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What Happened to the Australian Aquatic Biota 18 000 years Ago?

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Abstract

There is now ample evidence that hydrological conditions in lakes, rivers and the groundwater in south-eastern Australia have varied continuously during the last 50 000 years. The most dramatic event culminated around 18 000 years ago when most lakes dried. During this arid phase, much of the aquatic biota probably survived in lakes located near the coast. These lakes were subsequently inundated by a relatively rapid rise in sea level. The biota survived this phenomenon because it had good dispersal mechanisms. Some organisms of the arid phase also survived in a few inland bodies of water (notably in mound springs). It is important that limnologists and water managers remember that the key to full understanding of the present nature of Australia's aquatic environment is knowledge of past events.

Introduction

What would happen to the aquatic biota of Australia if most lakes and rivers dried? Would it survive so as to regenerate when water reappeared, and if so how? Has this phenomenon actually occurred in the not too distant past, and is it recurrent? In the event of such dramatic desiccation, how would the aquatic biota be affected in the long term, and is the present biota a direct reflection of such events? Are the life cycles of some species specially adapted to recurrent and extensive periods of drought, and can some species survive by constant migration?

Such questions are of more than academic interest because there is accumulating evidence that the Australian climate has indeed undergone extensive periods of aridity, with obvious limnological implications. However, the significance of recurrent aridity appears often to have been ignored by Australian limnologists. This contribution, then, aims to sharpen limnological focus on such events by summarizing present knowledge of the hydrological record. It goes on to consider the consequences of arid periods for the modern aquatic biota.

The Hydrological Record

Australia: a Stable Continent with a Long Lacustrine Record

In any consideration of the hydrological record, it should first be noted that Australia constitutes a portion of the earth's crust that has been geologically stable for a long period, viz for approximately the last 60 million years. During that time, Australia has been devoid of major rift-type tectonism and extensive mountain range building, such as would result from collision of lithospheric plates. In addition, Australia has not been covered by extensive ice sheets like those that have so obviously scoured Northern Hemisphere landscapes during the last glacial episodes of the Quaternary.

As well, some areas of Australia have been sites of lacustrine sedimentation for extensive periods. For example, near and south of Lake Eyre in central Australia, lake sediments date as far back as the end of the Cretaceous (Johns and Ludbrook 1963), and, similarly, some of the major elongated playa lakes in Western Australia, which occur in an ancient drainage network (Fairbridge and Finkl 1978; Van de Graaf *et al.* 1978), have accumulated lake sediments since the early Tertiary (Van de Graaf *et al.* 1978). There is, therefore, a substantial record of lacustrine sedimentation in some Australian basins. Study of these lake sediments can provide important information on the past hydrology of the lake basins in question, and on past climatic conditions. In addition, the associated fossil biota can provide information on the nature of past aquatic ecosystems and indicate how they changed through time and in response to hydrological changes.

Lakes, Rivers and Groundwater as a Reflection of Regional and Local Hydrology and Climate

In some cases, lake water level fluctuates only as a result of *local* climatic variation. The best-known examples are the maar lakes in western Victoria. Three of these have a well-documented record spanning the last 10 000 years (see Fig. 1 and Bowler 1981; De Deckker 1982*a*; Chivas *et al.* 1985). They are considered to be more or less in equilibrium with the local climate because there is little input from local groundwater and their catchment is small in area. They act, it has been said, as gigantic rain gauges. Other lakes have a much more extensive ratio of lake area to catchment area [see Bowler (1981) for tabulation of data]. They may receive water falling anywhere within their catchment, sometimes far from the depression (lake) itself. Lake Eyre is perhaps the best example: located in South Australia, it occasionally fills with water originating from rainfall in northern Australia. Bonython and Mason (1953) noted that in 1949 Lake Eyre filled with water that originated ~ 1000 km away and took nearly 4 months to reach the lake.

In general, most lakes and rivers are the surface expression of an extensive hydrological basin. In most lakes, therefore, overall water chemistry and salinity are controlled largely by groundwater composition. Chemical processes usually change more slowly below the lake than in the water column above because the latter is under the direct influence of local conditions, especially climatic ones. Thus, for a saline lake (e.g. >50 g l^{-1} salinity) to become fresh (<3 g l^{-1}), a significant dilution of the entire groundwater aquifer, or part of it, is necessary. To achieve this if the basin is large (e.g. >100 km^2), extensive hydrological changes are normally required. There must be either a simple dilution by input of fresh water, or salt flushing by an overflow of lake waters (or even the groundwater) from the basin. Associated with any process of salt dilution that may cause a lake to become less saline, the groundwater can also rise, thus producing higher lake levels and causing lake margins to extend. Similarly, with a groundwater rise, rivers will increase in flow and capacity, and formerly dry rivers might even start to flow again.

