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Drought, the “creeping disaster” Effects on aquatic ecosystems

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knowledge for managing Australian landscapes



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Abbreviations

BP	before present
CPOM	coarse particulate organic matter
DOC	dissolved organic carbon
ENSO	El Niño-Southern Oscillation
NDMC	National Drought Mitigation Center
PHDI	Palmer Hydrological Drought Index
POM	particulate organic matter
PDSI	Palmer Drought Severity Index
SOI	Southern Oscillation Index
SST	sea surface temperature



Foreword

For the past ten months I've read numerous papers, reports and books on the nature of drought as a climatic, meteorological and hydrological phenomenon, and on the impacts on, and responses of biota and ecological processes to hydrological drought. This has proven to be a fascinating and somewhat difficult task as the available literature is very scattered; quite a few papers only refer to drought obliquely, as studying drought was not a planned part of the ecological studies. The coherence of the literature varies tremendously. The literature on drought as a climatic and meteorological phenomenon, especially in relation to the El Niño-Southern Oscillation is readily accessible, whereas the biological/ecological literature is widely scattered.

The overall plan for this Research Fellowship was to read and digest the literature on drought and aquatic systems and their biota, to produce a report for Land & Water Australia on the major findings from the review of the literature, and to use this Fellowship effort to set up the writing of a book on drought and aquatic systems. The time to read about drought and think about what we know, in spite of some necessary interruptions, has been a very rewarding experience, and I am grateful to Land & Water Australia for giving me the opportunity to dig into the drought literature.

In this report I document the major findings evident from the literature, outlining some of the highlights I've encountered, and providing some suggestions on future research directions. The report deals with most of the areas that I have investigated. I am well aware of some areas that need to be pursued further, for example, how human activities in rivers and their catchments have served to exacerbate the impacts of drought. As Australia is the human-inhabited continent with the most variable rainfall and stream flow, and is affected frequently by drought, one would have thought that Australia would be a leader in drought research, especially in the ecology of drought. Sadly, this is not the case, with the exception of the excellent work on the meteorology and hydrology of drought.

P.S. Lake
1 July 2006



About the Senior Research Fellowships

During the peak of a researcher's career their most precious commodity is time. Many of our best scientific brains spend too much of their time on activities other than research—administration, management, writing research proposals, wrestling with budgets and so on. In a new approach to funding science, the Land & Water Australia Fellowships are expressly designed to “free up” the time of a select few leading researchers each year, to give them some time and space free from the constraints of everyday work. The intent is to sponsor reflective, synthesis research by people at the top of their fields—in mid-career, rather than in retirement.

The Senior Research Fellowships are designed to advance the way Australians think about, interact with and manage our natural resources. Each of the Fellows produces a major work, in written recommendations. Land & Water Australia expects these works will be thought-provoking and challenging, representing leading-edge thinking within their respective field.

Each year the Fellows are selected by the Land & Water Australia Board. The Fellowships are also made possible by the support of the Fellows' employers. Land & Water Australia thanks these organisations for their foresight and willingness to participate in this initiative.



Executive summary

As a general phenomenon to cover most situations, drought is difficult to define, though basically a drought is due to a severe, abnormal deficit in the rainfall of a region. Four major types of drought are recognised: meteorological drought, agricultural drought, hydrological drought and socio-economic drought. This report is mainly concerned with hydrological drought, which is manifested in both the availability of surface water and the levels of groundwater. There are numerous indices for drought detection and severity, and those applicable to hydrological drought are briefly examined.

Australia is a drought-prone continent with most of its drought generated by El Niño events. Since reliable records began in 1860 up till now, Australia has had major droughts for 78 of the 146 years. In spite of this, Australia as a nation has not been a leader in drought research, except for research on the climatic and meteorological components of drought.

Knowledge on the extent and severity of past droughts has come from dendrochronology and the examination of lake sediments, notably in North America. Of particular interest is the discovery of mega-droughts (droughts that last longer than one to two decades) in the Mediaeval Climatic Anomaly (~1150-1400 AD) and the 'Little Ice Age' (~1500-1700 AD).

Current knowledge on droughts has been generated with three types of studies. By far the most common type of study—the serendipitous one—occurs when drought intervenes into a study not specifically directed at drought. In this category many of the studies may lack pre-drought data and recovery from drought may not be followed. In the second and uncommon approach, the studies usually follow the onset and the recovery from drought even though the overall aims of the studies have been long-term ones not focused on drought. Finally and rarely, there are a few experimental field studies of the effects of drought.

