Lake) were midge larvae (Chironomidae). Although a total of 10 species of midge larvae were recorded from the two lakes, six did not appear in the samples until July, the remaining four appeared in June. In Thomsons Lake *Chironomus australis*, *C. greisidorsum* and *Prodadius villosimanus* were found in June. In Forrestdale Lake only *C. greisidorsum* and *Lymnophyes pullulus* occurred in June. Only one species, Prodadius sp. was not common to both lakes; this species, found only in Thomsons Lake, was not recorded in Edwards' (1964) key to the Chironomidae of South-Western Australia. In Forrestdale Lake, *C. australis* was the commonest species in sites 0 and 5 in July, in site 3 it was replaced by *C. curtivalva*. The remaining species never rose above densities of 50/m^2, compared to 1800 *C. australis*/m^2 at site 5. In July at Thomsons Lake *L. pullulus* was commonest in sites 0 and 5 (750 and 1080/m^2), whereas in site 3, *P. villosimanus* was the most abundant (300/m^2). In both lakes the total numbers of chironimids increased towards the centre of the lake.

Three species of the family Ceratopogonidae were found, two in Forrestdale Lake, and one in Thomsons Lake. The species in the latter was found only at the edge of the dry lake (Table 2). One specimen of a species of Tabanidae was found in Forrestdale Lake after flooding and a tipulid species was found in both lakes after flooding. The species of Sphaeroceridae was very common as pupae in the dry lake sediments, and adults emerged after the pupae were kept in moist sediment for two weeks.

Coleoptera: In Thomsons Lake this order was the most diverse taxon, with nineteen species, compared to eight in Forrestdale Lake. Four of the species of beetles in Thomsons Lake were found only in the dry/moist sediments, these being *Heterocerus flindersi*, *Atheta* sp.,

PHYLUM	CLASS	SUBCLASS	ORDER	FAMILY	GENUS/SPECIES	TLO MAR	JUL	TL3 MAR	JUN	JUL	TL5 MAR	MAY	JUN	JUL
PLATYHELMINTES	TURBELLARIA				spp.		•		•	•			•	•
ASCHELMINTHES	NEMATODA				sp.	•	•							
MOLLUSCA	GASTROPODA			PLANORBIDAE	*Physastra sp.*		•							
				PHYSIDAE	*Physa acuta*		•							
ANNELIDA	OLIGOCHAETA				sp. 1				•	•			•	•
					sp. 2				•					
ARTHROPODA	ARACHNIDA		HYDRACARINA	LIMNESIIDAE	*Limnesia sp.*		•						•	
				LIMNOCHARIDAE	*Limnochares australica*		•							
			ORIBATIDA (SUBORDER)		sp.		•		•					
			MESOSTIGMATA (SUBORDER)		sp.		•							
	CRUSTACEA	(ZOOPLANKTON)	CLADOCERA AND/OR COPEPODA		spp.		•		•	•		•	•	•
		OSTRACODA			*Mytilocypris ambiguosa*			•	•	•		•	•	•
					Candonocypris novaezelandiae		•		•	•			•	•
					Sarscypridopsis aculeata		•			•				•
					Gomphodella sp.		•							
					Eucypris virens				•				•	
					sp. 1				•					
					sp. 2		•							
		MALACOSTRACA	AMPHIPODA	CEINIDAE	*Austrochiltonia subtenuis*		•	•	•	•		•	•	•
			ISOPODA	PHREATOICOIDAE	*Paramphisopus palustris*		•			•				•
			DECAPODA	PARASTACIDAE	*Cherax quinquecarinatus*		•							
	COLLEMBOLA		COLLEMBOLA		spp.		•							
	INSECTA		ODONATA	SYNTHEMIDAE	sp.	•								
					unidentified nymph			•						
			HEMIPTERA	CORIXIDAE	*Sigara mullaka*							•		
					unidentified nymphs sp. 1		•					•		
					sp. 2							•		•
			DIPTERA		sp. (larvae)				•					
				CERATOPOGONIDAE	sp. 1	•								
					sp. 2		•					•		
					sp. 3		•		•				•	•
				TIPULIDAE	sp.		•							
				SPHAEROCERIDAE	sp.	•								
				CHIRONOMIDAE	*Chironomus australis*		•		•	•				•
					C. griseldorsum		•		•				•	•
					C. intertinctus		•			•				•
					C. alternans		•			•				
					Cladopelma curtivalva		•							•
					Dicrotendipes conjunctus									
					Procladius villisomanus		•		•	•			•	•
					Procladius sp.					•				
					Lymnophyes pullulus		•							•
					Tanytarsus fuscithorax		•			•				
			COLEOPTERA	HALIPLIDAE	*Haliplus sp.*		•							
				HYDROCHIDAE	*Hydrochus sp.*							•		
				CURCULIONIDAE	sp.		•			•				
				HELODIDAE	sp.		•							
				HYDROPHILIDAE	sp. (larvae)		•							
					Berosus sp. (larvae)		•			•				
					Hydrous sp.		•							
				HYDRAENIDAE	*Octhebius sp.*				•					
				HISTERIDAE	sp.		•							
				DYTISCIDAE	*Chostonectes*		•			•				
					Limbodessus compactus		•			•		•		
					Hydrovatus opacus								•	
				HETEROCERIDAE	*Heterocerus flindersi*			•						
				CHRYSOMELIDAE	*Donacia sp.*		•							
				CARABIDAE	sp.			•						
				STAPYLINIDAE	*Athera sp.*			•						
					Falagria sp.							•		
				PTILODACTYLIDAE	sp. (larvae)	•								
				HELMINTHIDAE	sp.		•							

Table 2: Species List for Thomsons Lake.

PHYLUM	CLASS	SUBCLASS	ORDER	FAMILY	GENUS/SPECIES	FLO FEB	JUL	FL3 FEB	JUN	JUL	FL5 FEB	MAY	JUN	JUL
ASCHELMINTHES	NEMATODA				sp.	•	•							
ANNELIDA	OLIGOCHAETA				sp. 1		•			•				•
ARTHROPODA	ARACHNIDA		HYDRACARINA	LIMNESIDAE	*Limnesia sp.*		•		•					
	CRUSTACEA	(ZOOPLANKTON)	CLADOCERA AND/OR COPEPODA		spp.		•		•	•		•	•	•
		OSTRACODA			*Mytilocypris ambiquosa*		•		•	•		•	•	•
					Candonocypris novaezelandiae		•			•				•
					Sarscrypridopsis aculeata		•		•	•				•
					Cypretta sp. (shell)									
					Alboa wooroa						•			
					Diacypris spinosa		•			•				•
					Eucypris virens		•		•	•			•	•
					Ilyocypris australiensis					•				•
					sp. 1								•	
		MALACOSTRACA	AMPHIPODA	CEINIDAE	*Austrochiltonia subtenuis*		•		•	•			•	•
			ISOPODA	PHREATOICODAE	*Paramphisopus palustris*		•							
	COLLEMBOLA		COLLEMBOLA		spp.				•	•			•	
	INSECTA		ODONATA		nymph							•		•
			HEMIPTERA	CORIXIDAE	*Micronecta robusta*						•			
					Agraptocorixa hirtifrons		•							
					unidentified nymph sp. 3							•		
			DIPTERA	CERATOPOGONIDAE	sp. 1		•		•					
					sp. 2				•					
				TIPULIDAE	sp.				•					
				TABANIDAE	sp.		•							
				CHIRONOMIDAE	*Chironomus australis*		•			•				•
					C. griseidorsum								•	•
					C. intertinctus					•				•
					C. alternans		•							
					Cladopelma curtivalva					•				•
					Dicrotendipes conjunctus									
					Procladius villisomanus									•
					Lymnophyes pullulus				•					
					Tanytarsus fuscithorax		•			•				•
			COLEOPTERA	HALIPLIDAE	*Haliplus sp.*		•		•	•				
				HYDROCHIDAE	*Hydrochus sp. 1*						•			•
					Hydrochus sp. 2		•					•		
				DYTISCIDAE	*Chostonectes sp.*				•					
				CHRYSOMELIDAE	sp.		•							
				CARABIDAE	sp.			•						
				STAPHYLINIDAE	*Atheta sp.*	•								
					Falagria sp.							•	•	

Table 3: Species List for Forrestdale Lake.

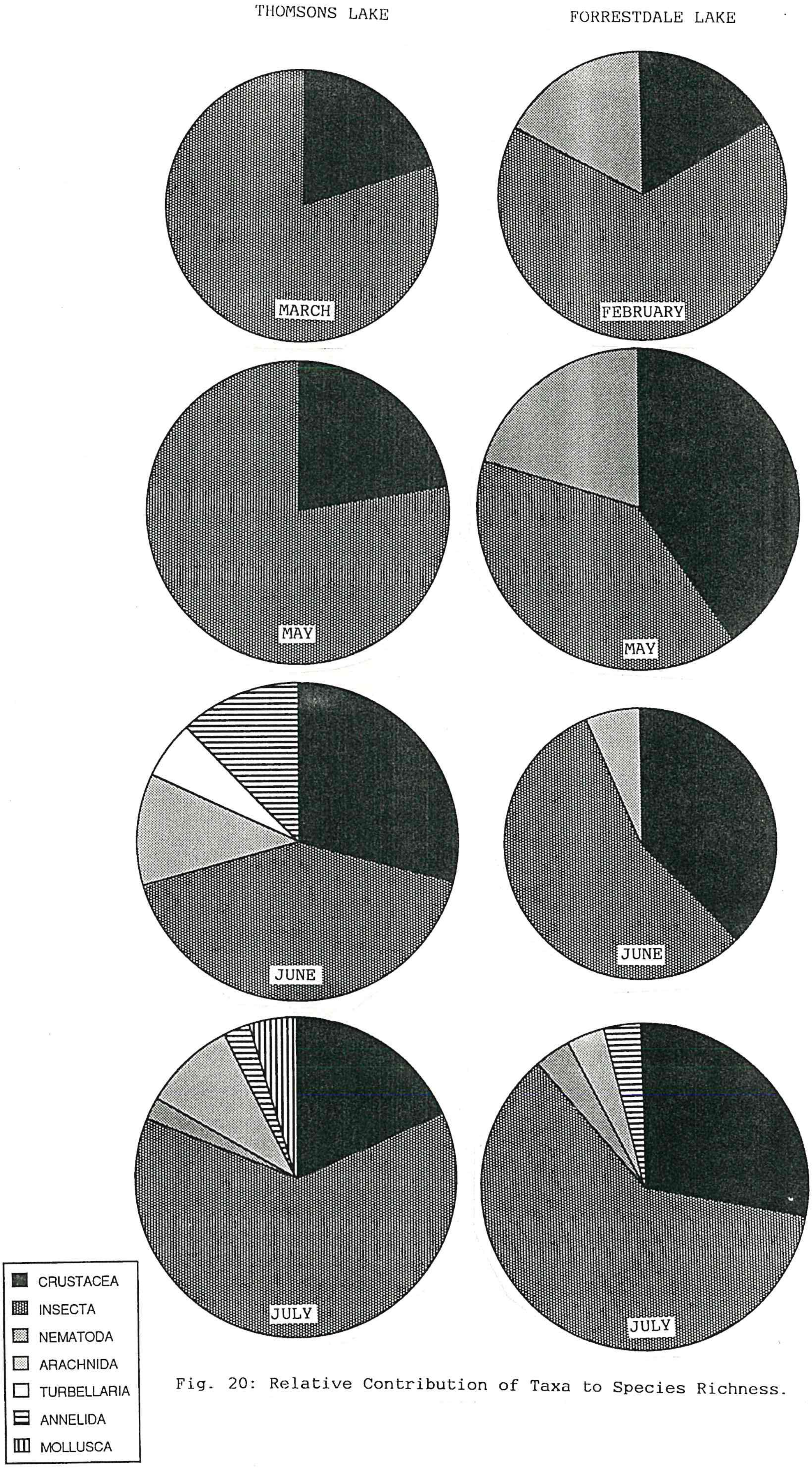


Fig. 20: Relative Contribution of Taxa to Species Richness.