The best-documented example of the relationship between groundwater and lake water is provided by Lake Tyrrell and the adjacent Lake Wahpool in Victoria (Macumber 1983). These two lakes, although only 10 km apart and experiencing similar climates, have underlying groundwaters of quite different salinity, and, when full, have quite different water (see Teller *et al.* 1982). The composition of the groundwater below Tyrrell and Wahpool would have to be dramatically modified for these lakes to retain not only a large amount of water but also to become less saline and permanent. Such profound modification has previously occurred, for there is evidence at Lake Tyrrell (which today rarely retains more than 50 cm of water: J. Luly, personal communication) of high water marks at ~ 13·5 m above the present-day lake floor and dating from before 30 000 years BP (Macumber 1983). Indeed, evidence of past water-level fluctuations at Lake Tyrrell is by no means unique in Australia. A substantial amount of information on water-level fluctuations for a number of lakes now exists, especially for those in south-eastern Australia [for a summary, see Bowler and Wasson (1984)].

Documentation is also now available on changes in river regimes in south-eastern Australia [for a summary, also see Bowler and Wasson (1984)], so that, considered with our knowledge of lakes, the hydrological history of south-eastern Australia during the past 50 000 years can be regarded overall as well documented. Of special note here are the two volumes published under the auspices of CLIMANZ (Chappell and Grindrod 1983); they provide palaeoclimatic information at particular times for Australasia, viz 32 000 ± 5000 years BP, 25 000–20 000 years BP, 18 000 ± 2000 years BP, 15 000–10 000 years BP, and 7000 ± 2000 years BP. Bowler and Wasson (1984) review most of the published information about glacial age environments of inland Australia.

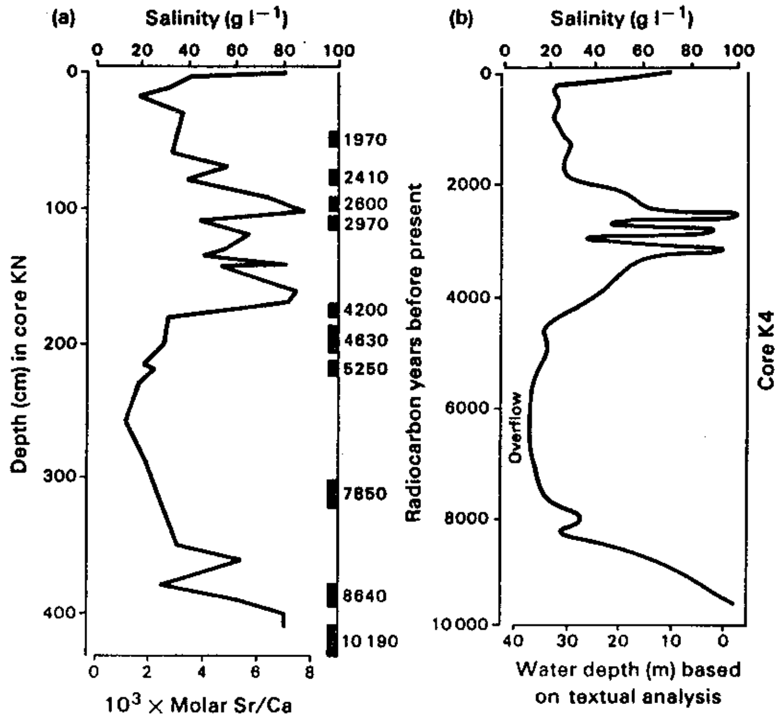

Fig. 1. Salinity curves for the last 10 000 years in Lake Keilambete, Victoria, reconstructed using two different methods. (*a*) Changes in the molar Sr/Ca in fossil ostracod shells recovered from core KN directly relate to salinity changes in the lake water by correlating the Sr/Ca of ostracod shells with the amount of Sr in their host water (see Chivas *et al.* 1985). (*b*) Changes in the size fraction of the sediment recovered in core K4 permitted Bowler (1981) to reconstruct a water-level curve for the lake; a salinity curve was also correlated to this water-level curve (see Bowler 1981).

