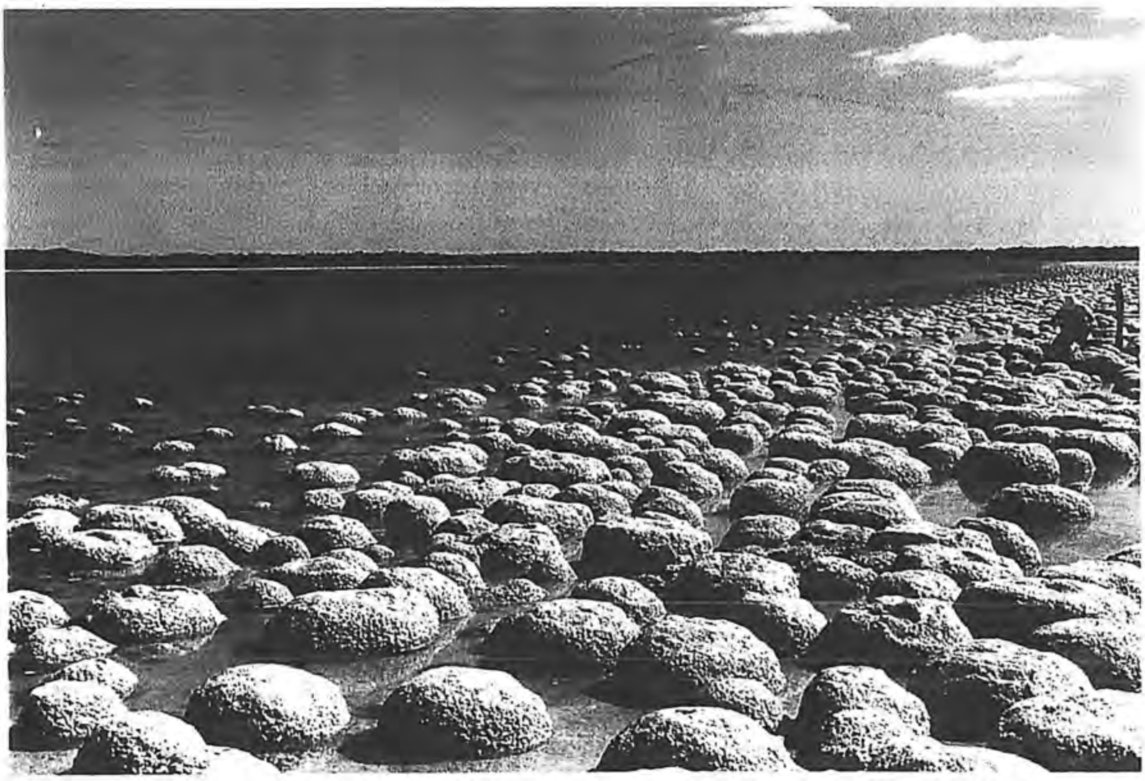
INTECOL V MID-CONFERENCE EXCURSION

THE WONDERS OF MICROBIAL MATS

Wednesday 25 September, 1996



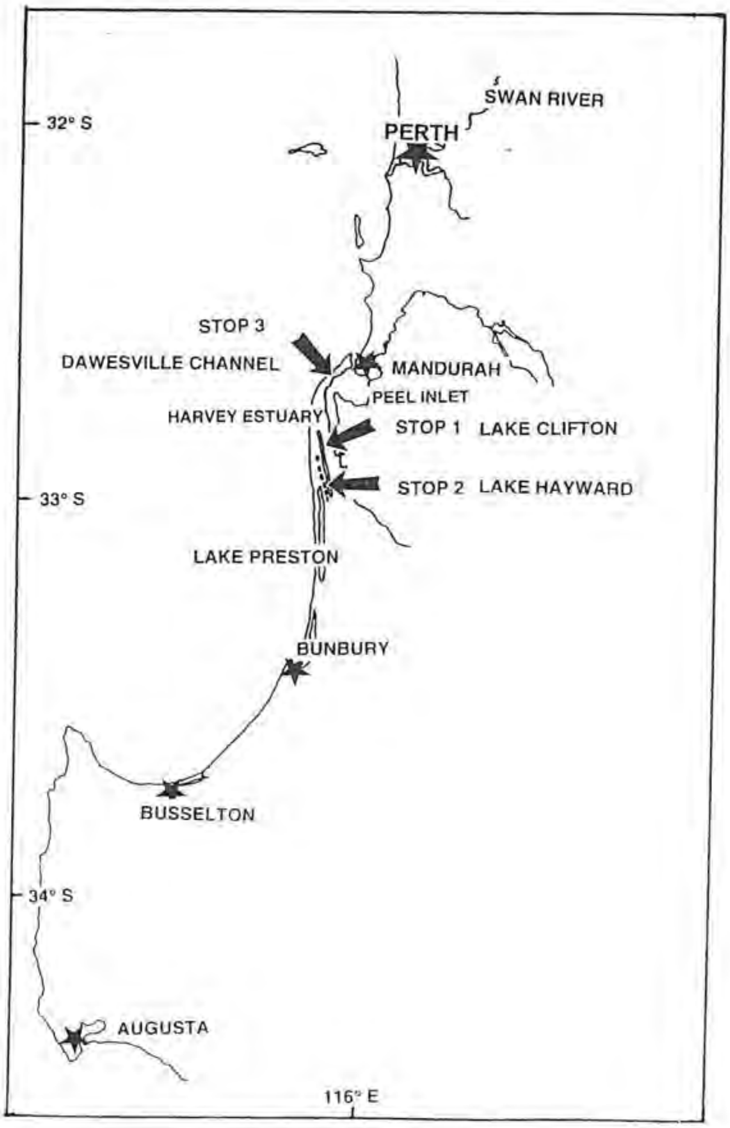
This document was compiled by Drs Brenton Knott, Jeffrey V Turner & Linda S Moore. The material contained in the docuemnt is drawn largely from the references cited, and acknowledgement is given to various co-authors.

ITINERARY

Stop 1: Mount John site, Lake Clifton

Stop 2: Lake Hayward

Stop 3: Dawesville Channel



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ACKNOWLEDGEMENTS

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REGIONAL CONTEXT

The landscape traversed on this excursion from Perth to Yalgorup National Park is dominated by two structural features, the Darling Scarp indicating the western limit of the Yilgarn Block and the Swan Coastal Plain. The Yilgarn Block, of Precambrian Archaean age, is the largest component of the Western Shield (Trendall 1975). The Swan Coastal Plain is the major onshore surface feature of the Perth Basin. The Darling Fault stretches for over 900 km from near the northern limit of the Perth Basin to the south coast. The geology of both the Shield and the Perth Basin is reviewed in detail in several Memoirs published by the Geological Survey of Western Australia. Seddon (1972), in his book entitled *Sense of Place*, provides a description integrating geology, geomorphology, climate, biology and utilization by man of the Plain. This has become a standard introductory reference to this environment; unfortunately, the book is presently out of print.

The Perth Basin (Fig. 1) approximately 1000 x 120 km, contains nearly 15000 m of sedimentary rocks dating in age from Permian to Tertiary (Playford *et al.* 1975). Quaternary deposits, laterite, limestone, dune sands and lake and swamp to a depth of 75 m, mantle much of the Perth Basin. Three major dune formations are described in Playford *et al.* 1975): the Quindalup Dune system, of recent age and comprising Safety Bay Sand, is formed from unlithified lime sand of foraminiferan and mollusc fragments with some quartz sand and heavy minerals; adjacent to this is the Spearwood Dune System, with its yellow sands and associated rock unit, the coastal limestone - often also known as the Tamala limestone; the most eastwards and oldest sands comprise the leached, grey quartz Bassendean sands of the Bassendean Dune System. Bastian (1996) produced evidence supporting the hypothesis that the yellow Spearwood sands are residual deposits derived from weathering of the underlying Tamala limestone instead of a central Australian origin. The landforms and their particular biological associations are briefly described by Seddon (1972).