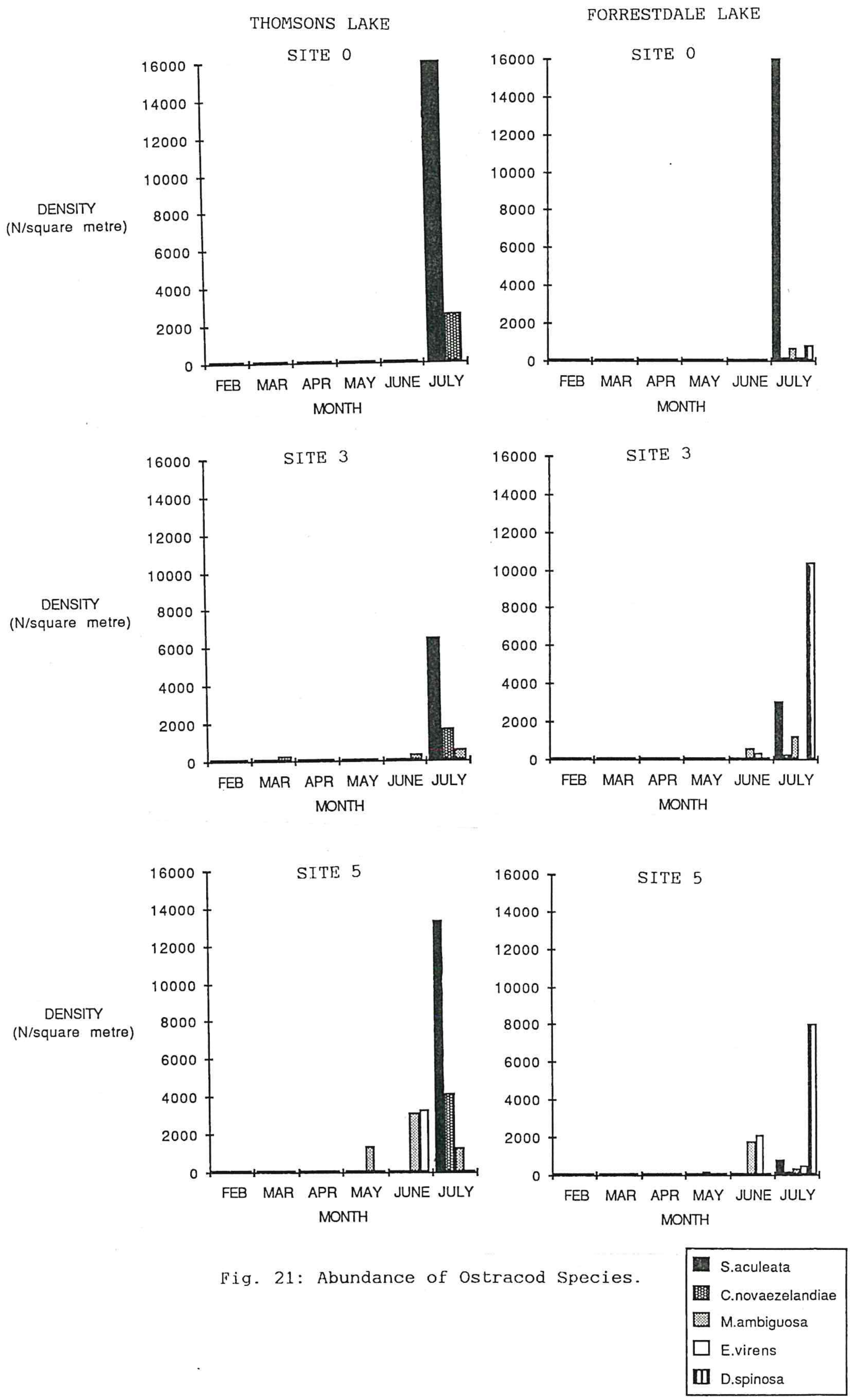


Fig. 21: Abundance of Ostracod Species.

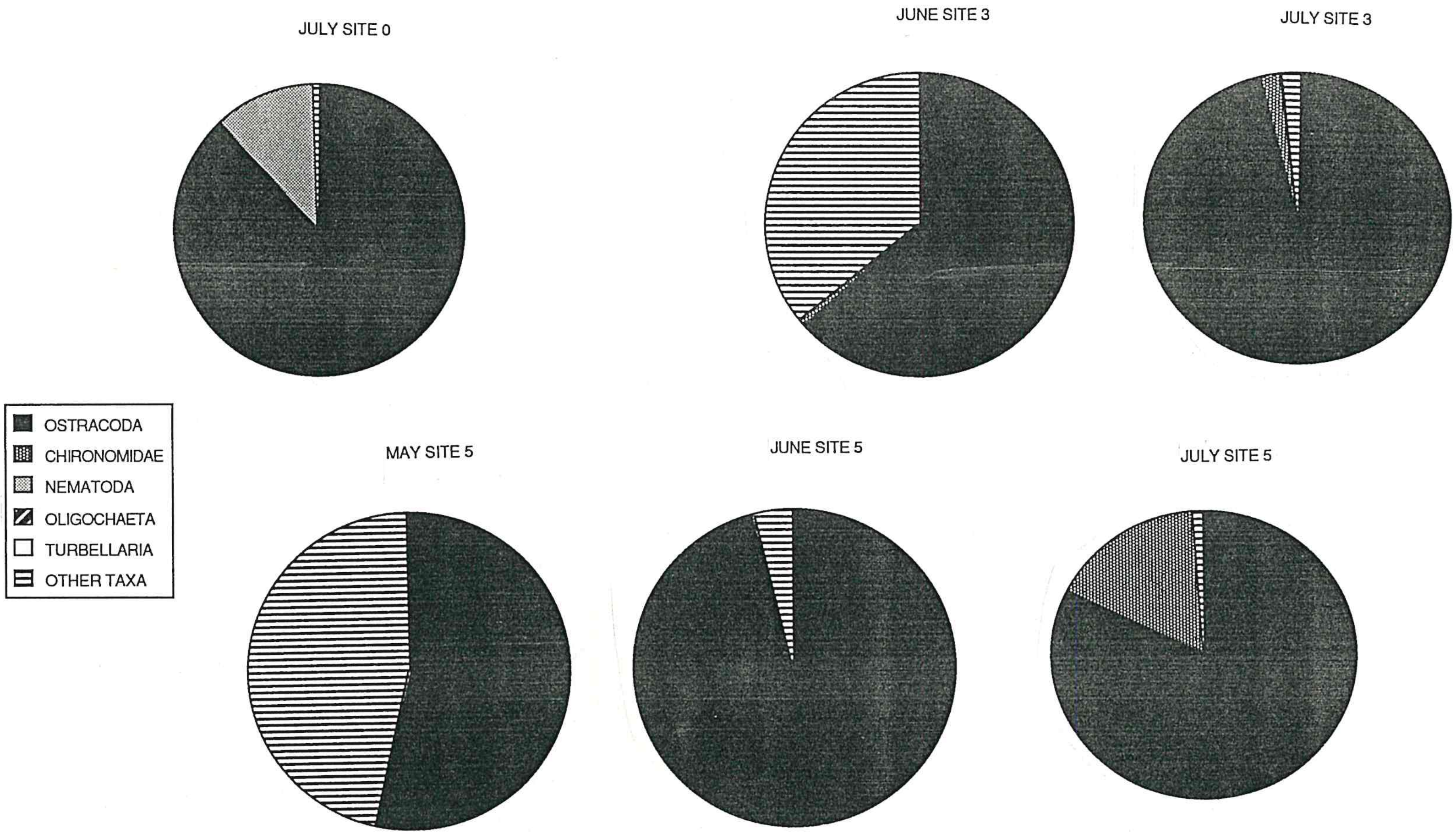


Fig. 22-a: Relative Contribution of Taxa to Abundance.
of Thomsons Lake.

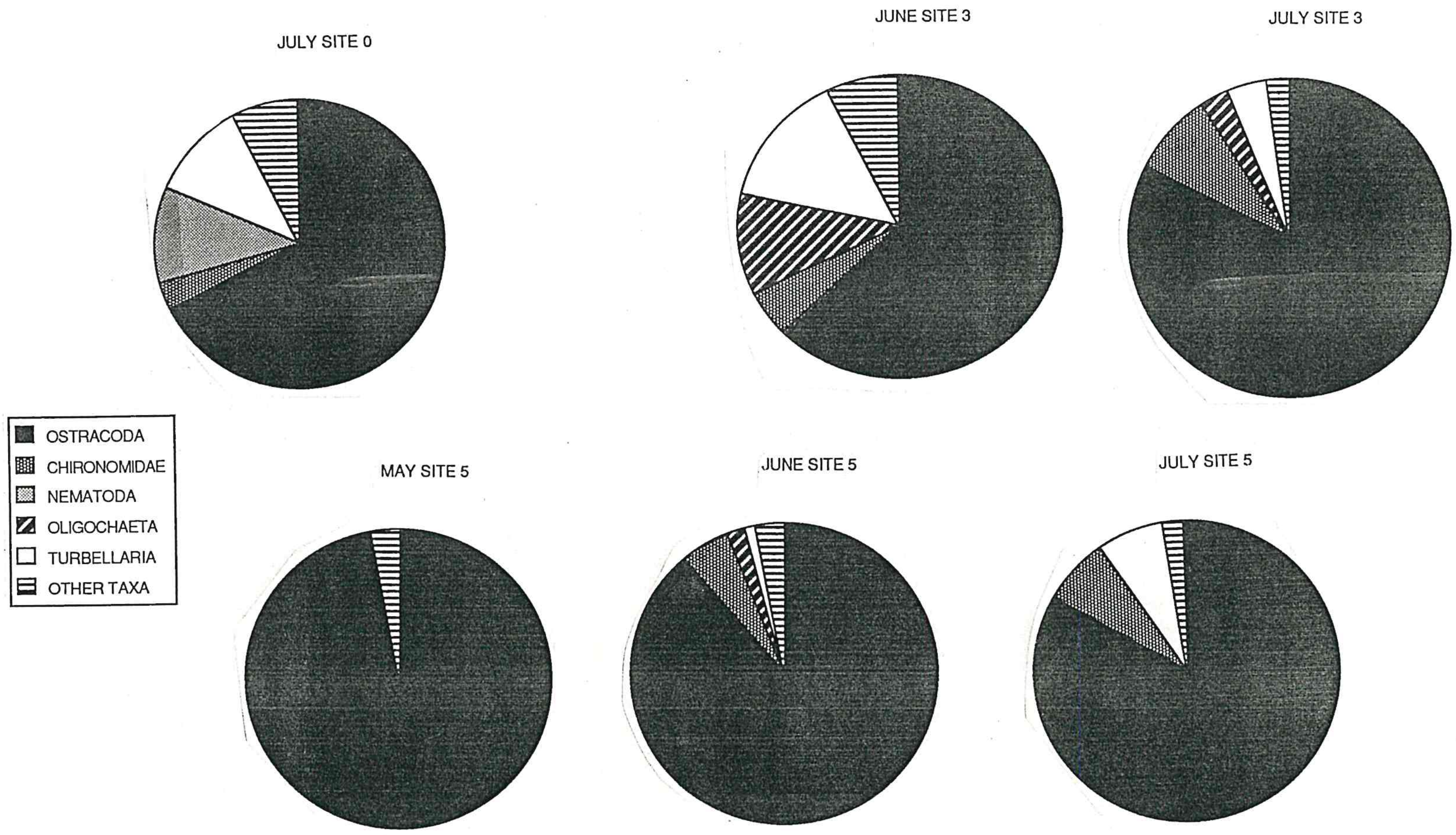


Fig. 22-b: Relative Contribution of Taxa to Abundance, of Forrestdale Lake.