Particularly valuable as part of the hydrological record is our knowledge of four regional components of the Australian landscape, namely (*a*) Lake Keilambete and other crater lakes of south-eastern Australia, (*b*) the Willandra lakes region, (*c*) the rivers of south-eastern Australia, and (*d*) the Mallee. Our knowledge of these elements is considered *seriatim*.

Lake Keilambete and Other Crater Lakes in South-eastern Australia. As mentioned, Lake Keilambete appears to function as a gigantic 'rain gauge' because it has little contact with regional groundwater and has a catchment limited to the crater rim: water level and salinity directly reflect the precipitation to evaporation ratio over the lake. Bowler (1981), De Deckker (1982*a*) and Chivas *et al.* (1985), using different methods of investigation, have reconstructed a water-level curve for this lake for the past 10 000 years (Fig. 1). Similar curves have been constructed for Lakes Gnotuk and Bullenmerri (two adjacent crater lakes approximately 25 km east of Keilambete) by De Deckker (1982*a*) and indicate a regional pattern of water-level change.

Unfortunately, no direct relationships can be accurately drawn yet between lake level and climatic changes. However, the following facts are significant. Levels in Lakes Keilambete and Gnotuk changed to such an extent that great salinity variations occurred over the past 10 000 years. These forced biological changes, which are particularly noticeable in Lake Keilambete for ostracods, cladocerans and foraminifers (De Deckker 1982*a*) and for aquatic macrophytes and algae (Tudor 1973; Dodson 1974). There is ample documentation that such biological changes commonly occurred over the past 10 000 years not only in Victoria but elsewhere in Australia [see Chappell and Grindrod (1983) for lists of references and sites]. A ready source of 'new' species must have always been available for dispersal into the lakes. Fish, for example, clearly reached Lakes Gnotuk and Bullenmerri on numerous occasions (De Deckker 1982*a*) (despite the fact that these lakes have elevated crater rims and are not connected to any stream). Birds were the likely agents for this form of passive transport. More details are given by De Deckker (1977). Note that both Lakes Gnotuk and Keilambete had also dried completely at some time before 10 000 years BP (Bowler and Hamada 1971; De Deckker 1982*a*); for these lakes, therefore, the aquatic biota has been completely reconstituted. Evidence that both have dried is given by the presence of a hard (soil?) layer below the 10 000 years old lacustrine sequence, and by their flat-bottomed topography.

The Willandra Lakes Region. This region has the best-documented palaeoenvironmental record in Australia: a chain of lakes connected by an old tributary of the Lachlan River record a succession of climatic events that have affected the region over the past 50 000 years. An account of these events is presented by Bowler and Wasson (1984) and is summarized in Fig. 2. The following points are relevant.

First, a 'wet lacustrine phase' started approximately 50 000 years ago and continued for well over 10 000 years. Then, around 35 000 years BP, lake levels dropped substantially before a rise about 30 000 years BP. From that time, lake levels fluctuated until approximately 12 000 years ago, when lacustrine deposition ceased.

Second, a short period (1000–2000 years) of intense aeolian activity associated with the lakes occurred about 18 000 years BP. This was a dune-building phase, and corresponded to the so-called Zanci phase of Bowler (1971). This Zanci phase started well before 18 000 years BP (probably around 25 000 years BP or even earlier), but climaxed about 18 000 years BP. The area of desert dunes in Australia was then dramatically large, and longitudinal dunes, characteristic of deserts, occurred even near Melbourne, on Kangaroo Island and in north-eastern Tasmania (Bowler 1978; Spriggs

1979). At the same time, the sea level had dropped by approximately 150 m below today's mean sea level (Chappell 1983). During this phase, lake levels dropped dramatically throughout south-eastern Australia and indeed there is no evidence that any large lake in the area retained water. Chappell and Grindrod (1983) indicate on their map of Australia that, at 18 000 ± 2000 years BP, 14 out of 15 sites investigated (but not necessarily lakes) in northern and southern Australia were drier than today.

Rivers of South-eastern Australia. Past and present hydrological regimes of rivers within the Murray Basin are better documented than any others in Australia. Available data on the Riverine Plain where the Lachlan, Murrumbidgee and Goulburn Rivers intersect the Murray Basin have been assembled by Bowler (1978) and are summarized in Bowler and Wasson (1984). Three principal hydrological phases within the Riverine Plain are recorded. They are represented graphically in Fig. 2.