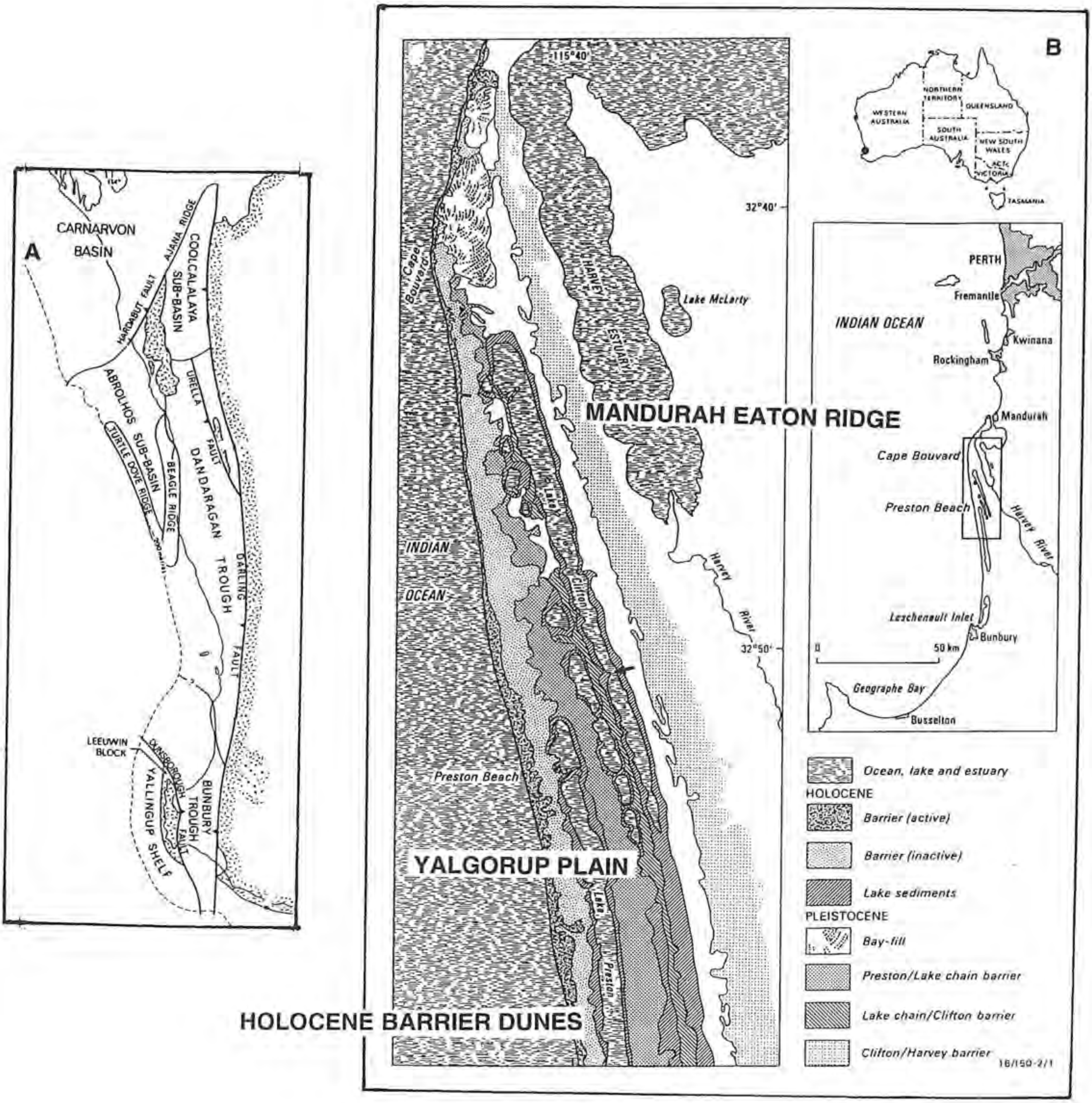

Fig. 1 (A) The Perth Sedimentary Basin (from Playford et al., 1975) and (B) geomorphic units of Yalgorup National Park (from Moore, 1993).

The lakes of the Yalgorup National Park occur in three, shore parallel lines, with Lake Preston and Clifton being considerably longer than the lakes of the inner line (Lake Pollard, Martins Tank, Lake Yalgorup, Lake Hayward, North and South Newnham). The lake waters are NaCl brines with ionic compositions approximating sea water but large salinity differences occur between lakes which may be only tens of metres apart (Burke and Knott 1989). The benthic communities of some of the lakes are very different. Lake Clifton has a large reef of thrombolites and extensive beds of the charophyte *Lamprothamnium papulosum*; Lake Pollard is dominated almost totally by *L. papulosum*. Lakes North Newnham, Hayward and Yalgorup all have cohesive, mucilaginous mats of benthic microbial communities (BMCs) across the sediments. As the source water for all lakes is similar (Commander 1988), it is likely that dominant processes currently operating in these lakes are quite different (Burke and Knott 1989). The best known BMCs, from the point of view of their structure and function, are those of the microbialites in Lake Clifton (Moore, 1987, 1993 and 1994) and the mucilaginous mats of Lake Hayward (Burke 1990, 1995).

CLIMATE

The climate of the region is Mediterranean; summers are hot and dry, winters wet and cool. Rainfall data from 1982 to 1989 have been collected at Yalgorup National Park (YNP) by Rangers of the Department of Conservation and Land Management (CALM) and can be found in Burke (1990). Additional data from 1990 to 1993 have also been collected by CALM. These combined data demonstrate rainfall to be seasonal, most falling between May and September with a maximum in June or July. Total annual rainfall values show a wide range, 642 to 1015 mm, with an average of 796 ±115 mm for all data. Because the time span of data collection is short (11 years), average rainfall values can be misleading and the standard deviation is large. For example the average rainfall between 1982-1989 is 769 mm, but from ‘88-’92 the average is 873 mm. Because of this variation, it is difficult to determine "normal" annual rainfall. Nevertheless, drought years and heavy rainfall years greatly effect the hydrology and hydrochemistry of the lakes. Burke’s study was conducted during one wet year and one "average" rainfall year (1991-1992), although the year preceding the study (1990) was a low rainfall winter. Evaporation rates measured by Hodgkin *et al.*

(1980) at nearby Peel Inlet show annual evaporation to be greater than twice the average annual precipitation

VEGETATION

The vegetation of Yalgorup National Park is summarised in the *Yalgorup National Park Management Plan 1995 - 2005.* Six vegetation complexes within YNP are recognized.

The Quindalup complex, found on the Quindalup Dunes, comprises the foredune shrub *Scaevola crassifolia* and grass *Spinifex hirsutus* and four age groups: the youngest shrubland (*Acacia rostellifera, Olearia axillaris*) second youngest of heath and shrubland (*Melaleuca acerosa*) and the two oldest (*M.acerosa, Pimelia ferruginea*). Older dunes with *Agonis flexuosa,* (peppermint) and *Xanthorrhoea preissii.*

The adjoining Cottesloe complex is of mixed eucalypt forest (tuart *Eucalyptus gomphocephala*, marri *E. calophylla*, jarrah *E. marginata*, red mallee *E. foecunda*) with tall understorey (*Banksia attenuata, Agonis flexuosa, Allocasuarina fraseriana*).

The Yoongarillup complex, tuart with a peppermint understorey surrounds Lake Clifton.

The Vasse complex, a wetter vegetation complex of tuart, jarrah, marri, flooded gum (*E. rudis*) and paperbark (*Melaleuca rhaphiophylla*) south of Lake Clifton.

The Karrakatta complex of mixed eucalyptus forest (tuart, jarrah, marri) and *Banksia* understorey occurs in the north eastern section of the Park.

In a narrow fringe around the lakes is a paperbark swamp vegetation complex of *Melaleuca cuticularis* and *M. rhaphiophylla*).

HISTORICAL DEVELOPMENT OF YALGORUP NATIONAL PARK (YNP) MANAGEMENT PLAN

The Fauna Protection Advisory Committee first discussed the issue of proclaiming the area about the Yalgorup lakes as a national park in 1946, and formally recommended that course of action in

1955 and again in 1957 (Chapter 3 in Western Australian Sub-Committee of the Australian Academy of Science Committee on National Parks 1963). However, Yalgorup National Park was not proclaimed until the 1970's and was listed on the National Estate in 1978. The Park currently covers an area of 12888 hectares and comprises 4 separate Reserves plus the Wellington Location. Although lakes Preston and Clifton were recognized to be important sites for waterfowl and the area about the lakes merited reservation for the "fine ocean beaches and very varied coastal scenery typical of that seen by the early settlers", early interest in having the area proclaimed as a national park possibly was based on the vegetation complexes present and the demand to use the lakes for recreation, particularly canoing (National Parks Committee Australian Academy of Science 1962): this may indicate the probable cause for the strong local opposition at the time to proclamation of YNP. Given the current interest in the benthic microbial formations in the several lakes, it is interesting to note that these lakes were described as having "bottoms .....covered with fine silts" (Western Australian Sub-Committee of the Australian Academy of Science Committee on National Parks 1963: p126). Within its boundaries lie a number of lakes of great scientific importance. The Peel - Yalgorup wetlands are recognized as Wetlands of International Importance under the Ramsar Convention. However, the increasing presence of humans, generated particularly by the population growth and increasing urbanisation in the Mandurah to Bunbury region are considered to pose a serious threat to maintenance of the lakes with their unquestioned scientific value. Already there have been wanton acts of vandalism such as riding of motorbikes on the thrombolite reef and the introduction of fish into Lake Clifton. Of greater significance is the fact that most of the Park lies close to privately owned land used for pasture and the production of lucerne and vegetables; furthermore, land eastwards of Lake Clifton has been extensively subdivided for hobby farms and semi-rural holdings relying on septic tanks. There is increasing pressure on the ground water, both through increased abstraction for agriculture and also from the increased introduction of pollutants, including nutrients. In response, the Department of Conservation and Land Management which manages on behalf of the National Parks and Nature Conservation Authority all parks and reserves vested with that Authority has prepared, after due process of consultation with a wide range of scientific, governmental and local community representatives, a management plan,entitled *Yalgorup National Park Management Plan 1995-2005*, designed, in the CALM Act (Section 56) statement of the broad objective governing the management of national parks

"To fulfill so much of the demand for recreation by members of the public as is consistent with the proper maintenance and restoration of the natural environment, the protection of indigenous flora and fauna and the preservation of any feature of archaeological, historic or scientific interest".