Carabidae sp., and a species of Ptilodactylidae. Of the remaining species, eleven were caught at site 0 (eight were confined to this site), compared to five in site 3, and four in site 5. Beetles reached their highest density at site 0 in July with species such as *Donacia* sp. occurring at densities of up to 108/m^2.

Of the eight species of Coleoptera that were present in Forrestdale Lake, two occurred only when the lake was dry, these being *Atheta* sp. and a carabid beetle. Of the remaining species, three occurred at site 0, two at site 3 and three at site 5. Numbers reached a maximum near the *Typha* beds, with 135 *Haliplus* sp. per m^2. In both lakes the densities of beetles increased towards the edge of the lake.

Figure 20 shows the relative species richness of each major taxa. In all cases, except the dry Thomsons Lake, insects were the dominant fauna in terms of numbers of species, mainly because of the large number of midge larvae and beetles. Nematodes appeared to be absent from the flooded lakes until July where they occurred at the edge of the lakes; however, they were found in the dry lake bed. The Turbellaria did not occur in the lakes until June and then only in Thomsons Lake. Crustacea always made up at least $^1/_6$ of the species present, mainly Ostracoda. Most taxa did not become abundant in the water until a few months after flooding of the lake.

Changes in Species Composition and Richness Between Dry Period and Initial Flooding

A. Forrestdale Lake

Five species of macroinvertebrates were found in this lake in February (Table 3), two at the littoral site and three at the lake centre. The species at the edge of the lake were *Atheta* sp. (Coleoptera) and

Nematoda, which emerged from sediment flooded in the laboratory, the beetle was probably present in the sediment prior to this flooding. The species at the centre were *M. robusta*, *Hydrochus* sp. and *Alboa wooroa*, the latter of which was observed only after several days of artifical flooding of a section of the core sample. The former two species were sampled with the sweep net. After flooding of site 5 (lake centre), the number of species rose to six; these were, however, different to species found in the dry lake bed or small pools. Each successive site to flood contained a greater number of species than the last; for example, after site 5 flooded in May six species were found; at site 3 in June thirteen species occurred, and at site 0 in July, twenty-one species were found. The lake was dominated by insects in terms of species richness, and the number of species of crustaceans remained low throughout the study (Fig. 20).

B: Thomsons Lake

A total of eleven species was found in March, (Table 2) but in sites 0 and 3 only, which contained five and six species respectively. The species found at the lake edge were mainly insects, though nematodes were also found when the cores were artificially inundated with water. The odonatan nymph was also found only after this laboratory flooding. Dipteran pupal cases were common, and several were placed in a shallow dish of moist sediment; after about two weeks an adult emerged and was identified as a member of the terrestrial family Sphaeroceridae. The ceratopoginid larvae and ptilodactylid larvae (Table 2), were found in core samples. Two crustacean species, *M. ambiguosa* (Ostracoda) and *A. subtenuis* were found at site 3 in core samples. Insects were again the most numerous in terms of species, being represented at site 3 by a dragonfly nymph, and three species of beetle in March (Table 2). Although site 5 had no invertebrate fauna in March, ten species were found in May after flooding, and of these only the two crustaceans (Table 2) were found elsewhere in the lake beforehand. As was the case for Forrestdale Lake, the number of species found at each site immediately after flooding increased as each successive site flooded, with 10, 16 and 40 species occurring at sites 5, 3 and 0 respectively when each site flooded. This trend is evident in Fig. 23 which shows total species richness for the lakes over the whole study period.

Changes in Species Composition and Richness over the Whole Study Period

At almost all sites the number of species recorded increased over time, reaching a maximum at the littoral site, where, in July, forty and twenty-one species were found in Thomsons and Forrestdale Lakes respectively (Fig. 23). Most of the differences in species richness between sites were not statistically significant at any particular date ($p < 0.01$), according to one-way analysis of variance results (Table 4). The only significant ($p < 0.05$) difference was between site 0 and the other 2 sites in July at Thomsons Lake. However the changes in species richness over time at any one site were always statistically significant (Table 4).

Jaccard similarity coefficients (based on presence/absence data) were calculated to determine whether species composition changed over time and space. The results of these calculations (Table 5) showed that as the lakes began to fill there were large changes in species composition (hence high Jaccard coefficients). Then at successive sampling dates the sites change less with time. For example a value of 1.0 was obtained for site 5 at Thomsons Lake between March and May, indicating a complete change. Between May and June similarity was 0.85, and between June

a

MONTH	SITES SAMPLED	F-VALUE	SITES COMPARED BY t-TEST	t-VALUE
JULY	0,3, AND 5	7.33 *	0 AND 3 3 AND 5 0 AND 5	3.83 ** 2.03 n.s. 1.84 n.s.
JUNE	3 AND 5	13.21 **	--	--

SITE	DATES SAMPLED	F-VALUE	DATES COMPARED BY t-TEST	t-VALUE
3	JUNE AND JULY	11.99 **	--	--
5	MAY,JUNE AND JULY	8.22 *	MAY AND JUNE JUNE AND JULY MAY AND JULY	0.72 n.s. 3.81 ** 3.09 *

b

MONTH	SITES SAMPLED	F-VALUE	SITES COMPARED BY t-TEST	t-VALUE
JULY	0,3, AND 5	4.32 *	0 AND 3 3 AND 5 0 AND 5	2.54 * 0.00 n.s. 2.54 *
JUNE	3 AND 5	0.9 n.s.	--	--

SITE	DATES COMPARED	F-VALUE	DATES COMPARED BY t-TEST	t-TEST
3	JUNE AND JULY	8.00 *	--	--
5	MAY,JUNE AND JULY	26.20 **	MAY AND JUNE JUNE AND JULY MAY AND JULY	4.028 ** 3.603 ** 7.206 **

c

MONTH	SITES SAMPLED	F-VALUE	SITES COMPARED BY t-TEST	t-VALUE
JULY	0,3 AND 5	1.36 n.s.	--	--
JUNE	3 AND 5	1.014 n.s.	--	--

SITE	DATES SAMPLED	F-VALUE	DATES COMPARED BY t-TEST	t-VALUE
3	JUNE AND JULY	8.00 *	--	--
5	MAY,JUNE AND JULY	12.37 **	MAY AND JUNE JUNE AND JULY MAY AND JULY	4.21 ** 2.41 * 4.92 **

Table 4: One-way Analysis of Variance,

Between Sites and Between Dates.

For Thomsons Lake.

(a); Abundance, (b); Species Richness,

(c); Diversity.

* = Significant at p 0 05

** = Significant at p 0 01

n.s. = Not significant

a

MONTH	SITES SAMPLED	F-VALUE	SITES COMPARED BY t-TEST	t - VALUE
JULY	0,3 AND 5	10.12**	0 AND 3 3 AND 5 0 AND 5	3.79** 0.192 n.s. 3.99**
JUNE	3 AND 5	15.68**	--	--
SITE	**DATES SAMPLED**	**F-VALUE**	**DATES COMPARED BY t-TEST**	**t - VALUE**
3	JUNE AND JULY	11.08 *	--	--
5	MAY,JUNE AND JULY	26.29 **	MAY AND JUNE JUNE AND JULY MAY AND JULY	2.50 * 4.86** 7.10**

b

MONTH	SITES SAMPLED	F-VALUE	SITES COMPARED BY t-TEST	t -TEST
JULY	0,3 AND 5	0.05 n.s.	--	--
JUNE	3 AND 5	3.04 n.s.	--	--
SITE	**DATES SAMPLED**	**F-VALUE**	**DATES COMPARED BY t-TEST**	**t - TEST**
3	JUNE AND JULY	52.22 **	--	--
5	MAY,JUNE AND JULY	143.81 **	MAY AND JUNE JUNE AND JULY MAY AND JULY	3.30 * 13.40 ** 18.35 **

c

MONTH	SITES SAMPLED	F-VALUE	SITES COMPARED BY t-TEST	t - VALUE
JULY	0,3 AND 5	4.25 *	0 AND 3 3 AND 5 0 AND 5	2.62 * 2.42 n.s. 2.31 n.s.
JUNE	3 AND 5	7.33 *	--	--
SITE	**DATES SAMPLED**	**F-VALUE**	**DATES COMPARED BY t-TEST**	**t - VALUE**
3	JUNE AND JULY	2.38 n.s.	--	--
5	MAY,JUNE AND JULY	321.62 **	MAY AND JUNE JUNE AND JULY MAY AND JULY	1.053 n.s. 4.68 ** 5.62 **

Table 4(cont.): One-way Analysis of Variance, Between Sites and Between Dates. For Forrestdale Lake.

(a); Abundance (b); Species Richness (c); Diversity

* = Significant at p 0 05

** = Significant at p 0 01

n.s. = Not Significant.

DATE	SITES COMPARED	SIMILARITY(JACCARD COEFFICIENT)	
		THOMSON LAKE	FORRESTDALE LAKE
FEB/MAR(*)	0 AND 3	0.909	0.75
	3 AND 5	0.875	0.75
	0 AND 5	0.833	0.8
JUNE	3 AND 5	0.444	0.72
JULY	0 AND 3	0.682	0.481
	3 AND 5	0.409	0.381
	0 AND 5	0.702	0.667
SITE	DATES COMPARED	SIMILARITY (JACCARD COEFFICIENT)	
		THOMSON LAKE	FORRESTDALE LAKE
SITE 0	FEB/MAR(*) AND JULY	0.978	0.954
SITE 3	FEB/MAR(*) AND JUNE	0.909	1
	JUNE AND JULY	0.591	0.692
SITE 5	FEB/MAR(*) AND MAY	1	1
	MAY AND JUNE	0.85	0.727
	JUNE AND JULY	0.5	0.762

Table 5: Jaccard Similarity Between Sites and Dates.

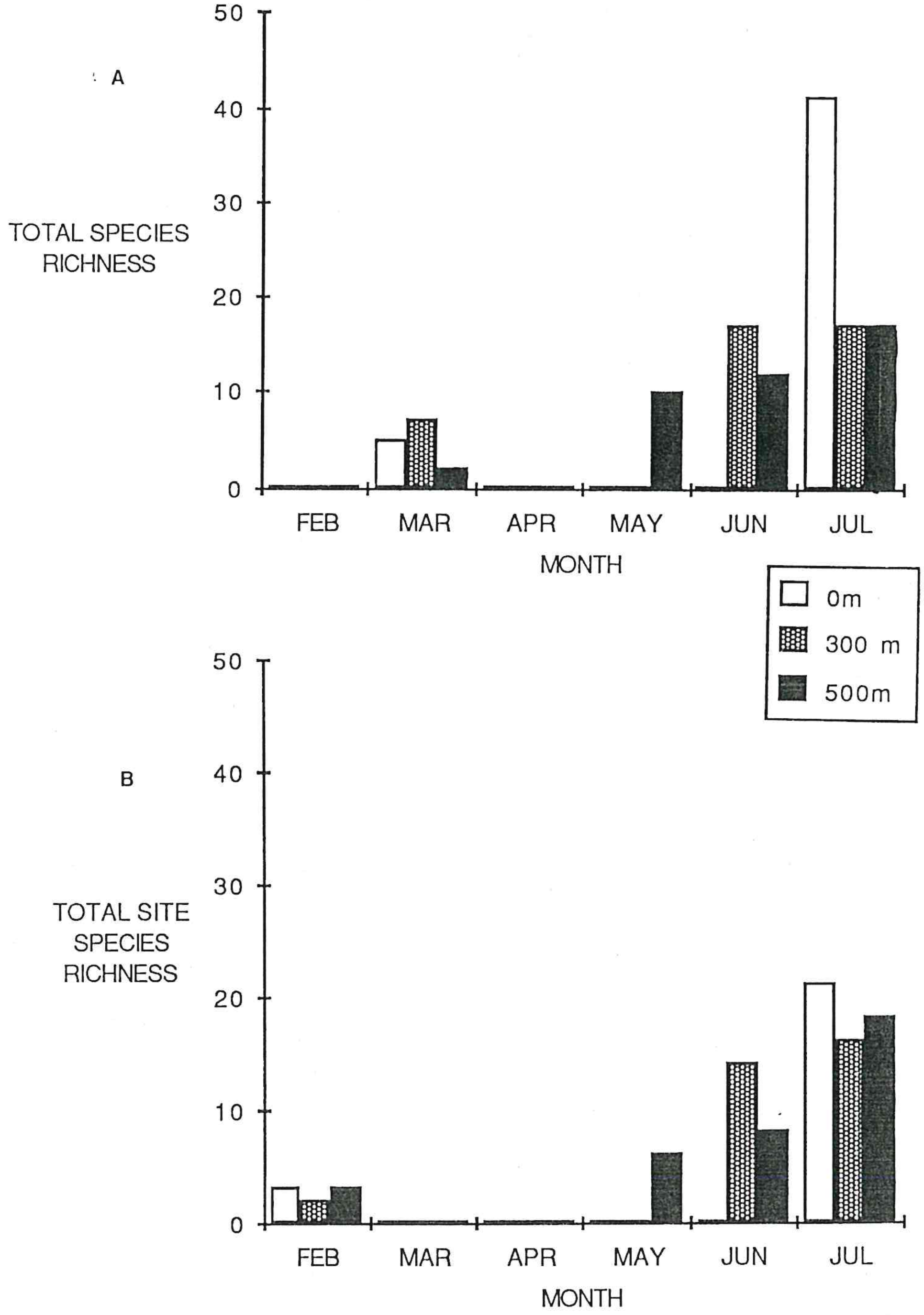


Fig. 23: Total Site Species Richness.(a) Thomsons Lake, (b); Forrestdale Lake.