Temporary water bodies are subject to periodic drying and this type of event needs to be separated from drought. Thus, drought affects water bodies when both meteorological and hydrological drought indices indicate regional drought. In many parts of the world, streams are normally subject to 'seasonal drought'—invariably not drought as defined by indices. Thus, most droughts are of long duration and are supra-seasonal. Streams that may have regular 'seasonal drought' can also be subject to supra-seasonal drought.

As a form of disturbance, drought is regarded as a ramp. The response to drought may also be a ramp, or a stepped ramp as there may be thresholds in the pattern of drying and in the biotic responses.

Drought as a disturbance in freshwater ecosystems causes declines in water level and volume, increased temperatures and evaporation and changes in water chemistry. In lakes lateral connectivity with the shoreline may be disrupted, whilst in flowing waters lateral connectivity may be lost, to be followed in many cases by a loss of longitudinal connectivity. Vertical connectivity with groundwater may also be lost. The larger the system, be it a river or a lake, the less serious are the effects of drought, provided that there are only minimal levels of human water extraction and river regulation.

Biota may survive drought by using temporal and spatial refugia. Temporal refugia involve such adaptations as having drought-resistant propagules, whilst spatial refugia involve movement into localities, such as pools in a drying stream, which allow persistence. Though it is relatively unexplored, there is clearly a variety of adaptations that have evolved to allow organisms to deal with drought.



Drought in standing waters, lakes and wetlands, has been rather neglected. Indeed it is from the study of lake sediments that we gain some idea of what droughts may do to lakes and their denizens. There are a few contemporary reports of direct changes in water chemistry, phytoplankton, zooplankton, benthos (especially the littoral benthos) and fish. Drought may also have indirect effects on lakes, such as the re-acidification of Canadian lakes as a result of drying of soil in the catchments and the subsequent re-wetting which releases sulphate into the lakes.

There is scattered but extensive information on the effects of drought on flowing waters, with a particular emphasis on invertebrates and fish. In large rivers, changes in the biota of the channels due to drought may be minimal, but the effects of extended drought on floodplain wetlands may be severe and long lasting.

With streams, drought causes loss of water volume, loss of habitat and disruption of connectivity, and if drying persists cease-to-flow can occur, usually breaking the stream up into a series of pools. In such pools lotic biota may be concentrated and water quality may steadily deteriorate with both hypoxia and hyperthermia—to such extent that fish kills can occur. The responses of ecological processes, even changes from autotrophy to heterotrophy and vice versa, have been very sparsely studied.

Biotic interactions between species may change or become accentuated with drought. Lentic and terrestrial predators and tolerant aquatic predators may exert strong pressure on their trapped prey. With habitat loss or the stress of drying, some sub-dominant species may temporarily become dominant. Parasitism may also rise in trapped populations.

With the breaking of drought, the positive responses of both algae and some short-generational invertebrates may be rapid, whilst the responses of aquatic macrophytes, large invertebrates and fish may take considerable time—a lag—to reach pre-drought levels. Severe drought may even cause local extinctions.

The effects of drought on estuaries has been the subject of a small number of studies. With reduction in the freshwater inputs into estuaries, there may be very significant changes in the level and distribution of salinity in the estuary with consequent effects on freshwater biota. Major changes may occur in productivity and in the trophic structure of the estuary and the risk of harmful algal blooms may rise. Such effects of drought or of reduced freshwater inputs into estuaries by virtue of river regulation and water extraction can severely damage estuarine fisheries.

Human activities, both direct and indirect, can exacerbate drought, or even create permanent drought-like conditions in waterways. With global climate change increasing the likelihood of increasingly frequent droughts, and/or increased duration, there is very clearly a need to better understand the nature and impacts of drought and to pro-actively plan and implement measures to effectively deal with drought.