The task of managing YNP, minimising destruction or alteration to the numerous biological and limnological assets of the area will be made much more difficult than is usually the case by the markedly irregular outline of the park and the proximity of farmland and encroaching urbanisation. The stance being adopted is that it is better to educate the public about the inherent interest and importance of these biological features than to try and hide them away. Where else in Australia are microbial slimes being highlighted as interesting and important components of a natural ecosystem instead of the standard warm and cuddly mammals? The board wald and display at the Mount John site of this excursion (Stop 1) has been built as a result of one of the recommerndations of the Yalgorup Park Management Plan.

GEOLOGICAL AND GEOMORPHOLOGICAL SETTING

Lakes of the Clifton-Preston System lie within elongate depressions that lie parallel to the coast and within the Yoongarillup Plain and Spearwood Dunes; a terrain comprised of Pleistocene limestone commonly mantled by quartz sand of variable thickness. A prominent ridge of the Spearwood Dunes, up to 80m high, defines the eastern edge of the lakeland system. Another ridge of the Spearwood Dunes forms a barrier between Lake Preston and the chain of smaller lakes (hereafter called the "lake chain") that includes Lake Hayward. The lake chain is separated from Lake Clifton by a relatively low sand barrier, and at times of high lake levels the most northerly lake in the chain (Swan Pond) is connected to Lake Clifton. Along the western margin, the Holocene Quindalup dunes form a 20 to 40 m high barrier to the ocean. Thus, the pre-Holocene framework of the Clifton-Preston area is one of multiple north-south trending dune ridges and depressions. These pre-existing features define, for the most part, present day lake morphology (Coshell and Rosen, 1994). In terms of Semeniuk's (1995) recent study of the area, the name Yoongarillup Plain (of McArthur and Bartle 1980) is replaced by Yalgorup Plain and lakes Clifton and Hayward lie between the Youdaland and Kooallup Land geomorphological units, themselves between the Mandurah - Eaton Ridge (to the east) and Holocene barrier dunes (to the west). Semeniuk (1995) recognized 10 separate lithologies within the Yalgorup Plain and three Pleistocene formations, Tims Thicket Limestone, Myalup Sand and Kooallup Limestone (all three previously being part of the Tamala Limestone). The evolution of the Yalgorup Plain is thought to have occurred through several stages of coastal progradation related to sealevel still-stands in the Pleistocene (Semeniuk 1995).

STRATIGRAPHY AND HOLOCENE HISTORY

Lake Hayward

The stratigraphy and holocene history of Lake Hayward and the Yalgorup lake system has been studied by Coshell and Rosen (1994). Surface features present around the margins of Lake Hayward include groundwater tepee structures, desiccation features (mudcracks etc.), crusts, gas escape structures, and accumulations of degrading benthic microbial mats (BMC's). Along the eastern and southern margin of lake Hayward, Pleistocene pinnacles of carbonate are exposed at the surface. These pinnacles acted as nucleations sites for carbonate precipitating microbialite communities to colonise. Microbialites are no longer living in Lake Hayward, but similar forms are still present in nearby Lake Clifton. In the lake center, the surface is generally covered with thick coatings of various non-carbonate precipitating BMC's. Below the BMC and capping the sequence is a thin surficial layer of gypsum. Gypsum is not present deeper in the sediment.

The stratigraphy established from 20 cores taken in various locations around the lake exhibit a disconformable transition from Pleistocene aeolian coastal dune sedimentation at the base of the cores (Unit A), to a Holocene limnic swamp phase marked by the accumulation of higher plant matter (including whole logs), peat horizons and the freshwater gastropod *Physatra georgiana* (Unit B). The limnic swamp phase has been dated by ^{14}C (uncorrected) as approximately 8,000 ±300 years BP (±1 s.d.). Holocene deposition was initiated by a rise in sea level resulting from rapid global warming in the late Pleistocene and early Holocene. The rising water table caused the freshwater swamp to develop over the Pleistocene dune sand and calcretised calcarenite in the depression. Wetland conditions gradually became predominant with progressively higher sea level and concomitant rise in water table. Ultimately, dune barriers were breached and Hayward became part of a complex marine inlet. Above the limnic swamp phase is a short interval dominated by marine microfauna and estuarine molluscs interpreted to be the marine inlet phase (Unit C). The top of this unit is dated at approximately 7,000 ±170 years BP (±1 s.d.) indicating that this surface marine connection was short-lived, probably less than 1000 yrs.

A gradual lowering of sea level isolated Hayward from the rest of the system, possibly aided by the accumulation of dune sand at the northern and southern end of the modern lake. From approximately 7000 yr BP, a saline lacustrine depositional environment has prevailed. Above the marine inlet, the sediments become more regularly laminated and are dominated by chemically and biologicially precipitated carbonates (Unit D). This unit comprises the bulk of the sediment and is interpreted to be the lacustrine phase. The transition from marine inlet to lake sedimention is marked by the abrupt disappearance of forams, certain bivalves and ostracods. The ostracod *Cyprideis australiensis* survived the marine/lacustrine transition and occurs throughout the lacustrine sequence. The lake sediments are dominated by aragonite and Mg-calcite, with subordinate amounts of calcite, of both primary chemical and biologic origin. However, significant concentrations of diagenetic dolomite have been found in both lake centre and lake margin cores. The lake centre cores also contain on average 25 % TOC. The occurrence of diagenetic dolomite has been documented in the sediments of Lake Hayward (Rosen and Coshell, 1992 and Rosen *et al.*, 1992).

Lake Clifton

At Lake Clifton, the latest part of a pre-lacustrine marine inlet phase has been dated at between 4670 and 3890 yr BP. A marine connection therefore existed at least during this time but no date on the initiation of the marine inundation or underlying stratigraphy is available. Certainly the marine phase at Lake Clifton appears to have ended later than that indicated for Lake Hayward. Hence, Lake Clifton's lacustrine record is shorter than the record at Lake Hayward. This interpretation of the Holocene history of Lake Hayward has significant implications for understanding how Lake Hayward evolved to its present hypersaline condition as well as the nature of other lakes in the Clifton-Preston system. Lake Hayward apparently became isolated from the ocean far earlier than Lake Clifton.

MORPHOMETRY OF THE LAKES

Lake Clifton

Lake Clifton is the second largest lake in the system. It is 21.5 km long with a maximum width of 1.5 km (Commander, 1988). Although the maximum area of open water is 17.8 km^2 (Commander, 1988), it is much less in summer when large areas of the southern end of the lake dry out completely. Groundwater enters the lake via seeps along the shore, through the middle of microbialite mounds and pinnacles (see Coshell and Rosen, 1994) on the bottom of the eastern shore of the lake, and via diffuse inflow. A wide, partially vegetated sand spit constricts the width of the lake to less than 200 m at a point approximately 7 km from its southern end. While much of the lake is less than 1.5 m deep, certain areas, such as the deep basin in the north and the channel passing around the spit, are up to 3 m in depth. Both the basin and mean annual water level of Lake Clifton are lower than mean sea level (Moore 1993). The microbialites form a reef-like structure with an abrupt 2-3 m drop off on the western margin of the platform. The western margin of the lake has no documented occurrences of microbialites. The presence o microbialites predominantly on the eastern shore has been related to the discharge of regional ground water on the eastern side of the lake which appears to be essential for vigorous microbialite growth (Moore and Turner, 1988). However, isolated microbialites have been reported on the north wester margin of the lake (Moore 1993). The western margin consists mostly of unconsolidated carbonate sand.