and July it had fallen to 0.5, indicating less change. As the water rose, the difference between any two sites in respect to species composition also decreased (Table 5). For example, the Jaccard coefficient between sites 3 and 5 at Thomsons Lake was 0.875 in March, 0.444 in June and 0.409 in July. This trend was apparent for all sites in both lakes.

The relative number of taxa contributing to the species richness is shown in Fig 20. All seven taxa represented in this series of graphs were only present together in Thomsons Lake in July. Turbellaria and Mollusca were never found in Forrestdale Lake. In general the number of taxa represented increased as the water levels rose, but the insects were always dominant in terms of numbers of species, and crustaceans usually made up a large proportion of the total number of individuals.

Density of Macroinvertebrates

Figure 24 shows the mean abundance per square metre for each site at each sampling date. Zooplankton were not included for reasons previously mentioned. In Thomsons Lake in March the lake was almost completely dry; in the only site that was moist, site 5, no fauna was found. The maximum abundance in the dry lake was at site 0 (6096 animals/m^2). The abundance increased in all sites over time reaching a maximum of 41283 individuals/m^2. Densities in sites 3 and 5 remained low in May and June even though site 3 flooded in June, and site 5 in May. Density appears to have increased greatly in July, except at site 3, where it remained relatively low. Analysis of variance (Table 4) revealed no statistically significant difference between sites 3 and 5 in June and July; however in July site 0 was different to both sites 3 and 5. Changes in densities at sites 3 and 5 over time were usually significant, except for site 5 between May and June. In May 96% of the fauna in site 5 was *M.*

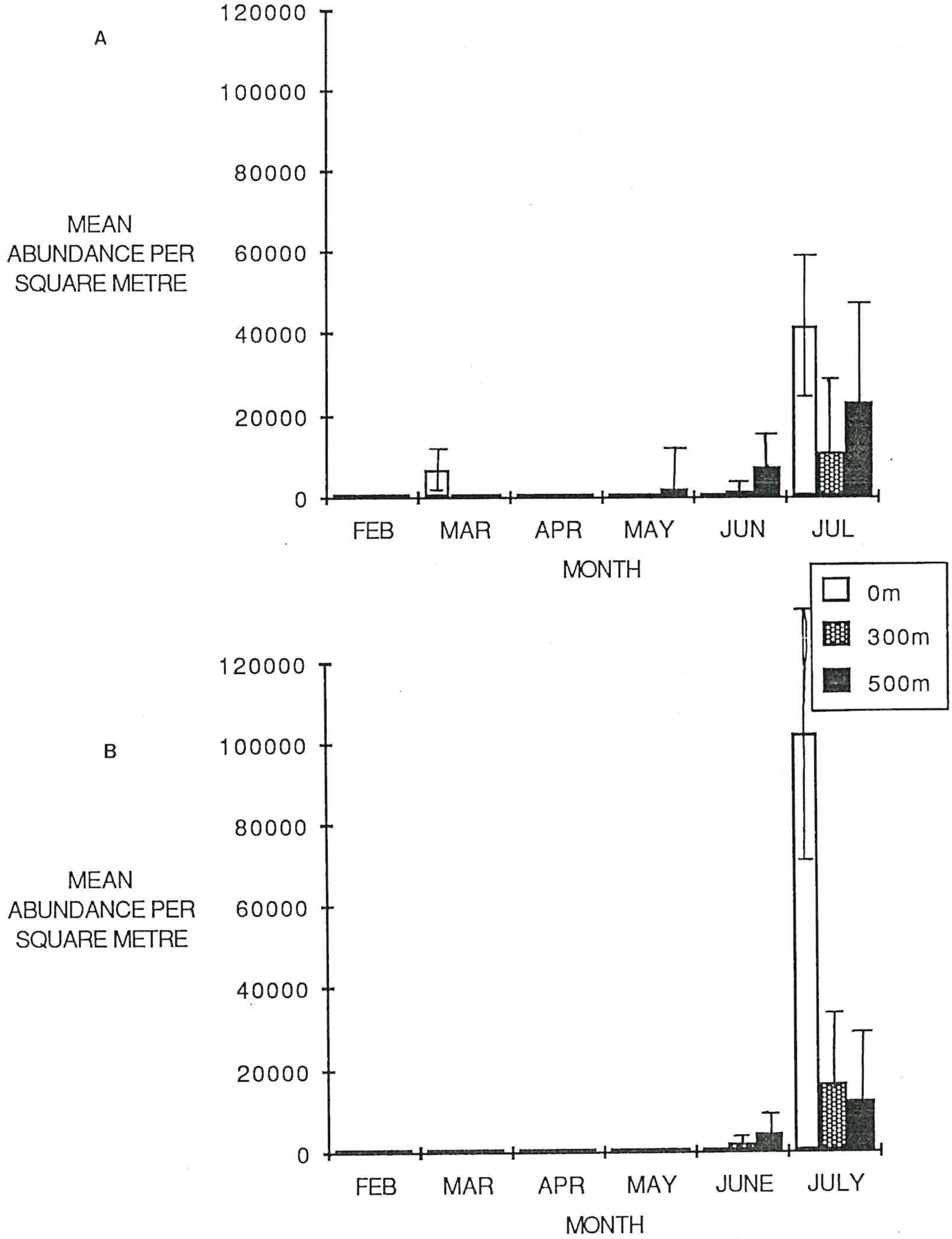


Fig. 24: Mean Density.(a); Thomsons Lake,
(b); Forrestdale Lake.

ambiguosa (Ostracoda), and in all other sites after flooding, in June and July, ostracods made up most of the numbers (Fig. 22). Flatworms (Turbellaria) and chironomids also had relatively large densities most of the time, as did the oligochaetes in June, site 3.

Usually Forrestdale Lake supported less animals per square metre than did equivalent sites in Thomsons Lake. However the site near the edge of Forrestdale had a density of 102 033/m^2 in July, two and a half times the density of the same site in Thomsons Lake in July. No fauna was found in February in quantitative samples at any sites in Forrestdale Lake, at least not before artificial inundation in the laboratory, therefore no values appear on Figure 24 for February. As in Thomsons Lake the density at all sites increased with each successive sampling date. Statistically significant differences were found between sites in both June and July (Table 4) and all sites were found to change significantly between sampling dates. In all flooded sites (May to July), most individuals belonged to the sub class Ostracoda (Fig. 22), though in the months immediately after site 5 and site 3 flooded (May for site 5 and June for site 3) a variety of other taxa were abundant. After this time chironomids and nematodes were the only other abundant taxa (Fig. 22).

Diversity of Macroinvertebrates

Diversity (Shannon-Wiener index (H^1)) brings together species richness and abundance into a single number, reflecting the distribution of abundances among the species present. Diversity increased over time, the highest diversity occurring in Thomsons Lake, where at site 0 the average diversity per sample was 0.59, in July (Fig. 25). Little difference between the lakes was found, other than the low diversity at site 0 in Forrestdale Lake after flooding (0.22) (Fig. 25). No diversity indexes were

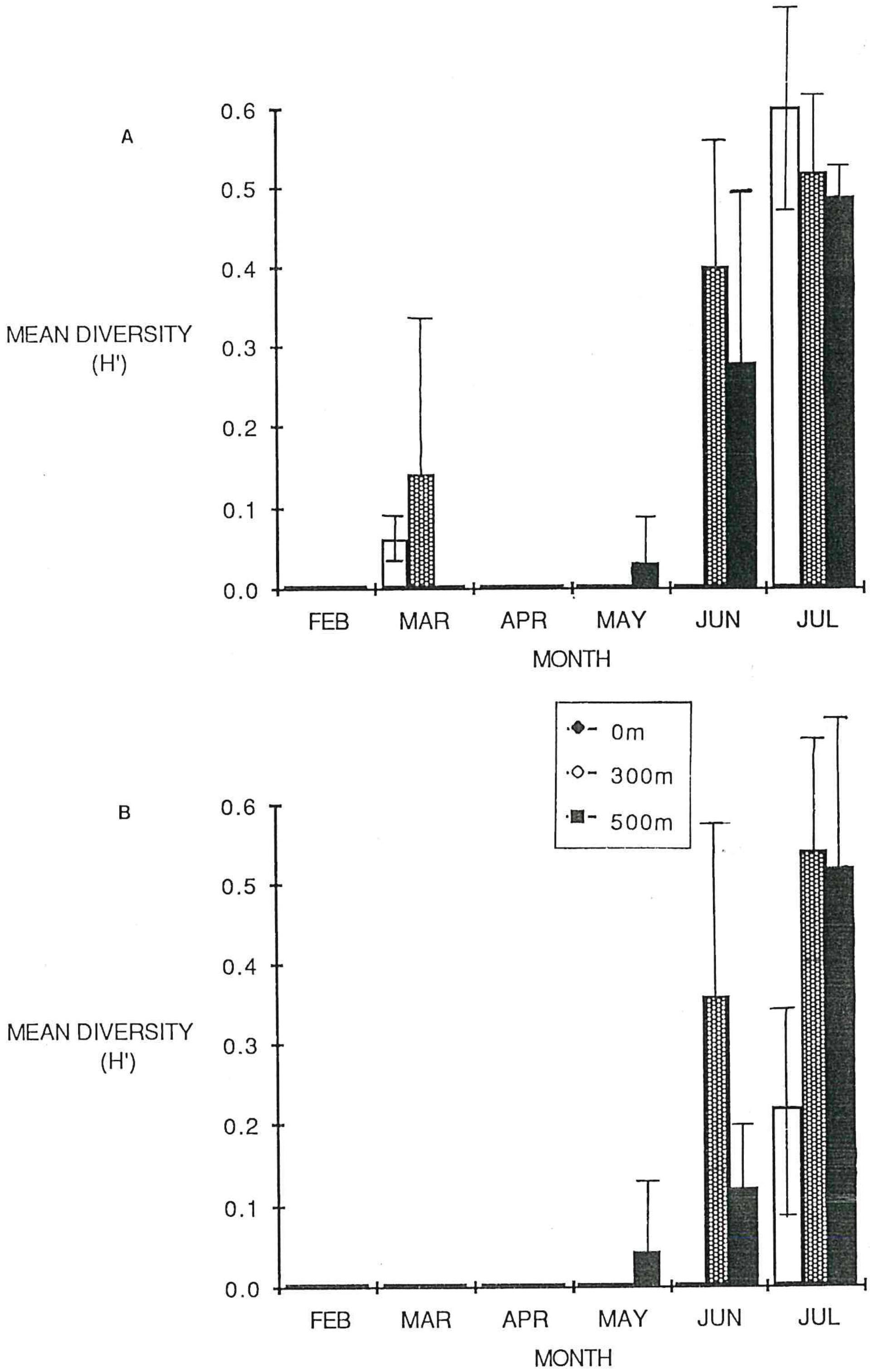


Fig. 25: Mean Shannon-Weiner Diversity.(a); Thomsons Lake, (b); Forrestdale Lake.

able to be calculated for the dry Forrestdale Lake, due to all the fauna being found by semi-qualitative techniques. Analysis of variance showed no difference between flooded sites at any particular date at Thomsons Lake (Table 4); however this is not surprising given the high variability as shown (Fig. 25). Some site differences were significant in Forrestdale Lake; however standard deviations did not overlap so much in these sites. Temporal changes in diversity appeared to be more statistically significant in Thomsons Lake than Forrestdale Lake (Table 4).