The Phenomenon of drought

Introduction

Drought is a normal recurring climatic feature and its frequency, duration, severity and extent vary with locality and with time. It has proven difficult to get a universal definition of drought; indeed “a universal definition is an unrealistic expectation” (Wilhite 2000). The numerous definitions tend to split into two forms; those that define as a natural phenomenon and those that define it as a hazard to human activities, especially agriculture. For example, the definition of Schneider (1996) is in the natural category, drought is “an extended period—a season, a year, or several years—of deficient rainfall relative to the statistical multi-year mean for a region”. Examples of the second category include that of Tannehill (1947) drought is “a deficiency of rainfall from expected or normal that, when extended over a season or longer period of time is insufficient to meet the demands of human activities”, and ‘a drought is a prolonged, abnormally dry period when there is not enough water for users’ normal needs” (Bureau of Meteorology, Australian Government 2006). In this report, drought is mainly regarded as a phenomenon affecting natural ecosystems rather than one affecting human activities.

As stressed by Hagman (1984) and Wilhite (2000) drought is a very complex phenomenon and it remains a poorly understood climatic hazard. Bryant (1991) ranked 31 different natural hazards ranging from drought to rockfalls in terms of nine hazard characteristics: degree of severity, length of event, area extent, loss of life, economic loss, social effect, long-term impact, suddenness and occurrence of associated hazards. Drought scored the most severely on all characteristics, except for the last two, and is clearly the most severe natural hazard in terms of duration, spatial extent and impact.

Drought needs to be distinguished from aridity. Accordingly, aridity applies to the situation where there is a high probability of rainfall below a low threshold for a long and indeterminate duration, whereas drought occurs when there is a low probability of rainfall for a given period below an arbitrarily low threshold (Coughlan 1985). Thus, in arid areas or areas that have marked dry seasons, provided there is a good long-term rainfall record, it is clearly possible to distinguish drought when it occurs in spite of the prevailing regime of low rainfall.

Drought is linked with famine (Field 2000) both now, such as in sub-Saharan Africa, and in the past. The two severe droughts of 1876–79 and 1896–1902 are estimated to have killed 12.2 to 29.3 million people in India and 19.5 to 30 million people in China (Davis 2001). Economic losses, mainly through reduction of agricultural production, can be severe. The 1987–89 drought in the USA is estimated to have cost “upward from \$US39 billion” (Riebsame et al. 1991), whereas the very severe drought of 2002–03 in Australia (Nicholls 2004) is estimated to have cost \$A7.4 billion in lost agricultural production (Australian Bureau of Statistics 2004).

Major characteristics of drought

As suggested by Tannehill (1947) when he labelled droughts “creeping disasters”, it can be difficult to detect the beginning of a drought, as the deficiency of moisture in a region takes time to emerge (e.g. Changnon 1987). As drought is a form of disturbance that steadily builds in strength, Lake (2000, 2003) suggested that it constitutes a ramp type of disturbance. It can also be difficult to detect the end of a drought. However, if the drought is linked with an El Niño event, it may be broken by severe flooding (Whetton 1997).



As a form of disturbance, a hazard, droughts are distinctive in not causing major geomorphological changes or damaging and destroying human structures. Droughts may cause some geomorphological changes, such as those due to accompanying dust storms with consequent wind erosion and deposition of soil and sand. Droughts are also distinctive in occurring over large areas. They differ from floods in being usually drawn-out ramp disturbances rather than rapid pulses and in being a type of disturbance from which recovery is also a drawn-out process.

Droughts have three major characteristics; intensity, duration and spatial extent (Wilhite 2000). Intensity refers to the degree of reduction in expected precipitation and to the rapidity with which the drought becomes evident. Duration refers to the length of the drought and is entirely dependent for its determination on the thresholds used to define the onset and the end of drought. Dependent on the indices used to detect drought, it usually takes two to three months for drought to become established. Spatial extent refers to the area covered by drought, and in mapping the areas, such as in continually updated US Drought Monitor (Svoboda 2000), the areas are delineated in terms of drought intensity, from Do abnormally dry to D₄ exceptional, and in drought type (A, Agricultural and H, Hydrological) (David Miskus, JANF, CPC, NCEP, NOAA 2006).

Types of drought

There is general agreement that there are three basic forms of drought: Meteorological (National Drought Mitigation Center NDMC 2005) or Climatological (Tate and Gustard 2000), Agricultural (e.g. NDMC 2005), and Hydrological (NDMC 2005). To this may be added Socioeconomic drought (NDMC 2005) or Operational Drought (Mawdsley et al. 1994). This report will be primarily concerned with the first three types.