Lake Hayward

Lake Hayward (at 0.6 km ^{2}) is one of the smaller lakes in the system. At times of high wate (approximately 0m Australian Height Datum: i.e. mean sea level), the lake is 1.3 km long, 0.5 km wide with a maximum surface area and depth of 0.6 km^2 and 2.75 m, respectively. The lake level fall approximately 1m annually, considerably reducing the area of open water (approximately a 1 m fal equates to 0.45 km^2). There are no living microbialites around the margins of Lake Hayward. However there are rare lithified remnants of dead microbialites attached to Pleistocene eolianite on the easter margin of the lake suggesting that at one time there may have been a microbialite reef along the easter margin of the lake (Coshell and Rosen, 1994). Groundwater enters the lake mainly as seeps along th eastern margin, although tepee structures (see Coshell and Rosen, 1994) found on the western margin o the lake indicate that groundwater is entering the lake from the west as well.

Lake Preston

Lake Preston, which is 27.5 km long and 2 km wide at its widest point, is the largest lake in the system The maximum area of open water is 29.6 km^2 (Commander, 1988), but this is substantially reduced i summer when the northern end of the lake dries out. Lake Preston has been artificially divided into tw lakes by a causeway across the northern end of the lake. North Preston is small and shallow and dries ou completely in summer. Although there are drainage culverts through the causeway, there is little to n flow between the two lakes at low water due to a natural limestone ridge which separates the basins South Preston comprises essentially 95% of the total lake area.

There is no bathymetric chart available for Lake Preston, but it appears to be a very shallow lake. The north end is less than 2 m deep and, although there are no measurements for the southern end of the lake, it appears that it is also less than 3 m deep.

Much of the Lake Preston margin is indurated with a shallow dipping carbonate crust. This suggests that most of the groundwater entering the lake seeps in around the margins of the lake. Extensive remains of low-lying relict microbialite mounds and teepee structures have been recorded on the eastern shore of the lake. There are also some unusual digitate/crustose formatiuons offshore beyond the teepee zone in water depths of 1-2 m which appear to be living.

REGIONAL HYDROLOGY & COUPLED SALINITY REGIMES

Hydrology

The Clifton-Preston Lakeland system lies at the coastal margin of westerly flow from the Myalup ground water flow system (Deeney, 1988,1989a). The origin of this fresh water is recharge to the Yanget Mound located approximately 10 km west of Lake Preston. The salinity of this water at the water table is low at the source (less than 250 g/ m^3 TDS), but increases to greater than 1000 g/ m^3 near the lakes. At the base of the aquifer the salinity at the source is approximately 500 g/m^3 and increases to over 7000 g/m^3 near the lakes (Deeney, 1988,1989a,b). Ground water flow is generally from east to west. However, in the vicinity of lakes Clifton and Hayward, the ground water flow turns northwest. Small amounts of dilute ground water flow into the lakes from the west due to fresh water stored in lens stored in the dune systems that enclose the lakes. The only water reaching the lakes is by either direct rainfall on to the lakes themselves or via ground water. The dominant winds that carry moisture (carrying marine-derived ions in solution) are from the west. The groundwater that flows from the Yanget Mound to the lakes also had its origin from marine derived aerosols.

The regional ground water study conducted by Commander (1984, 1988) in the area from Mandurah to Bunbury indicated that underlying the lakes is a wedge of hypersaline water ranging from 35 kg/m^3 to 64 kg/m^3 TDS. In general, the trend is for the water to become more saline from north to south. The interface between fresher ground water overlying the saline water is quite sharp except in the north. Commander (1988) suggested that tidal influences of the Peel-Harvey estuary blurs the interface. The influence of the Peel-Harvey estuary may also explain why the northern area has a lower salinity, similar to that of seawater, and may reflect a significant intrusion of seawater into the aquifer.

The lakes of the Clifton-Preston system receive virtually no runoff, but are maintained by direct rainfall and ground water inflow (Commander, 1988). Perhaps the only direct surface input other than rainfall occurs into Lake Clifton. Davies and Lane (1996) studied the inputs of surface water discharge along the eastern side of lake Clifton as part of a study into the role of the fringing buffer communities. Surface water discharge into the eastern side of Lake Clifton is markedly episodic, occurring only after >10 mm rainfall over a 48 hour period. Surface water discharge from small buffer (20-50m wide) zones was about 100 times higher and total nitrogen content was significantly greater compared with the medium (100-150m wide) and large (500-600m wide) buffer zones (Davies and Lane in press). Although not statistically significant, mean levels of total phosphorus ranged from 0.16, 0.04 and 0.07 mg/l from the small, medium and large zones respectively (Davies and Lane in press). The marked seasonality of the rainfall and evaporation produces a cyclic pattern of annual lake level rises and falls. The September or October lake level peak is three months later than the rainfall maximum, reflecting the ground water influence on the system.

Salinity

The hydrogeochemistry and nutrient cycling in Lakes Clifton, Hayward and Preston have been reported by Rosen *et al.*, 1996. Lakes of YNP exhibit a large range in salinities (14 - 207 kg/m^3 TDS) both seasonally within each lake and among lakes. The chemistry of all the lake waters in the system is a Na-Cl-SO_4 brine, similar to sea water composition. However, lakes Clifton, Hayward and Preston have less SO_4, Br, Sr, Mn, and probably Fe than seawater and the concentrations of Ca and HCO_3 vary seasonally. The variation of Ca and HCO_3 in all three lakes suggests that calcium carbonate is precipitated during the late summer and early autumn when evaporation is most intense. Stable isotopes of carbon and oxygen have been used to study the timing and composition of carbonate precipitation in Lake Hayward (Rosen et al., 1995)the and

In the upper and lower water layers of Lake Hayward, the most saline of the lakes in the system with a total salinity in summer > 200 g/l, the concentrations of conservative ions such as Na, Cl, and K decrease in winter and increase in summer, indicating dilution by winter rain and concentration via evaporation in the summer. Concentrations of total Fe and Mn in the lower layer increase in winter suggesting release from the sediments and/or decay of the benthic microbial mat on the lake floor.

TIN/PO_4-P ratios and TN/ PO_4-P ratios are high in all lakes suggesting that P is the limiting nutrient in the system. Observed increases of the macroalgae Cladophora in Lake Clifton suggests that any potential increase in the PO_4 load to the lake will be taken up by the invigorated growth of this algae and may not be detected by measuring lake water PO_4 concentrations. The increased growth of Cladophora is detrimental to the health of the well-established microbialite community on the eastern shore of Lake Clifton.

Coupling the hydrology and salinity of the lakes

Hydrologically and with respect to their salinities, the Yalgorup lakes appear to be coupled. While each lake in the system behaves independently with respect to their seasonal water and solute balances, characteristics such as their relative seasonal water levels, groundwater levels and their salinities show characteristics that can be explained at the regional scale. The most striking of these characteristics is the fact that Lake Hayward has the lowest water level of all the lakes (i.e amongst those that have been measured accurately) that in the system and its level is slightly below sea level for much of the year, as well as being below the level of Lakes Clifton and Preston. Lake Hayward is also the most saline of the lakes, reaching a salinity of about 220,000 mg/L. This is certainly no co-incidence and leads to the conclusion that Lake Hayward acts as a regional sink for groundwater, its only mechanism for discharge being evaporation which traps salt. There is good evidence however that densitry driven flow causes the brine in Lake Hayward to flow against the direction of hydraulic gradient between itself and Lake Clifton.

The following list of points summarizes the main observations to indicate the coupling of hydrology and salinity in the lake system:

- The groundwater and lake hydrology in the Yalgorup National Park Lakes is governed by hydraulic boundary conditions of the Peel-Harvey Estuary to the east and the ocean to the west.

- Lake and groundwater levels are coupled and respond seasonally - *almost* in phase. Seasonal tidal fluctuations in Peel-Harvey Estuary are about 3 months out of phase with the groundwater and lake water levels because they respond to differing forcing functions, viz. tidal influences, rainfall recharge and discharge by evapotranspiration.

- Water table gradients are very low due to the Peel Harvey Estuary and the ocean causing elevations are close to MSL & slightly below for Lake Hayward.

- Source of salt is from a high marine aerosol input. This is concentrated by evapotranspiration and due to the low water table gradients is *not* effectively flushed out of the system and returned to the ocean by groundwater flow

- Observed lake and groundwater levels & salinities and the position of freshwater/saltwater interfaces are a long term (1000's of years) quasi-steady state determined by
    - Seasonal periodic forcing (recharge, ET)
    - The rate of marine aerosol salt deposition
    - Groundwater gradients/Boundary conditions
    - Density effects with brines - Lake Hayward.