CHAPTER 4

DISCUSSION

Lake Sediments

Rybak (1969) studied a large number of Polish lakes and compared organic content of the lake bed sediments to the trophic status of the lakes. He found that eutrophic lakes had an organic content of 18-61%, compared to dystrophic lakes (77-83%), mesotrophic lakes (17-30%) and oligotrophic lakes (11-20%). In these studies only the first five centimetres of sediment were analysed, by ashing at 550°C for five hours (hence techniques were comparable to this study). By comparing the results in Fig. 10 to these northern hemisphere lakes, Thomsons Lake would appear to be eutrophic, whereas Forrestdale Lake is bordering on the mesotrophic/eutrophic level. However Williams and Wan (1972) have pointed out that although Australian lakes display features diagnostic of eutrophic water-bodies, the more obvious signs of eutrophication are often absent, indicating that care must be taken when applying northern hemisphere classifications to Australian lakes. Studies reviewed by Rybak show varying trends with regards to changes in organic content levels with depth, negative, neutral and positive trends being found; however Jonasson (1978) found that in general organic matter tends to collect in the centre of lakes. The precise distribution of organic material will in the end depend upon the morphological and botanical characteristics of the lake; in both Thomsons and Forrestdale Lake the organic content of the deeper sites (sites 3 and 5) were highest (Fig. 10). The low values for site 0 in Forrestdale Lake are presumably due to the hard rock bed zero to three centimetres under this site, which is covered mainly by fine and coarse sand (Fig. 12). This is supported by a high negative correlation (r = -0.92) between the amount of such sand and organic content, thus most of the organic content seems to be in the >2mm range. Qualitative observation of the samples seems to support this, the larger particles, (designated fine gravel by Briggs (1977)) were conglomerates of smaller particles and contained large amounts of vegetation debris.

Organic content values obtained in other Australian lakes vary greatly, but values obtained in this study were generally higher. For example in shallow semi-permanent wetlands studied by Briggs and Maher (1985) organic content ranged from 1.4 to 17.6%; however, chemical methods were employed rather than ashing. Deeper coastal lakes studied by Timms (1973) had sediments with organic contents of 7.1 to 26%, the shallowest lakes (two and three metres) had organic contents of 7.1 and 16.5%. Fulton (1983) studying deep Tasmanian reservoirs obtained organic contents of 5.6 to 39.5% which are very similar to values obtained in this study. The high organic contents recorded for Thomsons and Forrestdale Lakes may be a function of the extensive emergent macrophyte growth around the lake edges. Also both lakes have submerged aquatic macrophyte growth, Thomsons Lake more so than Forrestdale Lake. These submerged aquatic plants die annually as the lake dries, to be replaced by terrestrial vegetation. This annual growth and decay of aquatic and terrestrial vegetation means a continual source of decaying vegetation matter that would not occur to the same extent in permanent lakes.

The trend towards decreasing particle size in Thomsons Lake after flooding (Fig. 11) may be due to erosion of soil aggregates as observed by McLachlan (1974a) in temporary African lakes. No such trend was apparent in Forrestdale Lake (Fig. 12). However, the large particles contributed less to the total weight of the sediment to begin with, also the large conglomerate particles that were there had a high clay content and did not break apart so easily. It should be noted, however, that the process of sieving may also break up conglomerates of soil and organic debris.

Water Chemistry

According to Vollenweider's (1971) classification of trophic status, the inorganic nitrogen levels (Fig. 13 and 14) indicate that the lakes are both ultra-oligotrophic, having inorganic nitrogen concentrations of $<200 \mu g.l^{-1}$. Forrestdale Lake total phosphorus concentrations exceed Vollenweider's (1971) classification for polytrophism ($>100 \mu g.l^{-1}$) whereas Thomsons Lake only exceeded this level on one occasion (in mid-July). The average total phosphorus concentration of Thomsons Lake was $72.8 \mu g.l^{-1}$ which, according to Vollenweider (1971), classified the lake as eupolytrophic. These high phosphorus concentrations seem to exceed the $110 \mu g.l^{-1}$ that Conway (1942) claims to be world average for freshwaters (Williams and Wan, 1972).

St. John *et al.* (1976) classified the trophic status of Canadian lakes on the basis of chlorophyll concentrations; these are given in Newman and Hart (1976). By cautiously comparing these values with chlorophyll *a* concentrations measured for Thomsons and Forrestdale Lakes (Fig 16), then these lakes may be classified as mesotrophic to eutrophic, and mesotrophic respectively. The peaks in chlorophyll *a* concentration in the two lakes (Fig. 16) may reflect algal blooms, and this is why such measurements were carried out; however, artificial concentration of the phytoplankton due to wind induced currents is known to occur (Borowitzka pers. comm.). Assuming that algal growth is accurately measured by chlorophyll *a* determination, then nutrient concentrations can be discussed in terms of the chlorophyll *a* measurements. When, or soon after, the peaks in chlorophyll *a* concentrations occurred, peaks in organic phosphorus were observed, indicating high concentrations of particulate organic phosphorus in suspension, perhaps from algal cell breakdown. When the peak in organic phosphorus occurred in Forrestdale Lake (at the same time as the peak in chlorophyll *a*), phaeophytin concentration (the breakdown product of chlorophyll *a*) was 12.6 $mg.m^3$, almost as high as the chlorophyll *a* concentration (14.5.$mg.m^3$) indicating that the bloom was already in a state of decay. The peak in organic phosphorus in Thomsons Lake occurred later than the peak in chlorophyll *a*. This may be because of a later breakdown of the bloom; however phaeophytin measurements were not made in the end of month samples taken by S. Rolls of Murdoch University. In Thomsons Lake a rise in ammonia was observed soon after the peak in chlorophyll *a* ; this could be a result of zooplankton feeding on the algal cells, converting nitrogen to ammonia which is the nitrogenous waste product of most crustaceans (Barnes, 1980). However, such increases in ammonia were not observed until much later in Forrestdale Lake.

A detailed analysis of nutrient cycling in lakes would require a much more in-depth sampling programme, including measurements of denitrification, nitrogen fixation, and sediment/water interactions, as well as measurements of inputs and outputs to the system. The main purpose of measuring nutrients in this study was to gain some indication of the trophic status of the lakes. By international standards, on the basis of sediment organic matter, nutrient concentrations and chlorophyll *a* concentrations, both Forrestdale Lake and Thomsons Lake appear to be mesotrophic to eutrophic, Thomsons Lake being more eutrophic than Forrestdale Lake. Table 6 summarizes the trophic characteristics of the lakes.

The conductivity measurements are comparable to those of Congdon and McComb (1976) for Lake Joondalup, also on the Swan Coastal Plain, with the same pattern of decreasing conductivity with rising water levels

	THOMSONS LAKE	TROPHIC CLASSIFICATION	FORRESTDALE LAKE	TROPHIC CLASSIFICATION
ORGANIC CONTENT (%) (1)	27-51	eutrophic 18-60	2-33	mesotrophic 17-30
INORGANIC NITROGEN (ug/l) (2)	21-112	oligotrophic <200	30-62.5	oligotrophic <200
TOTAL PHOSPHORUS (ug/l) (2)	59-128	eu-polytrophic 30-100	165-365	polytrophic >100
CHLOROPHYLL a (mg/l) (3)	2-23	mesotrophic to eutrophic 2-15 to 10-50	5-14.5	mesotrophic 2-15

Table 6: Trophic Status of the Lakes, as Determined from (1); Rybak(1969), (2); Vollenweider(1971), (3); St.John et.al.(1976).

due to a dilution effect. In Lake Joondalup chloride was the dominant ion, and its concentration closely followed the change in conductivity. Congdon and McComb (1976) attributed this to the lake's close proximity to the ocean (Cl^- and Na^+ presumably being carried to the lake on the wind). These authors also made note of the unusually high calcium concentrations, no doubt due to the lake's close proximity to the aeolian limestone deposits. Similarly, Thomsons Lake is near to the ocean and received water from a limestone ridge to the west, perhaps explaining the slightly higher initial conductivity in Thomsons Lake compared to Forrestdale Lake. According to Metropolitan Water Authority data in Beckle (1984), both Forrestdale and Thomsons Lake become saline when water levels are very low; for most of the year Beckle (1984) describes them as brackish. Results obtained in this study indicate that they are both freshwater systems.

Both lakes are moderately alkaline, Thomsons Lake more so than Forrestdale Lake, as are most Western Australian wetlands (Hembree and George, 1978). The higher variability in Thomsons Lake (Fig. 18) may be due to the higher density of submerged aquatic macrophyte growth in this lake at the time of study affecting the dissolved carbon equilibrium. Carbon dioxide in solution gives acidity to the water by forming carbonic acid which is soluble:

i.e. $CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^- \leftrightarrow CO_3^{2-} + 2H^+$ (Hunter *et al.*, 1981). High levels of photosynthesis would thus reduce acidity by using carbon dioxide.

Fauna of the Dry Lakes

A total of thirteen species of macroinvertebrates were found to exist in the dry or moist lake beds in February and March (Tables 2 and 3) not including the gilgie (*Cherax quinquecarinatus*) which must have inhabited the dry lake bed of Thomsons Lake.These species can be classified into one of three categories; truly aquatic species that survive the dry period in the mud; semi-aquatic species; or, terrestrial colonizers. Wiggins *et al.* (1980, in Williams, 1985) grouped animals into four categories on the basis of how they coped with seasonal changes in water level. Williams (1985) then modified these to make them more applicable to semi-arid and arid zones. The lakes on the Swan Coastal Plain are subject to more temperate climatic patterns and so Wiggins' classifications may be more applicable to the fauna of these lakes. The four categories of Wiggins (1980, in Williams, 1985) are:

Group I - Permanent residents capable of only passive dispersal and dormant during the unfavourable period.

Group II - Residents capable of some active dispersal, dormant during unfavourable season, water needed for egg laying.

Group III - Residents capable of active dispersal, dormant during unfavourable period, water not required for egg laying.

Group IV - Residents capable of active dispersal, unfavourable season spent in permanent water elsewhere.

Most of the zooplankton (Copepoda and Cladocera) would fit into the Group I fauna, as they are mainly at the mercy of water currents. The Cladocera are known to produce drought tolerant ephippal eggs (DeDekker and Geddes, 1980) by sexual reproduction (Barnes R.S.K., 1980). After flooding these crustaceans rapidly reproduce asexually by parthenogenesis (Kenko, 1949). Survival by copepods varies between the three orders and even between species, some, such as members of the Harpacticoida can survive drying as adults. Williams (1980) and Kenko

(1949) state that both harpacticoid and cyclopoid copepods can survive for a while in dry mud in a lethargic state (drought torpor). In Thomsons and Forrestdale Lakes no adult copepods were found in cores unless the cores were artificially flooded, and then only harpacticoid copepods emerged, although as mature adults. Some cyclopoid copepods can survive as development arrested embryos (Williams, 1985) and both harpacticoid and cyclopoid species can encycst as immature stages or adults (DeDekker and Geddes, 1980). It appears that cladocerans and copepods form their resistant stages, whatever they are, before the lakes dry out, as no zooplankton were found in the pools at the centre of Forrestdale Lake.