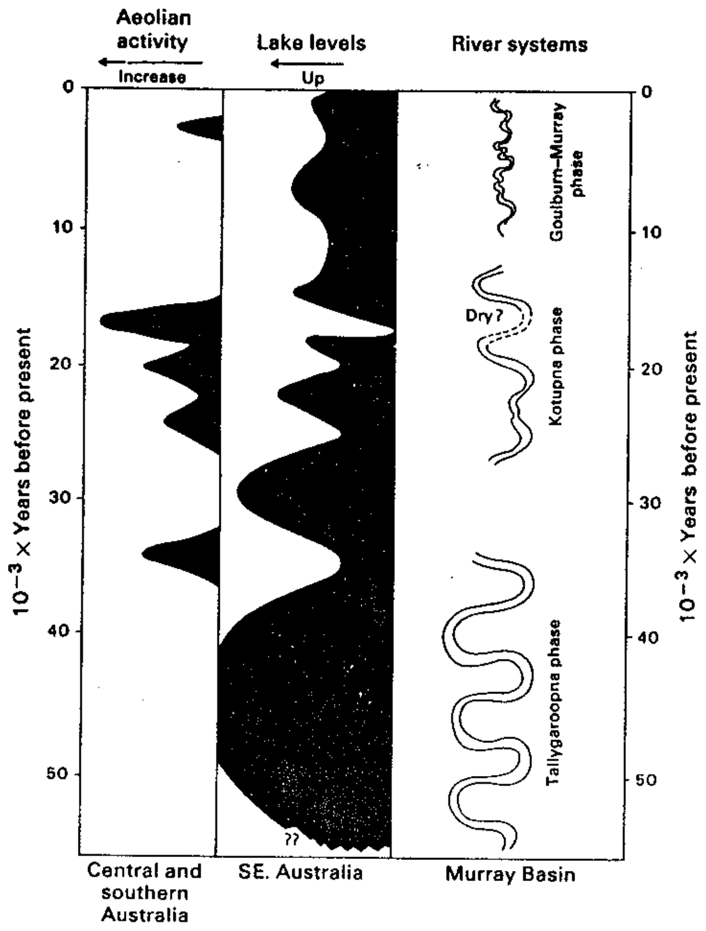

Fig. 2. Schematic diagram representing the timing of impulses of aeolian activity (mainly representing periods of dune formation), fluctuations in lake level, and major river morphologies that operated in south-eastern Australia (and central Australia for dunes as well) during the last 50 000 years. Diagram taken from Bowler and Wasson (1984) with updated information obtained by courtesy of J. M. Bowler.

The first phase, the so-called Tallygaroopna phase, was followed by the Kotupna phase. During both phases, rivers were characterized by large channels and meanders, and sand dunes were associated with their northern-north-eastern margins. Meanders during the second phase had smaller amplitudes than those during the first (see Fig. 2). The third phase, the so-called Goulburn-Murray phase, started approximately 11 000 years ago and lasted until today, although the exact time of transition between it and the previous phase is ill-defined (Bowler and Wasson 1984). The third phase is best characterized by having small, highly sinuous suspended-load channels. Bowler (1978) concludes that the first two phases involved much greater discharges. The same patterns occurred in the ancient record of the Darling River, which is now characterized by small sinuous channels (Bowler and Wasson 1984).

All events in the Riverine Plain reflect particular hydrological changes affecting the area. They must reflect major climatic phenomena that affected entire water budgets, including the groundwater. Thus, the large channels and meanders would have resulted from high groundwater levels, which in turn paralleled high lake levels.

The Mallee. Macumber's work on the hydrology of the Mallee region of north-western Victoria fully documents the presence there of a larger (60–100 m thick), generally saline, unconfined aquifer (within the marine sand unit—the Parilla Sand) below a thin cover of usually aeolian sediments (Macumber 1983). In the topographically low regions of the Mallee, especially in the northern portion, groundwater often reaches the surface and saline water, then seeps through the landscape into salinas. Macumber (1980) uses the term 'boinka' to describe these areas of saline groundwater discharge. They are sometimes quite extensive and are characterized by the absence of mallee vegetation, the occasional occurrence of halophytes, and the presence of salt flats and associated deflation features.

These saline groundwater discharge areas are now known to migrate laterally as well as vertically (Macumber 1983). This phenomenon depends on the movements of the groundwater aquifer. Moreover, Macumber (1983) has demonstrated that in parts of Victoria the saline seepage zones have recently risen topographically also, partly in response to human interference with the overall hydrology. In this respect, agricultural practices requiring vegetation clearance and irrigation are important. Groundwater migration of this sort is now closely monitored in Victoria (Macumber 1983, personal communication), and there is ample documentation that some rivers too are becoming more saline due to an increase of salt loading supplied by intersecting groundwater.