Thermal Stratfication - Lake Hayward

Although only 2.75 m deep at its deepest, Lake Hayward is thermally and chemically stratified between April and January. Burke (1990) argued cogently for the lake to be classified as monomictic rather than continuing to describe the salt lakes of the Swan Coastal Plain as seasonally meromictic - the appelation given to Serpentine Lake on Rottnest Island by Bunn and Edward (1984). During the summer of 1991-1992, the lake was unstratified for only 6 weeks from mid-March to the end of April (Figure 2). The abundant rainfall during the preceding winter of 1991, and a relatively cool summer that followed it, added large quantities of dilute ground water to the lake and reduced evaporation. These factors delayed mixing of the lake by several months. During 1986-1987 the lake was mixed for 4 months (Burke and Knott, 1989). However, the lake has mixed and stratified every year since 1986 when the lake was first monitored. The chemocline and thermocline are sharply defined with a maximum salinity gradient of 138.7 kg/m^3 in less than 10 cm of water and a temperature contrast of 19°C over the same interval.

Nutrients

Lake Clifton

Nutrient cycling in the lakes of the Yalgorup National Park has been reported by Rosen *et al.*, 1996. The concentration of nutrients in Lake Clifton is variable. Organic N accounts for essentially all of the nitrogen in the lake water. Although, Moore and Turner (1988) reported relatively high concentrations of organic P (up to 0.220 g/m^3) in the lake water, the samples we analysed were all below the detection limit of the equipment (<0.010 g/m^3). This may be because not all of Moore and Turner's samples were filtered (Moore and Turner, 1988). Orthophosphate (PO_4-P) concentrations average 0.007 ± 0.002 g/m^3. The ratio of total nitrogen (TN) to PO_4-P (TP excluded organic P) in Lake Clifton varies seasonally. High TN/PO_4-P ratios generally occur in late spring/early summer and autumn to mid-winter months and low ratios occur in summer and late winter/early spring. There is a significant correlation (r = 0.75) between Fe and PO_4-P concentrations when all of the analyses of the different lakes are plotted.

Lake Hayward

The TN/PO_4-P ratio in Lake Hayward shows a pattern of variation similar to Lake Clifton, with high TN/PO_4-P ratios generally occurring in late spring/early summer and autumn to mid-winter months and low ratios occur in summer and late winter/early spring. However, the TN/PO_4-P ratios in Lake Hayward are lower than those of Lakes Clifton and Preston. Although organic N accounts for essentially all of the nitrogen in the lake water for most of the year, during autumn and early winter, NH_4 may be very important when the lake is unstratified. Orthophosphate (PO_4-P) concentrations in Lake Hayward are higher than either Lake Clifton or Lake Preston, averaging 0.027 g/m^3. The concentrations in the mixolimnion (0.02 ± 0.01 g/m^3) are lower than the monimolimnion (0.03 ±0.01 g/m^3).

Lake Preston

The TN/PO_4-P ratio in Lake Preston varies in a pattern similar to, and intermediate between lakes Clifton and Hayward (Figure 6). Organic N accounts for nearly all of the nitrogen in the lake water; only a small portion of N is contributed by NH_4. Orthophosphate (PO_4-P) concentrations in Lake Preston are higher than Lake Clifton but lower than Lake Hayward, averaging 0.012 ± 0.003 g/m^3.

Biology

Lake Clifton.

Organosedimentary Structures

Thrombolites and stromatolites are two of several forms of organosedimentary structures considered to have accreted as a result of the activity of benthic microbial communities (BMCs). Collectively, these structures have been successively defined as *cryptalgal sedimentary rocks* or *rock structures* by Aitken (1967), *stromatolites* by Awramik and Margulis (1974), *microbial structures* by Kennard and James (1986), and finally as *microbialites* by Burne and Moore (1987).

Stromatolitic microbialites are the oldest known biological structures with a fossil record dating back to 3.5 billion years. This represents one of the earliest records of organised cellular activity and probably the first indication of life on the planet.

The decline of stromatolites at the end of the Proterozoic and the rise of thrombolites during the Cambrian have been related to the evolution of burrowing and grazing metazoans. Walter and Heys (1985) suggested that fossil thrombolites, including those described by Aitken (1967), were the result of burrowing animals disrupting the formation of stromatolitic laminae, and that the early Palaeozoic thrombolites provided the stratal evidence for the disruptive influence of metazoan life on stromatolites.

It is clear that thrombolitic fabrics are complex, show great variation and might have originated in several ways. In this context, studies on certain modern ecosystems such as Lake Clifton can elucidate the mode of thrombolite formation and the role of a co-existing metazoan fauna.

Microbial and Algal Communities

Benthic microbial communities (BMC's) of varied species composition and preservation potential are common in all the lakes of this system (Moore *et al.*, 1983; Neil, 1984). The BMC associated with the Lake Clifton microbialites is composed of a variety of cyanobacteria and eukaryotic algae. By far the most abundant cyanobacterium is *Scytonema* (*S. siculum*, Moore and Coute, unpublished), a relatively large filamentous organism with a sheath diameter of 20-40 µm. Other cyanobacteria within this BMC include *Oscillatoria, Dichothrix, Chroococcus, Gleocapsa,* *Johannesbaptista*, *Gomphosphaeria* and *Spirulina*. Periphytic and epiphytic diatoms are particularly numerous throughout the lake and are not exclusive to the BMC of the microbialites. The most common genera are *Amphora*, *Brachysira*, *Cymbella*, *Entomoneis*, *Mastogloia*, *Navicula*, *Nitschia*, and *Synedra* (J.John, Curtin University, WA, pers. comm.). Macroalgae also occur in the lake and include the charophytes *Lamprothamnium papulosum* and *Nitella* sp., as well as *Ruppia megacarpa* and recently *Cladophora vagabunda*.

The Thrombolites

Thrombolitic microbialites are presently forming in Lake Clifton, where lake water salinity ranges from 14 g L^{-1} in winter to 35 g L^{-1} in summer. The thrombolites are growing in an environment intermediate between an open-marine environment in which their early Palaeozoic counterparts flourished, and a continental setting from which most modern microbialites have been recorded. The Lake Clifton thrombolites occur principally along the eastern margins of the lake with some minor developments along the north-western shore. They lie on or are partially buried in the sediments of the lake basin. Radiocarbon dating of submerged thrombolites show ages ranging from 1 950 years BP to modern. Serially-dated examples imply minimum net growth rates of the calcified structure of 10 mm per 100 years.

The marine-derived waters of this former coastal lagoon support an abundant and diverse fauna comprising marine, estuarine and lacustrine elements, a situation permitting studies on microbialite formation in the presence of a wide variety of benthic metazoans. Such studies have a bearing on those interpretations which suggest that the origin of thrombolites, as well as the decline in the abundance and diversity of marine stromatolites, was mainly the result of burrowing and grazing animals. Lake Clifton, therefore, provides an important modern analogue for improving our understanding of the development of Phanerozoic microbialites and, more importantly, the origin of thrombolites.

External Morphology

The thrombolites of Lake Clifton exhibit a wide range of external morphologies including conical, domical, discoidal and tabular formations which vary considerably in size, as well as more irregular and columnar structures up to 1.3 m high. As documented by other studies of modern microbialites such as those in Shark Bay (e.g. Logan *et al.*, 1974; Playford, 1980), external morphology appears to be primarily the product of the environmental setting. In Lake Clifton, seasonal fluctuations in water depth, regional variations in sedimentation rates and the effects of prevailing winds and currents are major controlling factors.

Large tabular, discoidal and domical thrombolitic microbialites, which range in diameter from 20 to 150 cm, are found at the north end of the lake. Along the north-eastern shoreline they have coalesced to form an extensive wave-resistant structure over 6 km long and in several places up to 120 m wide. This can appropriately be termed a reef after both Heckel (1974) and Fagerstrom (1987). The tabular thrombolites comprise a platform area comparable with the >reef flat= of coral reefs. Thus the rear margin of the >reef flat= is the highest part of the formation, most regularly emergent and least exposed to wave activity, whilst the >reef platform= and >reef front= (although often emergent) are regularly exposed to wave activity.

The tabular thrombolites typically consist of a series of concentric rings 3-18 cm wide surrounding a central core. On the platform the rings often abut or overlap those of adjacent thrombolites, with outer rings encompassing two or even three formerly discrete structures. This growth pattern has clearly facilitated the development of a continuous and indurated platform in many areas. Processes thought to promote these Clifton ring formations are related to the lateral accretion of the structures where vertical growth is limited by shallow water. A similar process is involved in the formation of microatolls in modern corals (Stoddart and Scoffin, 1979; Scoffin and Stoddart, 1978). The marked delineations between the rings in the Lake Clifton structures are probably related to prolonged interruption and eventual resumption in BMC activity in a manner similar to the episodic growth of coral microatolls described by Woodroffe and McLean (1990).