Meteorological drought occurs when there is a deficit in the actual amount of precipitation received and the amount that may normally be expected for an extended duration. It is dependent in its determination on rainfall falling below threshold levels that are determined from long-term rainfall records. It is regionally specific and given the need for long-term records to define it, meteorological drought may be difficult to define in regions with highly variable rainfall, such as arid areas, or in regions with insufficient long-term rainfall data collection.

Agricultural drought “is typically defined as a period when soil moisture is inadequate to meet evapotranspirative demands so as to initiate and sustain crop growth” (Changnon 1987). It focuses basically on “soil moisture deficits and differences between actual and potential evapotranspiration” (Tate and Gustard 2002). It is primarily centred on the availability of soil moisture in the root zone of crops, though it may also refer to lack of water for plant growth to meet the needs of livestock (Changnon 1987).

Hydrological drought occurs when the amount of precipitation in a region is insufficient to maintain normally expected flows in stream/river (lotic) systems or normally expected levels or volumes in lakes/reservoirs (lentic) systems (NDMC 2005). It is usually defined at the basin or catchment level. In the natural state it is induced by shortfalls in precipitation affecting surface runoff and groundwater storage of water. However, hydrological drought may be not only induced by precipitation deficits, but also by water deficits created by human land use and water storage (NDMC 2005).

Hydrological drought has mostly been defined in terms of availability of surface water, but groundwater levels may also undergo drought. Groundwater drought can be defined as occurring when there is deficit of groundwater storages or heads in relation to normally



expected storage levels or heads (Van Lanen and Peters 2000). In the natural state, the drought is due to a reduction in groundwater recharge in relation to discharge. In the human-impacted state, groundwater drought can be created by extraction, and thus with excessive extraction groundwater droughts may be created completely unrelated to surface hydrological conditions.

In any one region, meteorological drought is the initial form of drought. This may, dependent on soil properties and crop type, lead on to agricultural drought. Hydrological drought, dependent on precipitation, evapotranspiration, and human land and water uses, usually takes time to set in. If the drought is relatively short, groundwater drought may not occur, but with a drought of extended duration groundwater drought sets in, and its onset and severity may be greatly accelerated by human groundwater extraction.

When meteorological drought breaks with increased precipitation, agricultural drought may be ended shortly afterwards. Hydrological drought usually takes time, with considerable lags, to recover, and groundwater drought may have long lags in recovery.

Socioeconomic drought is the most difficult to objectively define as it arises from the interaction between meteorological, agricultural and hydrological drought and social and economic drivers of water use in a region. It occurs “when the demand for an economic good exceeds supply as a result of a weather-related shortfall in water supply” (NDMC 2005). Its announcement may be strongly influenced by political pressures (Heathcote 2000).

Drought indices

The World Meteorological Organization (1992) defined a drought index as “an index which is related to some of the cumulative effects of a prolonged and abnormal moisture deficiency”. There are numerous drought indices, many designed to meet particular needs or purposes. Heim (2002) provides a detailed history of the development of numerous drought indices in USA, along with an evaluation of 13 of these indices from those of Munger (1916) to the Drought Monitor (Svoboda 2000). It is perhaps not surprising, given the difficulty in getting a universal definition of drought, that there has been such a proliferation of drought indices. In an ideal world, drought indices could be used to compare droughts from region to region at any one time, to compare current droughts with those of the past, to identify drought-prone areas and to determine whether there are trends in droughts with time. Rather than review a wide range of indices, I will provide some details on widely used indices, especially those used to quantify hydrological drought.

In terms of impacts on freshwater ecosystems, meteorological and hydrological droughts are the most important, although one of the most widely used drought indicators, the Palmer Drought Severity Index (Palmer 1965, 1968), is basically for agricultural drought. I will deal with only a selected set of indicators that are widely used and relevant to this report.

For the detection and assessment of meteorological drought, I'll deal with just two widely used indices: rainfall deciles, and the Palmer Drought Severity Index (PDSI). The rainfall deciles method (Gibbs and Maher 1967) is the major one used in Australia. This method depends on the availability of long-term rainfall records for localities. Normal (Gaussian) graphs about the median of the frequency distributions of rainfall are compiled, usually for monthly data. The graph is divided into 10 deciles, with the lowest decile (ninth percentile) being very much below average. Drought is detected by comparing the ranked observed precipitation totals for the past three months against the long-term record for that period. Drought is present if the observed three-month total falls into the lowest decile of the long-term record. A drought is deemed to have broken when the precipitation “for a given month is at or above the 30

percentile of the three month period beginning in that month, or the rainfall over a three-month period is above the 70th percentile for that period” (Gibbs and Maher 1967).