Macumber (1983) has found evidence of relict boinkas in other parts of north-western Victoria, indicating that saline groundwater seepage is by no means a recent phenomenon. Elevation of the salinity levels in some rivers no doubt also occurred in the past. Such changes, of course, were the result of natural phenomena, most probably climatic changes.

Consequences of Aridity

Our increased knowledge of the hydrological record of south-eastern Australia (which must correspond to that elsewhere on the continent, though not necessarily congruent in time) provokes several questions, the most important of which is: how did these hydrological changes affect the aquatic biota, and, in particular, how did it survive the extreme aridity of around 18 000 years ago?

Answers must currently be speculative for most of the biota because our knowledge of historical events is restricted largely to a knowledge of the fauna of lake systems where fossil deposition has occurred and to groups that fossilize well, such as ostracods, gastropods, diatoms and pollen or seeds of macrophytes. On the basis of such knowledge, however, there is no evidence that any important element of the fauna of Australian lowland lakes became extinct at that time. Indeed, some species now found only as fossils, in Late Quaternary sites (e.g. some ostracods at Pulbeena and Mowbray Swamps, Tasmania: De Deckker 1982*b*) will likely be found living as the Australian aquatic biota becomes better known. So, where did the biota seek refuge 18 000 years ago? The most probable answer is in coastal lakes that the sea has since transgressed. A chain of lakes, like those associated with the Coorong today and paralleling the coast, must have occurred along the continental platform 18 000 years ago at an altitude of ~ −150 m compared to the present sea level. These ancient lakes must have provided a refuge for much of the aquatic biota from the increasingly drier Australian interior. There is no direct evidence of the presence of these coastal lakes, but maps of the contemporary pattern of rainfall (Gaffney 1975) show that it is more predictable and abundant along most of the Australian coast. If this phenomenon is caused by coastal proximity, it is fair to assume that it also existed 18 000 years ago. Tasmania could also have acted as a refuge for some species as some large lakes there probably did not dry.

After the dry period of 18 000 years BP, sea level rose rapidly to transgress much of the Australian continental platform. Between 18 000 and 9000 years BP, sea level rose by 130 m (Chappell 1983), a rate of 1 m per 70 years; and between 18 000 and 6000 years BP, the surface areas of the Australian continent shrank by approximately 20%! Thus, having survived extensive aridity, the biota was faced with the need to survive a relatively rapid marine inundation of refuge areas.

It seems likely that survival of marine inundation was not the problem it might have been because the biota was already long adapted to an environment that required good dispersal mechanisms. Prior periods of aridity, involving both salinity change and periods of drought and associated sediment deflation (including deflation of eggs, cysts and seeds), had resulted in the evolution of organisms that had very effective transport mechanisms (Williams 1985). No doubt such species were frequently transported by birds, stuck to feathers and within their gut, or by other means to localities that often proved unsuitable, so that there was, in a sense, a continual 'testing' of habitats for suitability. And, of course, many habitats were only ephemerally suitable so that to secure survival, even in the absence of a marked climate change, the species must have been able to withstand periods of desiccation and dehydration. Additionally, tolerance of individuals and eggs to a broad spectrum of salinity, chemistry and other environmental conditions must have been a recurrent phenomenon.

It is not suggested that *all* elements of the aquatic biota of inland Australia survived in coastal refuges during the arid period 18 000 years BP. Some inland waterbodies also provided refuges. Of these, the most notable perhaps were mound springs (see Ponder 1986). To survive in these, however, the biota needed to be adapted to (or adapt to) a more or less constant environment. Note that some mound springs, especially those marginal to the Great Artesian Basin, have been actively flowing for perhaps millions of years. Consequently, some host a series of endemic species of gastropod and crustacean [for ostracods, see De Deckker (1979); for isopods, Mitchell (1985)], which probably evolved within the springs. Other occupants may be regarded as 'refugees'. This could be the case for two ostracod species (*Cyprideis* sp. and *Limnocythere* aff. *inopinata*) found in mound springs along the south-eastern margin of the Great Artesian Basin (De Deckker, unpublished data). These species are probably the residual few of a group that lived in numerous lakes when different water types existed in the region (viz in Lakes Eyre and Frome). *Cyprideis* requires permanent water to regenerate, and *Limnocythere inopinata* prefers highly alkaline waters (see Forester 1983). These two water types and conditions are very rare in central Australia today.