The tabular structures comprising the >rear margin= are more widely spaced, lower in height, and have fragmented and incomplete rings. These features give this area a disorderly and rubbly appearance reminiscent of the rear margin of coral atoll reef flats. That the tabular microbialites might represent the eroded remains of once domical or conical structures which had formed when lake levels were much higher, is difficult to accept for a variety of reasons. For example, their wide diameter would mean that 'giant' domical or conical thrombolites formed within a relatively short period of time. Moreover, there is no sign of relict or >stranded= microbialites above the highest water mark of the present-day shoreline.

In front of the emergent platform, mainly domical thrombolites pass offshore into a deeper area (1-3 m), where the structures are more isolated and interspersed with unconsolidated sediments (Fig. 3a). The permanently submerged structures lying beyond these often partially-emergent domes are typically conical and up to 1 m high (Fig. 3d). Gross >external laminae= of these conical thrombolites are often present (Fig. 3d). They are semi-detached from the core of the structure, thereby producing a distinct outer shell or 'cloak' under which lakewater can readily circulate (Fig. 4c). Since the connections between the cloak and core are tenuous, the cloak is often fragile and easily dislodged (Burne and Moore, 1987). This is not the case, however, for the coalescent rings of the tabular thrombolites forming the platform. The fragility of the cloaks may in part be related to the steep sides and offshore location of the conical thrombolites, features which discourage sediment accumulation, infilling and the subsequent stabilisation of these layers.

To the south of the reef-like formation, there is a gradual transition to smaller and generally more widely separated thrombolites on a broad, gently-sloping shore of fine sands and silts. Discrete and mainly discoidal thrombolites, which range from 2 to 50 cm in diameter, are partially buried in unconsolidated sediment near and beyond the mean annual low water mark. However, many thrombolites, particularly those which lie at or just above the mean low water mark, are ring or partial ring structures surrounding a 'necrotic' centre of low-relief. These have been described as Apustular doughnuts (Moore *et al.*, 1983). Grey and Thorne (1985) suggest that the formation of the necrotic centre may be due to emergence of the top of these thrombolites during periods of low water levels, a process similar to the genesis of microatolls. Subaerial exposure of the upper surface restricts growth to the margins of the structure producing a rim. The rim then serves to trap sediments which further inhibit growth and help produce the necrotic centre, thereby leading to a ring-like structure. It is likely, however, that a combination of processes may be involved, including wave action *per se*, as well as those processes operating during occasional periods of complete exposure. These include differential wicking (i.e. capillary draw) of groundwater and wetting by spray, both of which would tend to favour BMC growth on the perimeter of these thrombolites.

Towards the southern end of the lake and lying across the narrow, deep-water channel which passes around the sand spit, are discoidal, domical, sub-spheroidal and columnar thrombolites (Fig. 4d). These microbialites exhibit a wide range of sizes, with the largest (up to 1.3 m in height) being found in the deeper parts of the channel. Those lying along the scalloped edges of the sand spit are partially or almost completely buried by fine sediments, and many prove to be club-shaped upon removal.

The thrombolites in the channel are subjected to strong and alternating north/south currents over summer and autumn. These wind-driven currents result from afternoon south-westerly sea breezes giving way to nocturnal easterly winds. Compared to the structures of the north-eastern shore, the channel thrombolites are far more irregular in shape, have much flatter tops, and often have one or more holes up to 15 cm in diameter facing the direction of the wind-driven currents. It is not yet clear whether the irregular shapes of the channel thrombolites have arisen as a consequence of continual exposure to such currents, or whether they are the result of cyclical periods of burial, re-exposure and erosion.

The currents have eroded sediments from the base and sides of the channel, cutting down to the horizon of the former marine phase, exposing the band of shells dominated by *Katelysia*. Many of these shells form a substrate for thrombolite formation, with small structures 1-5 cm wide and 2-4 cm high attached to the upper surface of the shells. Since the surface sediments within the channel are continually disturbed by the currents, the tops of *Katelysia* shells exposed above the sediment provide the only stable substrate at the sediment-water interface that allows the formation of new thrombolites. Despite their location in such a dynamic environment, both the external and internal morphology of these small thrombolites are remarkably similar to those of their counterparts in much calmer areas of the lake.

Apart from the small thrombolites forming on the *Katelysia* shells, the Clifton microbialites are not attached to hard substrates, but lie on or are partially buried in the unconsolidated sediments of the lake basin. Moreover, despite the number of artificial and natural hard substrates present in the lake, such as wooden fence posts, limestone and clay bricks, PVC tubing, driftwood and outcropping limestone, the BMCs colonising these surfaces do not contain *Scytonema* and do not lithify. It is not yet clear why *Scytonema* is absent.

The three major types of thrombolite (ie. tabular, domical and conical/columnar) often comprise distinct, parallel bands along much of the shore. Since the height of the thrombolites is limited by the maximum lake level, it is not surprising that a recent study of external morphological variation along several transects perpendicular to the shoreline shows significant correlations between mean water depth and thrombolite height and shape (Moore, 1993). There is also a significant positive correlation between thrombolite height and energy of the environment, with taller thrombolites occurring in higher energy locations where fine sediments do not accumulate, and shorter, oblate or club-shaped structures occurring in lower energy areas where they protrude only slightly above the surrounding fine sediment.

Knowledge of the way in which the wide variation in thrombolite morphology in Lake Clifton reflects environmental factors may assist in understanding the environments which influenced the external morphology of Palaeozoic microbialites.

The Cambrian thrombolites from the Shannon Formation (Amadeus Basin, Australia) and Petit Jardin Formation in Newfoundland represent excellent fossil analogues of the Lake Clifton thrombolites. There are strong similarities between the large thrombolites from the deepwater channel in Lake Clifton and the thrombolite pillars of the Shannon Formation. According to Kennard and James (1986), these pillars also grew on a loose substrate and had high synoptic relief before becoming enveloped by wave-rippled sediments indicative of a relatively high-energy environment.

Internal Morphology

Although gross morphology varies between and within localities, the internal framework and dominant microbial components of the thrombolites are remarkably consistent throughout the lake. The internal structure consists of a calcified framework composed of mesoscopic clots (mesoclots) of microcrystalline aragonite, and an interframework (*sensu* Kennard and James, 1986) of fenestrae and detrital sediment.

Examination of thin sections of thrombolites from various parts of the Lake demonstrates that remnants of *Scytonema* filaments occur within the aragonitic mesoclots (Fig. 2b), indicating that this organism has been present since the genesis of the thrombolites. The filaments appear as radial arrays of golden-brown threads. This colour is most likely due to 'scytonemine', the persistent extracellular sheath pigment characteristic of *Scytonema*. The close association between living *Scytonema* filaments and the developing carbonate structure has been highlighted through the use of scanning electron microscopy (SEM), which shows the arrangement of dense clusters of aragonite crystals around individual filaments, as well as aragonitic crystals between filaments. However, the presence of *Scytonema* on and within the thrombolites does not necessarily imply any causal relationship with the genesis of the structure, and the above features alone do not provide sufficient evidence for microbially-influenced deposition of carbonate. The $d^{13}C$ values for the carbonate forming the mesoscopic framework of Lake Clifton thrombolites are markedly elevated (+7.1 $^{o}/oo$) compared to those of the lake water (-7.0 $^{o}/oo$) and groundwater (-11.7 $^{o}/oo$). The fractionation evident in the Lake Clifton thrombolites is most probably the result of CO_2 uptake by the photosynthesising BMC, and indicates that the precipitation of the carbonate constituting the mesoclots is biologically-influenced (Moore, 1988; Moore and Turner, 1988). These data support the view that the major process involved in the formation of the Lake Clifton thrombolites is the precipitation of aragonite in a microenvironment determined by *Scytonema* and other members of the BMC, i.e. a process of biologically-influenced, non-skeletal mineralisation.

The clots are non-laminated and are the essential frame-building component of all thrombolites (Kennard and James, 1986; Burne and Moore, 1987). X-ray diffraction analyses and SEM with EDAX demonstrate that the mesoclots, which vary in width from 3-12 mm and exhibit a variety of geometrical shapes, arise from the accretion of arrays of 10-200 mm aragonitic crystal laths. These crystals are initially precipitated at the surface of the thrombolite, immediately around the mucopolysaccharide sheaths of *Scytonema* (Figs 2c, 6c).