Nematodes are also known to survive in dry sediments by being resistant to a certain degree of desiccation as adults, this is known as cryptobiosis (Williams, 1985).

The Amphipoda (*A. subtenuis*) are entirely aquatic, but are able to withstand a wide range of salinities (Williams, 1980). This ability is an obvious advantage if it is to survive in the moist mud of the lakes in the dry season, as Thomsons Lake salinity has been known to reach 5400 mg/l before drying (Beckle 1984). This, and other species of the subclass Malacostraca cannot produce resistant eggs (Williams, 1975), yet *A. subtenuis* was found in the moist layers of the Thomsons Lake sediment. Isopods are also known to survive by remaining, as adults, underneath decaying vegetation and stones where moisture remains (Williams, 1985). The gilgie (cf. p. 36) has a perennial life cycle and so must remain as adults when drying occurs. It does so by burrowing down to depths where moisture remains, and its burrows were seen in the dry lake sediments of Thomsons Lake. The time that any of these malacostracans can remain in the sediments of the dry lake would be limited because of the requirement for moisture. The Malacostraca then seem to fit into the second group of Wiggins (1980, in Williams, 1985).

The Ostracoda were the dominant fauna (excluding zooplankton) after flooding, reaching numbers of up to 89 775/m^2 in Forrestdale in July (Fig. 22). Before flooding only two species were found, *A. wooroa* in Forrestdale Lake and *M. ambiguosa* in Thomsons Lake (Tables 2 and 3). Adults of *M. ambiguosa* were found in moist mud in Thomsons Lake, indicating a degree of resistance to high salinities and desiccation. Edwards (1968) notes that the Ostracoda are usually the last remaining crustaceans in temporary waters, although in this study *A. subtenuis* was also observed in the mud. Even after flooding *M. ambiguosa* was initially the dominant ostracod when salinities were high in May. Hembree and George (1978) found that *M. ambiguosa* was the only species of ostracod present in the lakes of highest salinity. In general ostracods survive by means of resistant eggs (DeDekker and Geddes, 1980), the eggs consisting of two calcified layers enabling aestivation for long periods (Kenko, 1949). Some may also remain as immature or adult forms in the dry mud (Kenko, 1949), the hard shells no doubt helping to prevent water loss. As water is required for the laying of eggs by the ostracods (Hembree and George, 1978) they appear to belong to Wiggins' Group II.

Many insect species can escape the drying lake as flying adults; for example the midge larvae (Chironomidae) inhabit the flooded lake as larvae before pupating and emerging as adults, which leave the water. Though in this study no midge larvae were found in the dry lake, chironomid burrows have been found to depths of over 20 cm into exposed sediments by Klaster and Jacobi (1978). Other Diptera larvae were found in the exposed sediments; these were a ceratopogonid, (biting-midge) species and a species of Sphaeroceridae. The latter is a terrestrial species whose larvae or pupae are not usually associated with aquatic environments; it would seem that this species uses the lake bed as a terrestrial habitat after drying. The ceratopogonid larvae were found in dry cores at the edge of Thomsons Lake; this family is usually aquatic or semi-aquatic (Williams, 1980). As the same species was found in the flooded Forrestdale Lake it would appear to be an aquatic species that remains after water levels have receded. What happened to this species after further drying is not known because no further sampling was carried out, after February and March, until flooding occurred in May.

Micronecta robusta is a hemipteran and so can leave the lake after drying by flying to other water bodies. In Forrestdale Lake it was present only in the small pools in the centre of the lake. Recolonization by the Hemiptera occurs when invertebrates immigrate to the flooded sites (Davis, pers. comm.) although by July *M. robusta* had not returned to this lake. Other hemipteran species had returned however, for example *Sigara mullaka* were found after flooding, and presumably recolonized the lake by flying in from other water bodies. This species was also found in temporary rock pools in granite outcrops in Western Australia (Bayley, 1982).

The five species of Coleoptera that inhabited the dry lake beds were mainly of sub-aquatic or terrestrial origin. *Hydrochus* sp. 1 was a truly aquatic species, being found only in pools of water in Forrestdale Lake prior to flooding. Such aquatic beetles leave temporary water-bodies when conditions become adverse, as was observed for various members of the super-family Hydrophiloidea (to which *Hydrochus* sp. 1 belongs) by Landin (1976). The carabid beetles are either terrestrial or sub-aquatic, one-quarter of Australian species being sub-aquatic (Williams, 1980). The species of Carabidae found in this study was found only in the dry lake and so was probably a non aquatic species that had colonized the lake bed. *Heterocerus flinderii* would also seem to be a terrestrial colonizer of the dry lake, as was observed for dry lake beds in N.S.W. by Maher (1984). A species of Ptilodactylidae larvae was found in the sediments in March near the edge of Thomsons Lake, this family is semi-aquatic according to

Williams (1980), the larvae inhabiting water or damp terrestrial places. This species may have emerged from eggs laid in the shallow water or moist mud at the end of summer by terrestrial adults which normally inhabit marginal vegetation. The insects capable of flight away from the dry lakes fit into Wiggins (1980) Group IV as no mention of resistant eggs was found in the literature surveyed.

The macroinvertebrates remaining in the dry lakes were thus either semi-aquatic or terrestrial colonizers or species capable of survival during the dry season in the sediments. Survival in the sediments would be made possible by a variety of life-cycle and physiological adaptations.

Recolonization after flooding

Williams (1985) found four life cycle strategies while studying arid and semi-arid zone aquatic invertebrates. Firstly, there were the species that remained in the sediments as a dormant form when conditions were unfavourable. Secondly, some of the species that remained dormant also had some input from more permanent water bodies after flooding. Thirdly, some species had no dormant form and annually recolonized the ephemeral waters from more permanent ones; when the temporary water bodies dry these animals leave. Lastly some invertebrates moved between ephemeral water bodies that dried up at different times. If crustaceans have no methods of movement between water bodies not linked by streams or drains then they must fit into the first of these groups. However, several authors have suggested that water-birds may carry invertebrates in their feathers and so distribute them between wetlands (Mann, 1980; Barnes, 1980 and Williams, 1985). As both Thomsons and Forrestdale Lakes support a large water-bird population after flooding, which moves between Perth wetlands and rivers (Jennings, 1985), it is not unreasonable to suggest that some species of invertebrates may be re-introduced via the avian colonizers. Insects are able to fly between water bodies and so will fit into either the third or fourth of the above categories; while insects reproduce by eggs, they are usually not resistant to the stresses of the drying lake.

So recolonization of the flooded lakes occurs when invertebrates in the sediments hatch out or emerge (crustaceans, molluscs, nematodes) or fly in (or are carried in) from other wetlands (Coleoptera, Diptera, Hemiptera). Of the insects that fly back to the flooding lake, some may initially recolonize the waters edge, especially species in which only the larvae are aquatic. This is true of the midges (Chironomidae), the adults laying eggs at the moist waters edge (Maher and Carpenter, 1984); the cycle of emerging and egg laying may then occur several times before flooding is complete (Maher, 1984).

Species Richness and Composition of Flooded Lakes

The number of species found in the two lakes in this study appears to be relatively high by Australian standards. However the majority of other Australian studies are of more permanent water bodies, and so species lists have not included semi-aquatic and terrestrial colonizers. A total of 62 taxa were found in Thomsons Lake, of which 54 were recovered from flooded sites. The average number of taxa from studies of thirty Australian lakes, by various authors, is 30 ± 14, ranging from four in Lake Guraga (Western Australia) to 52 in Arthurs Lake, Tasmania (Fulton, 1983). While these figures are useful as a general comparison, it must be remembered that the water bodies used are of a very diverse nature, although no zooplankton were included in the calculation. Marchant (1982) studied temporary billabongs in the Northern Territory, and found an average of 45 taxa in the flooded billabongs and 18 when they were dry, giving a total of 90 taxa, and this did not include the number of species of Ostracoda, chironomids and mites. Contrasting this are the 32 taxa found in temporary ponds in New Zealand (Stout, 1964); however this is high compared to permanent New Zealand lakes (Timms, 1982). The 62 and 41 taxa found in Thomsons and Forrestdale Lakes is intermediate between those of the billabongs and the temporary New Zealand pools but, unfortunately, the lack of study of temporary freshwater bodies makes it difficult to rate these two lakes in terms of similar Australian wetlands. Previous studies of wetlands on the Swan Coastal Plain have resulted in species richness much lower than those presented here, the highest published values being 30, for Forrestdale Lake, by van Alphen (1983). In the study by van Alphen (1983), temporary waters were compared to permanent ones, and the former were found to contain the most species for both fresh and saline lakes. The limited literature available on overseas seasonal wetlands such as Klaster and Jacobi (1978) mainly concentrate on the dominant taxa, and species richness values are not given. However, studies by McLachlan (1974a) have shown temporary African lakes to have very low species richness, 6 and 11 species being found for two large lakes after reflooding.

The relatively small differences in species richness observed over the transects (Fig. 23 and Table 4) may be attributable to the relatively shallow depth of the entire lake (Fig. 19) and the more or less even cover of submerged aquatic macrophytes, making the sites very similar physically. Over time the changes in species richness were always significant statistically (Table 4). However analysis of variance results must be used with care, as populations are assumed to be normal and with equal variances (Walpole, 1982) and while these assumptions were not tested it is clear from Figs. 24-25 that variances were not always equal. Also over time, species composition changes occurred (Fig. 20) no doubt due to increasing immigration, hatching and habitat development. The sites changed less over time with respect to species composition, as can be seen from Table 5. This may reflect the initial habitat change after flooding, though changes were still quite noticeable, hence the similarity never fell below 0.5 when sites were compared over time. The differences in species composition between sites is evident from the numbers of species endemic to single sites. In Thomsons and Forrestdale Lakes, over the whole study period, 56 and 50% of species respectively were found at one site only, 26 and 21% were restricted to two sites. In Thomsons Lake 32% of species were found in the littoral site, compared to 17% of Forrestdale Lake species. High species richness, abundance and diversity are characteristic of flooded emergent macrophyte areas, as was found by Hembree and George (1978) for other Perth wetlands. In a review of lake zoobenthos Jonasson (1978) concluded that a peak in species richness usually occurs in the littoral region. The reason for this may lie in their value as a habitat protected from wind and wave, and as a food source for herbivores and their predators.

Density of Macroinvertebrates

Mean densities of macroinvertebrates for June and July in Thomsons Lake for all pump samples are $4104 \pm 5080/m^2$ and $24900 \pm 16275/m^2$. For Forrestdale Lake samples for June and July respectively, the mean densities are $2592 \pm 2155/m^2$ and $43\,366 \pm 48\,993/m^2$, the number of samples being 12 in each case. The June values are about average compared to other studies around Australia; for example, in two Tasmanian lakes, Fulton (1983) recorded an average value of 1626 individuals/m^2 for 12 sites, the maximum being being 3328/m2. Timms (1973) observed mean values of 585/m^2 and 432/m^2 for two Victorian coastal lakes, the maximum values being 934 and 1300/m^2 respectively. Murrumbidgil Swamp and Lake Mirramajeel are wetlands that occasionally dry up during the summer in New South Wales. The average densities in these lakes were 5922/m^2 and 5551/m^2 (Maher, 1984). In a study of twenty New Zealand lakes, densities between 75 and 7307/m^2 were observed (Timms, 1982). The July densities are extremely high in comparison with these Australian studies, though some studies could not be compared as data were in different units (for example biomass or numbers/m^3). In this study numbers per m^2 were used, as most of the macroinvertebrates were considered to be benthic, or at least not evenly distributed throughout the water column; thus numbers/m^3 would have overestimated the density.