The Palmer Drought Severity Index (PDSI) is really an agro-meteorological index and it is the major index used in USA. The PDSI is calculated using precipitation and temperature data along with available water content of the soil for any particular locality. From these inputs, an overall water balance equation is calculated and produces a value for the overall availability of moisture, the moisture anomaly index or Palmer Z index. Values around zero signify normal conditions, while values of - 4 or less signify extreme drought. By using soil moisture values it considers antecedent conditions. If the long-term trend is not considered, the PDSI becomes the Palmer Hydrological Drought Index PHDI (Karl et al. 1987). As the PDSI is a measure indicating the potential for plant growth, dendrochronological records can be used to calculate PDSI of the past, providing an indication of past aridity and “megadroughts” (Cook et al. 2004).

In an evaluation of six meteorological drought indices using six different criteria, the PDSI was rated the lowest and the Rainfall Deciles index was rated the most superior (Keyantash and Dracup 2002). However, a shortcoming of the Rainfall Deciles Index is that it does not indicate hydrological conditions, whilst the PDSI can provide a soil moisture index as well as provide the PHDI.

Hydrological drought may be determined from measuring a range of parameters in different types of water bodies, from flows in natural streams and rivers to water volumes in storages. In general, hydrological drought is determined from changes in flow in flowing waters (Tate and Gustard 2000), especially unregulated systems, though increasingly these systems may get harder to find. The key difficulty lies in discriminating drought from natural base flow conditions, especially in streams with high seasonal variability (Smakhtin 2001). There are a wide variety of hydrological drought indices, most based on low flow properties, and there is little standardisation of these indices worldwide. Links between meteorological indices and hydrological indices are few. The PDSI is linked with the PHDI, but for most other hydrological indices there is no obvious link between precipitation and the determination of the hydrological index.

For particular rivers, droughts may be defined using long-term flow records. Low flow frequency curves based on monthly or yearly flow volumes can be constructed (Gordon et al. 2004, Smakhtin 2001). In such curves there may be a break in slope, such that flows above this point are normal baseline flows and those below may be considered drought flows (Institute of Hydrology 1980, Gordon et al. 2004). These points vary with locality, for example with streams in UK the break point occurs at a low flow exceedance probability of 65% (Institute of Hydrology 1980), whereas for streams in Victoria it occurs at around 80% (Nathan and McMahon 1990).

A robust method of hydrological drought determination and description is the Total Water Deficit or Drought Severity (D) (Dracup et al. 1980). In producing this value, it is first necessary to derive a truncation level below which drought is deemed to occur. Drought severity is the product of the duration (D) that flows are below the truncation level, and the magnitude (M), the average departure of the flows from the set truncation level (Dracup et al. 1980). This method has been widely applied in the USA along with PHDI. In the previously mentioned study of Keyantash and Dracup (2002), Total Water Deficit index was ranked the best of four indices and the PHDI was ranked the lowest.

Groundwater drought usually sets in quite some time after hydrological drought has been established. It appears that it is still difficult to effectively characterise groundwater droughts (Van Lanen and Peters 2000, as it is difficult to assess groundwater storage volumes. Under



natural conditions, groundwater droughts may be characterised by a reduction in groundwater recharge with a consequent lower groundwater head, which can be readily measured. However, if there is human extraction of groundwater, drought may be difficult to effectively characterise. Groundwater droughts can have lasting deleterious effects on springs, streamflow, wetlands and riparian condition.