Although fine laminae are sometimes conspicuous in the top 2-5 mm BMC layer of a thrombolite, continued precipitation of aragonite and the formation of mesoclots leads to their destruction. Thus microscopic examination of the mesoclots lying just below the living BMC frequently reveals numerous radially-arranged and intact filaments of *Scytonema* embedded in a microcrystalline matrix i.e. the forming mesoclot. It is not yet clear, however, whether the continued precipitation of aragonite in the layers immediately below the surface of the Clifton thrombolites is due to *Scytonema* alone, or to bacteria, physico-chemical processes or a combination of all three (see, e.g. Monty, 1976; Chafetz and Folk, 1984).

The fenestrae comprising the interframework are either open, thereby creating convoluted cavities and tubes, or filled with fecal pellets, quartz sands and unconsolidated carbonate sediments, including the carapaces of ostracods, shells of bivalves (*Arthritica semen*) and gastropods (principally *Coxiella*). Open fenestrae occur predominantly near the surface, a feature probably related to the activities of metazoan inhabitants. The pattern of growth exhibited by the Lake Clifton thrombolites strongly indicates that these fenestrae are intrinsic, and that their formation is primarily related to the topography of the surface of the developing microbialite rather than to excavation of the structure by metazoan activity.

Many of the open and filled fenestrae are lined by a dark brown coating up to 0.5 mm thick which covers the surface of the mesoclots. This lining is characteristically smooth when wet and cracked when desiccated, and SEM with EDAX and XRD have shown the layer to be composed almost entirely of non-crystalline silica. The origin of this amorphous silica probably results from the dissolution of diatom frustules and subsequent reprecipitation.

The formation of fenestrae is related far more to the surface topography of developing thrombolites than to the activities of the diverse and abundant metazoan fauna which they harbour. The presence of an amorphous-silica coating in both filled and unfilled fenestrae is consistent with this view. This is not to say that metazoan activity cannot lead to minor modifications of the cavities. The fauna also contributes to the eventual infilling of fenestrae via transportation of lake sediments and deposition of fecal pellets.

The internal structure of the Clifton thrombolites parallels that of Cambrian thrombolites, with the various shapes of the mesoclots and the interframework of infilled fenestrae comparable with those found in the Shannon Formation (Kennard and James, 1986), although the size range of the Clifton mesoclots is somewhat smaller. Their size is, however, close to that of the mesoclots of the middle-Cambrian thrombolites from the Petit Jardin Formation of Newfoundland (Kennard, Chow and James, 1989).

The Lake Clifton thrombolites develop from the biologically-influenced precipitation of aragonite within a BMC microenvironment dominated by the filamentous *Scytonema*. Kennard and James (1986), on the other hand, suggested that microstructures within the calcitic mesoclots of most Cambrian/Ordovician thrombolites resulted from *in-situ* calcification of coccus-dominated communities. Apart from the remains of the *Scytonema* filaments, complex microstructures are not discernible in the Lake Clifton mesoclots. Kennard and James (1986) also suggested that Athrombolites *sensu stricto* do not appear to occur in any carbonate environment today, since they believed that the closest analogous modern structures are only partially clotted where-in the individual microbial clots are generally poorly-defined. However, the Lake Clifton microbialites clearly exhibit well-defined mesoclots throughout their structure and a recent comparative study by Kennard (1988) has confirmed that close analogies can be drawn, not only between Cambrian thrombolites and those in Lake Clifton, but also with those in Great Salt Lake, Utah (Halley 1976) and Green Lake, New York (Eggleston and Dean, 1976; Thompson, Ferris and Smith, 1990).

In summary, both modern and Cambrian thrombolites appear to be actively lithifying structures able to coexist with a grazing and burrowing fauna. This feature is not inconsistent with the fact that throughout the Phanerozoic, a suite of microbial structures (stromatolites, thrombolites and endostromatolites [*sensu* Monty, 1984]) continued to make significant contributions to reefs of more mixed assemblages. Calcifying BMCs were able to persist as >cryptoflora= in marine reefs, and continued to form significant carbonate formations in certain environments after the Palaeozoic, such as the Upper Permian reefs of the Zechstein basin in central Europe (Paul, 1980).

The modern thrombolites of Lake Clifton and the fossil thrombolites of the Shannon Formation exhibit a complex microbial-metazoan ecosystem. Kennard and James (1986) state that the Cambrian thrombolites Awere commonly inhabited by an abundant and diverse skeletal and soft-bodied metazoan fauna which included various trophic groups such as grazers, detritus feeders, suspension feeders and carnivores@, as is also the case in Lake Clifton.

Modern microbial mats, however, appear to be particularly susceptible to the pressures of grazing and burrowing. An apparent vulnerability to burrowing and grazing has been used to explain the crisis in stromatolite diversity and abundance at the end of the Proterozoic (e.g. Garrett, 1970; Awramik, 1971, 1991; Stanley, 1973; Walter and Heys, 1985). It has also been suggested that fossil thrombolites represent stromatolites that were burrowed and bored and, hence, owe their origin to the activity of these animals (Walter and Heys, 1985).

However, the internal structures of stromatolites that have been burrowed and bored are distinct from those of thrombolites. Moreover, the pattern of growth exhibited by the Lake Clifton thrombolites strongly indicates that their fenestrae are intrinsic, further supporting the view that bioturbation need not be the principal cause of fenestrae within fossil thrombolites.

If it is accepted that at least the Palaeozoic thrombolites were able to withstand grazing pressures, their eventual demise in oceanic and littoral environments must then be attributed to factors other than non-competitive exclusion by grazing organisms. Proposed factors have included competition for nutrients, competition for space, and/or changing chemical conditions (Monty, 1973, 1984; Grotzinger, 1990).

Competition for nutrients is unlikely to have been a significant factor in the decline of marine microbialites. The low nutrient demands of microbialite forming BMCs (see, e.g. Skyring and Bauld, 1990) strongly support this view. Indeed, low nutrient levels would tend to favour BMCs by inhibiting metaphyte growth. In this context, increasing phosphate levels in Lake Clifton as a result of human activities has been paralleled by increased growth of the green alga, *Cladophora* *vagabunda* in many parts of the Lake, including the thrombolite reef (Moore and Turner, 1988). The development of *Cladophora* can be seen as a form of spatial competition between this epiphytic macroalga and the BMC forming the thrombolites rather than competition for nutrients.

So far as competition for space is concerned, early thrombolites were able to co-exist with archeocyathans, early corals and stromatoporoids which grew at similar rates (Eicher and McAlester, 1980; Pratt and James, 1982: Pratt, 1984). A significant factor causing the decline of marine thrombolites may have therefore been the evolution of faster-growing, calcifying and reef-building organisms capable of outstripping the 10cm/100 year growth rates of lithified microbialites (Pratt and James, 1982; Kennard and James, 1986; Fagerstrom, 1987).

Kennard and James (1986) suggested that Achanges in the composition of the earth's atmosphere or oceans may have promoted the penecontemporaneous mineralisation achieved by BMCs associated with Cambrian thrombolites. The rapid lithification and durable nature of the Lake Clifton thrombolites is consistent with the fact that the Cambrian examples were able to diversify and radiate despite the concomitant explosion of metazoan life. However, calcification and rapid mineralisation by the BMC in Lake Clifton is clearly being facilitated by the seepage of carbonate-enriched groundwaters into a saline environment. Thus it remains unclear to what extent the subsequent decline of marine thrombolites during the Ordovician was due to spatial competition from the more rapid eukaryotic calcifiers or to changes in sea-water chemistry affecting cyanobacterial mineralisation.

Metazoan Communities

An abundant and diverse community of metazoans is associated with the Lake Clifton thrombolites (Table 1). The fenestrae within the structures provide an important habitat for isopods, amphipods, coleopteran and trichopteran larvae, shrimps and juvenile gobiid fishes *(Pseudogobius olorum)*. Other fauna frequently encountered within, or close to, the thrombolites include nematodes, polychaetes, ostracods, copepods and two other species of teleost fish. Abundance can be appreciated by the fact that several thousand animals have been extracted from single thrombolites less than 30 cm in diameter (B. Knott, pers.comm.). In view of the grazing habits of much of this fauna, it is reasonable to assume that the thrombolites provide both a source of food as well as refuge from predation (Moore *et al.*, 1983).

Two species of gastropod are generally found grazing on the sediment in the shallow regions of the foreshore rather than on and within the microbialites. In addition, colonial bryozoans have been found in a number of areas where they not only colonise the thrombolites but are also incorporated into the framework of some of these structures. The sea anenome, *Haliplanella luciae*, a species widespread in Australian estuaries, is common in the northern portion of Lake Clifton, where it colonises both the thrombolites and areas of coarse sediments.