Unlike species richness, site differences were common though there was usually no significant difference between sites 3 and 5 (see Figs. 5 and 7) in June and July (Table 4). In June the sites at the lake centres (site 5) were higher in both lakes than site 3; however, by the time site 0 became deep enough to pump sample in July it had by far the highest densities in both lakes (Fig. 24). In a review of the zoobenthos of lakes, Jonasson (1978) concluded that a peak in species richness usually occurs in the littoral region, while abundance usually peaks in the sublittoral; however in this case sublittoral means the depth below light penetration, and so is not applicable to this study, where littoral is taken to mean the zone of fringing vegetation. The index of diversity plotted on Fig. 25 must be analysed with care, and is not necessarily an index of community complexity; it merely brings together species richness and abundance. In general the individuals were spread more evenly over the species present as time passed; however site 0 in Forrestdale Lake in July had an unusually low index of diversity (Fig. 25). This low value may be due to the dominance of two taxa at this site (Nematoda and the ostracod *S. aculeata*) (Figs. 21 and 22). At site 3 in this lake in July ostracods are even more abundant; however several chironomid species replace the nematodes, and the numbers of ostracods are spread more evenly over more species (Fig. 21) thus raising the Shannon-Wiener Index (Fig. 25).

The differences in abundances between the present study and those of previous studies lies not only in the total abundance, but also in the distribution of these individuals amongst the major taxa. In most previous studies, the chironomids and/or oligaochaetes have been the dominant component of the zoobenthos; however, at the conclusion of sampling in this study, the Ostracoda was the most abundant taxon in both lakes (Fig. 22).

The Ostracoda appear to undergo a pattern of succession; prior to July *M. ambiguosa* was almost always the most abundant (Fig. 21), although *E. virens* was often common. *M. ambiguosa* appears to be able to withstand relatively higher salinities (Hembree and George, 1978) and this is supported by data in Fig. 21, where it can be seen that *M. ambiguosa* is usually the first to occur in any abundance. In July *S. aculeata* was dominant at all sites in Thomsons Lake, but only at site 0 in Forrestdale Lake, where *D. spinosa* was dominant at sites 3 and 5. To determine the reasons for these changes in ostracod numbers, more detailed study would be required; however, it is probably due to a combination of life-cycle details and environmental requirements for hatching and reproduction.

In the Kemerton group of wetlands in Western Australia, Bunn (1986) found the ostracods to contribute between 7 and 41.5% to overall abundance. Van Alphen (1983) found the ostracods to be very common in Forrestdale Lake, especially *S. aculeata*, which was the dominant ostracod in the present study by July (Fig. 21). Studies in the other states reveal chironomid and oligochaete dominance, with occasionally high abundances of isopods (Fulton, 1983 and Timms, 1983) and molluscs (Fulton, 1983). In temporary billabongs of the Northern Territory, Marchant (1982) found no dominant taxa; however the Chironomidae, oligochaetes Ostracoda and Ephemeroptera were all abundant. In a North American temporary reservoir Klaster and Jacobi (1978) found chironomids and oligochaetes to represent 98% of the benthic macroinvertebrates. McLachlan (1974b) found that during the flooding phase of a temporary African lake (Lake Chilwa) chironomids dominated the fauna (90%); during the drying phase *Berosus* spp. dominated (81%). The ostracod dominance seems to be an unusual feature of Thomsons and Forrestdale Lakes; however, it may be that the changes in fauna abundance may not have been complete by cessation of sampling in July.

Productivity in Seasonal Lakes

The high densities are consistent with the temporary nature of the lakes, such lakes being considered highly productive. The reasons for this appears to be primarily due to the regeneration of inorganic nutrients such as phosphorus and nitrogen. Aquatic macrophytes decay aerobically when seasonal lakes dry, releasing nutrients to the soil (Briggs and Maher, 1985). These nutrients are then released into the water when the soils flood (Briggs *et al.*, 1985). The macrophytes and zoobenthos that die as the lakes dry up also lead to high organic content in temporary wetlands (Briggs and Maher, 1985). The regenerated nutrients (leading to high aquatic macrophyte reproductivity) and the organic content of the soils lead to high lentic productivity, including invertebrates. Maher (1984) found that the highest biomass of invertebrates occurred when annual macrophyte growth was highest, and wetting and drying cycles are essential to maintain this high macrophyte growth each year, more permanent water bodies not being so productive. Livingston and Loucks (1978) also stated that such cyclic events were necessary if lakes were to maintain high productivity. A commonly held view is that diversity is higher in more stable communities, though according to Paine (1969) this is not always true. If species richness is any indication of diversity (according to Mason (1977) species richness alone may be a more accurate measure of community differences than a diversity index) then the diversity of Thomsons and Forrestdale Lakes are high, despite their 'instability'. The fact that they are seasonal, however, does not necessarily mean that they are unstable; stability can mean a regularly changing environment, compared to one that changes irregularly. These lakes do have a regular hydrological cycle, and the fauna seem well able to cope with this. According to Parsons (1980) the seasonality of temporary wetlands tends to select for fauna with r-strategy life cycles. The fauna recorded in this study certainly have many of the attributes of r-selected animals, including living in a variable environment, catastrophic mortalities, yearly life-cycles, yearly recolonization of habitat, short life-cycles (Krebs, 1978). Hughes (1980) also concluded that seasonally predictable stresses selected for animals with annual life cycles. Weller (1978) stressed that stability, in terms of unchanging environments is neither common nor beneficial, and that drying and reflooding induce periodic nutrient release which is reflected in periodic population responses. Large scale unpredicted catastrophes greatly reduce species richness, and habitats with very low levels of disturbance have usually reached equilibrium with the elimination of ineffective competitors. Regular intermediate levels of disturbance often create the greatest species richness, this is known as the Intermediate Disturbance Hypothesis (Giller, 1984). It is based on the theory that such systems have enough time to recruit new species but not enough time to eliminate many of these through competition.

Comparison of Lakes

In many respects Thomsons Lake and Forrestdale Lake are similar, in fact analysis of variance concludes that there is no significant difference between the lakes with respect to density, species richness, diversity nor similarily of sites (Table 7). While the total lake species richness of Thomsons Lake is much greater than Forrestdale Lake (Tables 2 and 3), Figure 23 reveals little difference between the lakes at any one date, apart from the littoral sites in July; this is where the major difference in species richness and abundance occurred in the flooded lakes. Another major difference was the observation of fauna in the dry/moist core samples in Thomsons Lake, whereas no fauna was found in the Forrestdale Lake cores unless artificially flooded. The slightly higher species richness in Thomsons Lake may be due to a combination of factors, including more extensive submerged macrophyte growth by July (mainly *Myriophyllum*). This plant has a more complex structure than the main aquatic annual in Forrestdale Lake (*Ruppia polycarpa*) and several authors have found that aquatic plants with more complex morphologies support a more diverse fauna (Driver, 1977). The higher organic content may provide more food for the macroinvertebrates; this may especially help to explain the comparatively low species richness in the littoral site at Forrestdale Lake. Thomsons Lake is surrounded by other wetlands and swamps, to a much greater extent than Forrestdale Lake, perhaps these may act as sources for recolonizing insects. This is supported by the results of Tables 2 and 3, which show that the high species richness of Thomsons Lake is due largely to a greater number of Coleoptera species.

Conclusions

DATA COMPARED	F-VALUE AND SIGNIFICANCE
ABUNDANCE (NUMBERS PER SQUARE METRE)	0.25 n.s.
SPECIES RICHNESS (AVERAGE PER SAMPLE)	0.18 n.s.
SPECIES RICHNESS (TOTAL PER SITE)	0.85 n.s.
DIVERSITY (SHANNON-WEINER)	1.00 n.s.
SIMILARITY BETWEEN SITES AT SAME DATE (JACCARD)	0.20 n.s.
SIMILARITY BETWEEN SAME SITE AT DIFFERENT DATES (JACCARD)	0.239 n.s.

Table 7: One-way analysis of variance between the lakes.

Both lakes appear to be very productive, in terms of macroinvertebrates species richness and abundance, by Australian standards. This is consistent with the meso-eutrophic nature of the lakes as determined from standards obtained from northern hemisphere studies. The high productivity also reflects the seasonality of the wetland.

The fauna of the lakes appear to be well adapted to the seasonal cycle of drying and flooding, re-colonization by many species occurring fairly rapidly, others remaining as resistant eggs or adults. The dry lake bed has a distinctive fauna including several semi-aquatic and terrestrial colonizers. After flooding species richness, abundance and diversity continue to increase over time. However the temporal differences are usually greater than the spatial differences at any one sampling occasion. The class Insecta was found to contain the most number of species (66% and 63% of the species in Thomsons and Forrestdale Lakes respectively). In terms of abundance, the subclass Ostracoda (Crustacea) was the dominant taxa after flooding. The sites near the perennial emergent macrophyte vegetation have the highest species richness and abundance in both lakes.

Overall, the lakes studied, Thomsons and Forrestdale Lakes, are quite similar, the main difference being a more abundant dry lake fauna, and a higher littoral species richness in Thomsons Lake. Forrestdale Lake had a much higher density of macroinvertebrates in the site near the *Typha*. The general patterns of change in the fauna appear to be very similar in both lakes.

BIBLIOGRAPHY

Allen, A.D. (1981). Groundwater resources of the Swan Coastal Plain near Perth, Western Australia. *Groundwater Resources of the Swan Coastal Plain.* Proceedings of a Symposium held at the University of Western Australia 21-22 May, 1981.

van Alphen, J. (1983) *Floral and Faunal Differences with Season, Salinity and Drying in Four Lakes South of Perth, Western Australia.* Murdoch University, Perth.

Arnold, J.M. and Wallis, R.L. (1986) *Wetlands: A Consideration in the Development of the Unconfined Groundwater Systems Underlying Perth, Western Australia.* Australian Water Resources Council Conference - Groundwater Systems Under Stress. Brisbane, 1986.

Ayre, D., Colreavy, M., Coster, P., Fisher, K., Hill, A., Lymberg, A., McShane, P. and Threlfall, T. (1977) *A Limnological Survey of Lakes Jandabup, Joondalup and Loch McNess.* Thesis. University of Western Australia, Perth.

Barnes, R.D. (1980) *Invertebrate Zoology.* Saunders, Phil.

Barnes, R.S.K. (1980). The unity and diversity of aquatic ecosystems. R.S.K. Barnes and K.H. Mann (Eds.) *Fundamentals of Aquatic Ecosystems.* Blackwell Scientific Publications, London.

Bartle, J., Graham, G., Lane, J., Moore, S., (1986). *Forrestdale Lake Nature Reserve, Draft Management Plan.* Department of Conservation and Land Management, Perth.

Bayly, I.A.E. (1982) Invertebrate fauna and ecology of temporary pools on granite outcrops in southern Western Australia. *Aust. J. Mar. Freshwat. Res.* 33: 509-606.

Beckle, H. (1984) A comparative review of lakes in the Perth Metropolitan area. *West. Geogr.* **8**: 61-77.

Briggs, D. (1977). *Sources and Methods in Geography.* Butterworths, London.

Briggs, S.V. (1980). Chemical studies of four swamps on the northern tablelands of New South Wales. *Aust. J. Mar. Freshwater Res.* **31**: 729-36.

Briggs, S.V. and Maher, M. (1985) Limnological studies of waterfowl habitat in south-western New South wales. II: Aquatic Macrophyte Productivity. *Aust. J. Mar. Freshwater. Res.* **36**: 707-15.

Briggs, S.V., Maher, M. and Carpenter, S.M. (1985) Limnological studies of waterfowl habitat in south-western New South wales. I: Water Chemistry. *Aust. J. Mar. Freshwater. Res.* **36**: 59-67.

Bunn, S. (1982) *Aquatic Invertebrate Survey of the Western Chain of Wetlands, Kemerton Region, W.A.* Preliminary Report.

Commonwealth Scientific and Industrial Research Organization (1977). *Insects of Australia.* Melbourne University Press, Melbourne.

Congdon, R.A. and McComb, A.J. (1975) The nutrients and plants of Lake Joondalup, a mildly eutrophic lake experiencing large seasonal changes in volume. *J. Roy. Soc. West. Aust.* **59** (1): 14-23.