Survival may also have occurred in those few inland waterbodies that, for various reasons, escaped the full impact of arid conditions. The cosmopolitan aquatic herb *Ruppia maritima* may provide an example of such survival. Perhaps its present patchy distribution in salt lakes, mound springs and artesian bores in central Australia (Brock 1979; Jacobs and Brock 1982) indicates that it is part of a relict flora (Brock 1979, p. 150: M. A. Brock, personal communication) that thrived during wetter periods in the interior of the continent. Note that coastal records of this species may be erroneous because of misidentification (M. A. Brock, personal communication) and that fossil *Ruppia* seeds have already been recovered in a core from Lake Frome (De Deckker, unpublished data), although no *Ruppia* grows there when the lake fills today.

The above discussion leads naturally to a consideration of whether the endemicity of some elements of the Australian aquatic biota within restricted regions results from past climatic fluctuations and past aridity. This matter has already been considered by Walker (1981) when attempting to explain the disparate distribution of some freshwater mussels within the Australian zoogeographic region. It has also been considered by Geddes (1983), who looked at the distribution of halobiont anostracans. He concluded that the high endemism of *Parartemia* species in Western Australia results from the fact that chances of dispersal are limited because eggs sink and remain within sediments. Williams (1984) further pointed out that *Parartemia* adults are fragile and cannot withstand desiccation. In addition, extensive latitudinal and altitudinal gradients in Western Australia have also favoured speciation and endemism (Geddes 1983). Williams (1984), on a more comprehensive level, explained the regional differences in the fauna of Australian salt lakes on the basis of climatic shifts (of increasing or decreasing aridity). Such shifts would cause either an areal regression or an extension of salt-lake districts (see Williams 1984, fig. 2), and have occurred since at least mid-Tertiary times. Williams (1984) also briefly indicated the probable direction of faunal movements. However, there are at present insufficient data on the zoogeographical distribution of organisms and past climatic shifts to reconstruct migration patterns with any confidence. More fossil data are needed for this type of work.

Perspectives

Limnologists and those involved in management of the Australian aquatic environment need to know that aquatic environments have undergone natural change through time in Australia and are likely to continue to do so. This is important because, for limnologists, present biological distributions can only be explained against the historical background. Similarly, knowledge of past conditions might perhaps help explain some aspects of the behaviour or tolerance that aquatic organisms display to particular conditions and that are inexplicable in terms of their present-day aquatic environment. For water managers, past knowledge is also the key to understanding fully present changes induced by man. When considering the management of the River Murray and of its biota, for example, it is important to know that the salinity of this river was higher in the past. This is particularly relevant when examining present rises in salinity level and in studying the effects these would have on the biota. At least some species currently inhabiting the river must be adapted to these changes. We need to know these organisms better and to study their life cycles and salinity tolerances to predict what will happen should the River Murray become even more saline.

We should not forget that Australia is an arid continent characterized by strong climatic contrasts and frequent droughts. Attempts at managing its water systems [e.g. by regulating river flow: for reviews see Walker (1980, 1985)] in the fashion done elsewhere under the influence of a very different climate is a formidable task. Managers of water systems in Australia have to know that the aquatic biota, when facing changes, will have to do what it has always done in the past—adapt, or move elsewhere where the conditions are more suitable. The aquatic biota is used to an ever-changing environment. If one now regulates the aquatic environment and arrests the on-going changes, the biota will either have to adapt or move again. It is more than likely that some species will leave the regulated systems and not return into them until they become irregular once again. Some species may even face possible extinction as a result of this! This would be an expensive price to pay for a continuous supply of water. To interfere with above-ground water levels and salinities is perhaps manageable in the short term, but management of the groundwater, as well, is a formidable task, which our engineers are not yet equipped to handle.

Our rivers in the past have been characterized by irregular flows, our lakes have often dried and undergone marked salinity change, and the composition of Australian groundwaters has often varied. Similar natural changes are likely in the future. The aquatic biota is here today as a testament to the fact that its ancestors managed well enough through these changes. Let us find these organisms and determine their methods of coping with environmental changes. We need to learn more about the strategies and mechanisms for species' (re)introduction into new environments, and how species are preparing themselves for coping with future changes. It may even be possible that the Australian aquatic biota is better equipped to handle environmental change than we are.

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