Lake Hayward.

Burke (1990, 1995) recognized four types of BMC: *Microcoleus* BMC, *Cyanothece* BMC, *Chromatium* BMC and 'sulphate reducing' BMC.

The *Microcoleus* BMC is confined to the littoral zone of the lake above the 0 m contour and is seasonally inundated and desiccated. The most common cyanobacterial species is *Microcoleus chthonoplastes*, but *Chroococcus* spp. are also common. When the community is inundated, prolific growth of diatoms occurs on the surface across the top of the *Microcoleus* BMC.

The *Cyanothece* BMC occurs towards the centre of the lake within the 0 m contour and generates a very mucilaginous community. The BMC is dominated by two sizes of *Cyanothece* spp. which invariably occur together. High numbers of cells of *Gloeothece* sp., usually as dead ghost cells, occur. Other common, but minor, species include *Spirulina* sp. and *Phormidium* spp. The *Cyanothece* BMC, covering the FeS zone, is formed of three layers; most cyanobacteria occur in the bottom layer. The *Cyanothece* BMC 'holds' the autumnal brine and consequently is permanently inundated with water above 150 salinity units, although the edges of the community may be seasonally desiccated depending on the amount of rainfall and evaporation.

The *Chromatium* BMC appeared in the centre of the lake following a bloom of purple sulphur bacteria in the water column. This BMC had a pale pink mucilage 3 mm thick on top of a deep red layer 1 mm thick on FeS. A motile *Chromatium* sp. and a nonmotile coccus (possibly *Thiocapsa*) sp.) were very abundant in the red and pink layers respectively. However, greenish brown 'hillocks' of mucilage were evident on the surface comprising the two *Cyanothece* spp., *Spirulina* sp. and, infrequently, *Phormidium* sp.

The 'sulphate reducing' BMC consists of areas of FeS, $CaCO_3$ and $CaSO_4.2H_2O$ with a thin mucilage which is sparsely populated with cyanobacteria.

Homeostasis

Photosynthesis by the BMCs is sufficient to supersaturate the bottom water during periods of stratification. However, following an unusually dry year in 1987, salinity increased to 260 g L^{-1} and gypsum precipitated throughout the lake. The resulting turbidity was sufficient to obscure completely the benthos despite the shallowness of the lake (< 2 m). Consequently, the BMCs were greatly altered and the amount of oxygenic photosynthesis reduced. During the following winter (1988) the bottom water during stratification became anoxic and sulphurous. However, during the next few years, the BMCs reestablished and were able to again supersaturate the bottom water. The BMCs consequently, are believed to function as a strong homeostatic mechanism enabling long term stability of the current limnological characteristics of lake Hayward (Burke and Knott in preparation).

Artemia Biology

The dominant metazoan grazer inhabiting Lake Hayward are parthenogenetic brine shrimps of the genus *Artemia* (Anostraca). Specimens of *Artemia* occur naturally in hypersaline systems. Their restriction to hypersaline waters is thought to result from the lack of predation. *Artemia* are efficient filter feeders: it is something of an anomaly, therefore, to find these brine shrimps in a lake with very limited phytoplanktonic production (Savage 1994). Savage (1994) showed, however, that the biology of the population of *Artemia* resident in Lake Hayward is modified from the pattern that could have been expected for a parthenogenetic species inhabiting a permanent lake. Indeed, Savage (1994) has shown that these brine shrimps are quite plastic in their ability to exploit BMCs and that much of their life history is controlled by the salinity stratification which develops during winter. The monomictic behaviour of Lake Hayward is quite regular and predictable, and the growth and development of the brine shrimps is cued into this regular hydrological pattern. The main start to the population occurs with the hatching of cysts in winter, these cysts having been produced during the previous summer period and are dormant until the lake fills and surface salinity and rainfall are suitable for hatching (Savage 1994). Cysts are concentrated on the shoreline and rainfall is probably a significant feature in their activation and hatching. Towards the end of winter the adult Artemia also contribute to the population size by generation of nauplii through ovoviviparous reproduction (Savage 1994). Despite the continuous production of nauplii, recruitment into the adult population is limited to once each year - from diapause cysts occurring in late summer as lake salinity increases and the population starts to age (Savage 1994).

With respect to feeding, the Artemia in the central regions of Lake Hayward feed predominantly on cyanobacteria and heterotrophic bacteria which are derived from BMCs, although how these bacterial aggregates enter the water column of the lake has not yet been determined (Savage 1994). The Artemia in the peripheral regions of the lake were shown to graze directly on the BMCs (Savage 1994).

THE DAWESVILLE CHANNEL

The *raison d'etre* for digging the Dawesville Channel are given in a number of reports most recently in that of Eliot (1993) from which source the following information is summarised.

The twin basins of the Peel Inlet - Harvey Estuary receive riverine inputs from the Murray and Serpentine (Peel) and Harvey rivers. All three river systems drain catchments which are extensively modified for agriculture. Consequently, nutrient levels in the estuary have increased leading in the mid 1960's to increased growth of *Cladophora* sp. (also known locally as goat weed). *Cladophora* in the Harvey Estuary grows particularly well under the high temperature, high light levels of summer, utilizing nutrients recycled from dead microalgal cells at the sediment surface. However beginning in 1973 *Nodularia* sp. blooms provoked considerable public comment because of the nauseous smell, water discolouration and fish kills which led eventually to the formulation of a Stage 1 ERMP which recommended weed harvesting, changes in the fertilisers used, drainage control, replacement of pasture by forests, dredging the Mandurah Channel, and digging the DawesvilleChannel. The interaction between P and the algal elements *Cladophora* and diatoms is documented in detail in McComb *et al.* (1981). McComb *et al.* (1981) report the following changes in concentration of nutrients

	Much of year	At end of winter
NO_3/NO_2 nitrogen	< 2μg/l	2000μg/l
NH_4 nitrogen	20μg/l	300μg/l
Total nitrogen	400μg/l	4000μg/l
PO_4 phosphorus	25μg/l	300μg/l

The values in the Table above are averages from 6 sites in the Peel Inlet and 1 from mid-Harvey Estuary. The distribution of nutrients was not uniform: N levels were higher in the Peel, and P higher in the Harvey. McComb *et al.* (1981) concluded that N was the limiting nutrient in summer and autumn, and P was the limiting nutrient in winter and spring. Phytoplankton (predominantly cyanophyta in the Harvey) concentrations are high immediately following the winter input of nutrients.

The underlying cause of the nutrient build-up initially was the limited water-exchange between the estuary and the ocean. Maximum water depths in the elongate Harvey estuary and circular Peel Inlet are 2 m and 2.5 m, respectively; 60% of the Peel inlet is < 1 m deep. Average tidal range at Dawesville is 0.9 m, a value which can be increased by up to 0.6 m given appropriate barometric effects: barometric influences (with a periodicity of 5 - 15 days) can increase the tidal range by 0.3 - 0.5 m; annual period tides (due basically to the seasonal expression of the Leeuwin Current) can add a further 0.22 m to the tidal range; storms of significant magnitude are rare events. The barometric and annual tides suffer little attenuation between the ocean and the basins. The single high tide per day shows a 14 day cycle of strong to weak tides. However, because of friction the tidal wave passing into the estuary through the Mandurah Channel is significantly attenuated, reducing to an astronomical tide of 0.12 m in Peel Inlet and 0.07 m in Harvey estuary. Winter input into the Harvey estuary reduced salinity to 2 pss, temperature 11-12° C, mean light attenuation coefficient 0.69; in summer salinity in the Harvey may rise to 52 pss, temperature 26-27° C, mean light attenuation coefficient 0.98.

The 1.7 km long Dawesville Channel, dredged to depths ranging between 2 - 6.5 m was opened in 1994. It is predicted that water levels in both basins will increase, by up to 40% of the daily ocean tidal range in the Harvey Basin. Uncertainty as to precisely what the new water levels will be is due to the fact that the flood and ebb cycles in the Mandurah and Dawesville Channels are largely out of phase.

It is also predicted that there will be a 3 fold reduction in the estuarine flushing time.

Details of the flow through the Dawesville Channel are as follows:

	SUMMER	**WINTER**
Peak flood tide flux	850 m^3/s	1200 m^3/s
Peak ebb tide flux	800. m^3/s	1200 m^3/s
Peak ebb discharge velocity	0.80 m/s	1.20 m/s
peak volume exchange/tide cycle	$22.03 \times 10^6 m^3$	$33.01 \times 10^6 m^3$

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