Congdon, R.A. (1979) *Hydrology, Nutrient Loading and Phytoplankton in Lake Joondalup.* Department of Conservation and Environment Bulletin No. 67, Perth.

Crook, I.G. and Evans, T. (1981) *Thomsons Lake Nature Reserve.* West. Aust. Nat. Reserve Manage. Plan No. 2. Department of Fisheries and Wildlife, Perth.

Davis, J.A. and Rolls, S. (1986) *An Ecological Study of the Invertebrate Fauna of Selected Urban Wetlands of the Swan coastal Plain.* Report for the Department of Conservation and Environment and the Water Authority of Western Australia. Draft Report.

DeDekker, P. and Geddes, M.C. (1980) Seasonal fauna of ephemeral saline lakes near the Coorong Lagoon, South Australia. *Aust. J. Mar. Freshwater Res.* **31**: 677-699.

Driver, E.A. (1978). Chironomid communities in small prairie ponds: some characteristics and controls. *Freshwater Biol.* **7**: 121-33.

Edward, D.H. (1968) *A guide for naturalists* by A.R., Main. Handbook. West. Aust. Nat. Club No. 4.

Fulton, W. (1983) Macrobenthic fauna of Great Lake, Arthurs Lake and Lake Sorell, Tasmania. *Aust. J. Mar. Freshwater Res.* **34**: 775-785.

Giller, P.S. (1984) *Community Structure and the Niche.* Chapman and Hall, London.

Gordon, D.M., Finlayson, C.M., and McComb, A.J. (1981). Nutrients and phytoplankton in three shallow, freshwater lakes of different trophic status in Western Australia, *Aust. J. Mar. Freshwater Res.* **32**: 541-53.

Hart, B.T. and McKelvie, I.D. (1980) Chemical limnology in Australia. *Limnology in Australia* (Ed.)

Hembree, D. and George, R.W. (1978) The Aquatic Invertebrate Fauna of the Northern Swan Coastal Plain. *Faunal Studies of the Northern Swan Coastal Plain - A Consideration of Past and Future Changes.* Western Australian Museum, Perth.

Hodgkin, E.P. , Sanders, C.C. and Stanley, N.F. (1979) Lakes, rivers and estuaries. *Environment and Science.* B.J. O'Brien (Ed.) University of Western Australia Press, Perth.

Hughes, R.N. (1980) Strategies for survival of aquatic organisms. R.S.K. Barnes and K.H. Mann, (Eds.) *Fundamentals of Aquatic Ecosystems.* Blackwell Scientific Publications, London.

Hunter, R.J., Simpson, P.G., Stranks, P.G. (1981) *Chemical Science.* Science Press, N.S.W.

Jennings, P. (1985) Wetlands at the Crossroads. *Environment W.A.* **7** (4): 3-6.

Jonasson, P.M. (1978). Zoobenthos of lakes. *Verh. Internat. Verein Limnol.* **20**: 13-37.

Kenko, R. (1949) *The Animal Life of Temporary and Permanent Ponds in Southern Michigan.* Ann Arbor University of Michigan Press, Michigan.

Klaster, J.L. and Jacobi, G.Z. (1978) Benthic macroinvertebrates of a fluctuating reservoir *Freshwat. Biol.* **8**: 283-290.

Krebs, C.J. (1978). *Ecology: The Experimental Distribution and Analysis of Distribution and Abundance.* Harper and Row, New York.

Landin, J. (1976) Seasonal patterns in the abundance of water-beetles belonging to the Hydrophiloidea (Coleoptera). *Freshwat. Biol.* **6**: 89-108.

Livingston, R.J. and Loucks, O.L. (1978) Productivity, trophic interactions, and food-web relationships in wetlands and associated systems. *Wetland Functions and Values: The State of our Understanding.* Proceedings of the National Symposium on Wetlands. P.E. Greeson, J.R. Clark, and J.E. Clark (Eds.) American Water Resources Association, Technical Publication Series, U.S.A.

McLachlan, A.J. (1974a). Recovery of the mud substrate and its associated fauna following a dry phase in a subtropical lake. *Limnol. Oceanogr.* **19** (1): 74-83.

McLachlan, A.J. (1974b) Development of some lake ecosystems in tropical Africa, with special reference to the invertebrates. *Biol. Rev.* **49**: 365-97.

Magdych, W.P. (1981). An efficient, inexpensive elutriator design for separating benthos from sediment samples. *Hydrobiologia* **85**: 157-59.

Maher, M. and Carpenter, S.M. (1984) Benthic studies of waterfowl breeding habitat in South-Western New South Wales. II. Chironomid populations. *Aust. J. Mar. Freshwater Res.* **35**: 97-110.

Maher, M. (1984) Benthic studies of waterfowl breeding habitat in South-Western New South Wales. I. The fauna. *Aust. J. Mar. Freshwater Res.* **35**: 85-96.

Major (1972) Standard Methods for the analysis of wastewater. C.S.I.R.O. Canberra.

Mann, K.H. (1980). The total aquatic system. R.S.K. Barnes and K.H. Mann, (Eds.) *Fundamentals of Aquatic Ecosystems.* Blackwell Scientific Publications, London.

Marchant, R. (1982) Seasonal variation in the macroinvertebrate fauna of billabongs along Magela Creek, Northern Territory. *Aust. J. Mar. Freshwater Res.* **33**: 329-42.

Marshall, B.E. (1978) Aspects of the ecology of benthic fauna in Lake McIlwaine, Rhodesa. *Freshwat. Biol.* **8**: 241-249.

Mason, C.F. (1977) The performance of a diversity index in describing the zoobenthos of two lakes. *J. Appl. Ecol.* **14**: 363-67.

Metropolitan Water Authority (1983) Progress of Investigations. Perth Urban Groundwater Balance, Metropolitan Water Authority.

Murkin, H.R. and Kadlec, J.A. (1985) Responses by benthic invertebrates to prolonged flooding of marsh habitat. *Can J. Zool.* **64**: 65-72.

Newman, P. and Hart, L. (1984) Deepening urban wetlands: An assessment of water quality in four wetlands on the Swan Coastal Plain, Western Australia. *Water* **June**: 12-16.

O'Connor, D. (1976). *The Cockburn Wetlands: An Environmental Study.*

Paine, R.T. (1969) A note on trophic complexity and community stability. *Am. Nat.* **103**; 91-93.

Parsons, T.R. (1980). Zooplankton production R.S.K. Barnes and K.H. Mann (Eds.) *Fundamentals of Aquatic Ecosystems.* Blackwell Scientific Oxford.

Rybak, J.I. (1969) Bottom sediments of the lakes of various trophic type. *Ekologia Polska - Seria A.* **17** (35): 1-52.

St. John, B.G., Carmack, E.C., Daley, R.J., Gray, C.B.J. and Pharo, C.H. (1976). The limnology of Kamloops Lake. B.C. Environment. Canada. Reference from Newman, P. and Hart, L. (1984)

Seddon, G. (1972) *Sense of Place: A Response to the Environment, the Swan Coastal Plain, Western Australia.* University of Western Australia Press, Perth.

Smith, B.J. and Kershaw, R.C. (9179) *Field Guide to the Non-Marine Molluscs of South Eastern Australia.* A.N.U. Press, Canberra.

Stout, V.M. (1964) Studies on temporary ponds in Canterbury, New Zealand. *Verh. Internat. Verein. Limnol.* **10**: 209-214.

Technicon Industrial Systems (1977) *Industrial Method 329-74W/B* Technicon Industrial Systems, Terrytown, New York.

Technicon Industrial Systems (1977) *Industrial Method 158-71W/Preliminary (1972) Nitrate and Nitrite in Water and Seawater.* Technicon Industrial Systems, Terrytown, New York.

Timms, B.V. (1973) A limnological survey of the freshwater coastal lakes of East Gippsland, Victoria. *Aust. J. Mar. Freshwater Res.* **24**: 1-20.

Timms, B.V. (1980) The benthos of Australian lakes. *An Ecological Basis for Water Resources Management.* W.D. Williams (Ed.) pp. 23-39 A.N.U. Press, Canberra.

Timms, B.V. (1982) A study of the benthic communities of twenty lakes in the South Island, New Zealand. *Freshwater Biol.* **12**: 123-38.

Vollenweider, R.A. (1971) *Scientific Fundamentals of the Eutrophication of Lakes and Flowing Waters, With Particular Reference to Nitrogen and Phosphorus as Factors in Eutrophication.* O.E.C.D. Paris.

Walpole, R.E. (1982) *Introduction to Statistics.* Macmillan, New York.

Weller, M.W. (1978) Wetland habitats. P.E. Greeson, J.R. Clark and J.E. Clark (Eds.) *Wetland Functions and Values: The State of Our Understanding.* Proceedings of the National Symposium on Wetlands. American Water Resources Association, U.S.A.

Williams, W.D. (1975). Australian Inland Waters. H.A. Nix and M.A. Elliot, (Eds.). *Managing Aquatic Ecosystems.* Ecological Society of Australia, Brisbane.

Williams, W.D. (1980) *Australian Freshwater Life.* Macmillan, Melbourne.

Williams, W.D. (1985) Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. *Hydrobiologia* **125**: 85-110.

Williams, W.D. and Wan, H.F. (1972) Some distinctive features of Australian inland waters. *Water Res.* **6**: 829-836.

List of References used in Identifying Fauna

Bayly, I.A.E., Bishop, J.A. and Hiscock, I.D. (1967) (Eds.) *An Illustrated Key to the Genera of Crustacea of Australian Inland Waters.* Australian society for Limnology, Melbourne.

Charpentier, R. (1967) A monograph of the family Heteroceridae (Coleoptera) of the Notogean region. Arkiv. Für Zoologi., **20** (11): 205-241.

C.S.I.R.O. (1970) *The Insects of Australia.* A Textbook for Students and Research Workers. Division of Entomology, C.S.I.R.O. Canberra.

Edward, D. (1964) Chironomids of S.W. Australia. Ph.D. Thesis, University of Western Australia. Zoology.

Knowles, J.N. (1974) A revision of Australian species of *Agraptocorixa* Kirkaldy and *Diaprepocoris Kirkaldy* (Heteroptera: Corixidae). Aust. J. Mar. Freshwat. Res., 25: 173-91

Lansbury, I. (1970) Revision of the Australian *Sigara* (Hemiptera - Heteroptera, Corixidae). J. Nat Hist., **4**: 39-54.

Mathews, G. (1982a) A Guide to the Genera of Beetles of South Australia. Part 1. South Australian Museum, Adelaide.

Mathews, G. (1982b) A Guide to the General of Beetles of South Australia. Part 2. South Australian Museum, Adelaide.

Merrit, R.W. and Cummins, K.W. (1984) (Eds.) An Introduction to the Aquatic Insects of North America. 2nd ed. Kendall/Hunt, Iowa.

Morrissy, N. (1977) *Marron of Western Australia.* Department of Fisheries and Wildlife, Publication No. 5. Department of Fisheries and Wildlife, Perth.

Smith, B.J. and Kershaw, R.C. (1979) *Field Guide to the Non-Marine Molluscs of South Eastern Australia.* A.N.U. Press, Canberra.

Watson, J.A.L. (1962) *The Dragonflies (Odonata) of South-Western Australia.* Handbook No. 7, Western Australian Naturalists' Club, Perth.

Watts, C.H.S. (1963) The Larvae of Australian Dytiscidae (Coleoptera). Trans. Roy. Soc. Aust., **87**: 23-40.

Watts, C.H.S. (1978) A Revision of the Australian Dytiscidae (Coleoptera) Aust. J. Zool., **57**.

Williams, W.D. (1962) The Australian Freshwater Amphipods. Aust. J. Mar. Fresh. Res., **13**: 198-216.

Williams, W.D. (1980) Australian Freshwater Life. The Invertebrates of Australian Inland Waters. Macmillan, Melbourne.

Wroblewski, A. (1970) Notes on Australian *Micronectinae* (Heteroptera: Corixidae). Polskie Pismo Entomologiczne, **40**: 681-703.