El Niño-Southern Oscillation and drought

Although it has been suggested that droughts can be caused by a number of major forces including sunspot activity (Tannehill 1947) and solar forcing (Hodell et al. 2001), a powerful and persistent creator of droughts resides in El Niño-Southern Oscillation (ENSO) phenomenon. ENSO is the dominant climatic event creating not only year-to-year climate variability, but also extreme events or disasters, floods and droughts (Bouma et al. 1997). This phenomenon is now relatively well understood (e.g. Allan et al. 1996, Couper-Johnston 2000) and is regarded as a powerful force in the world's climate. Basically, it is closely linked to the Southern Oscillation Index (SOI), which refers to significant changes in air pressure between Tahiti and Darwin. When the SOI is positive (La Niña), air pressure is low over Australia and high in the central and eastern Pacific, and sea surface temperatures (SST) along sub-tropical South America are cold. When SOI has high positive values major flooding may occur in Australia, Indonesia, India and possibly southern China and east Africa. When the SOI is strongly negative (El Niño), with high sea surface temperatures off South America, drought may occur in Australia, Indonesia, China, India and east Africa (Allan et al. 1996). El Niño events may be terminated by the rapid onset of La Niña, sometimes with severe flooding (Whetton 1997). Ecologically, ENSO has very strong effects on both terrestrial (e.g. Holmgren et al. 2001) and aquatic ecosystems, through floods and droughts.

The age of ENSO is uncertain; biological adaptations to high rainfall variability suggest that "ENSO has been operating and affecting Australia for millennia" (Nicholls 1989). Evidence from lake deposits from Ecuador suggest that ENSO is at least 11,000 years old (Moy et al. 2002), whereas evidence from fossil coral from northern Indonesia (Hughen et al. 1999) and from peat sediments (covering 45,000 years) from Lynch's Crater in north Queensland (Turney et al. 2004) suggests that ENSO was active in the last glacial-interglacial period.

El Niño events cause major changes in rainfall and consequently surface runoff and streamflow. A strong El Niño signal causing low streamflow and drought occurs in Australia (e.g. Simpson et al. 1993, Chiew et al. 1998, Chiew and McMahon 2002). Rainfall and the SOI and streamflow and SOI are both lag correlations (Chiew and Mc Mahon 2002). Links between low streamflow (droughts?) and ENSO events have been reported for India (Ganges) (Whitaker et al. 2001), New Zealand, northeast South America, central America, and to a lesser extent north and south-eastern Africa (Chiew and McMahon 2002).

Drought in Australia

Being in the mid latitudes, the flattest of continents and at the western dipole of the ENSO phenomenon, it is not surprising that the major part of Australia is arid and the continent as a whole is drought-prone. From 1860, when reliable records began, until 2006, Australia has had severe droughts for 78 of the 146 years (McKernan 2005, Bureau of Meteorology 2006). Drought has clearly been a force moulding the patterns of land use and abuse in Australia, but has not been fully recognised as such a force by historians, with some notable exceptions, for example Griffiths (2005) and M. McKernan (2005). Indeed, as persistently argued by Heathcote (1969, 1988, 2000), the reality of living in a drought-prone continent has taken a very long time to be fully accepted by European settlers. If anything it appears that Australia as a nation has been locked into the "hydro-illogical" cycle of drought described by Wilhite (1992). In this

cycle drought arises and there is alarm, but when the drought breaks things go back to the pre-drought state, without any anticipatory and pro-active measures to contend with the next drought. Both Keating (1992) and McKernan (2005) contend that it was the sharp and severe 1982-83 drought that effectively made dealing with drought a central part of Australia's politics and economy.

Australia has had major and memorable droughts, such as the Centennial drought (1888) (Nicholls 1997), the Federation drought (1895-1903), the droughts of the two World Wars (1911-1916, 1939-45) and the drought of 1982-83 (Keating 1992, McKernan 2005). With drought, severe bushfires tend to occur, such as Black Friday of 1939 and Ash Wednesday of 1983 (Keating 1992). Most, but not all, droughts are linked with ENSO events (Nicholls 1985, Whetton 1997).

Meteorological droughts of any duration lead to agricultural and hydrological droughts. In the USA with reliable regional data on the correlations between precipitation deficits, soil moisture content and streamflow, it is possible to deduce the resultant effects of meteorological drought and to use parameters such as tree rings and lake sediments to deduce drought indices such as the PDSI (Woodhouse and Overpeck 1998, Cook et al. 1999). However, at this stage, such a reconstruction of past droughts is not possible in Australia.

The recent drought (2002-2006?) has been both severe and long, indeed the most severe since the long droughts of 1939-1945 and 1946-1949 (Watkins 2005) and may now rival the Federation Drought (1895-1903). Nicholls (2004) noted that in the drought of 2002 (that has extended to 2005; Watkins 2005) temperature (and evaporation) were very high and he suggested that the nature of Australian droughts may be changing, being exacerbated by the enhanced greenhouse effect. This suggestion is supported by Karoly et al. (2003), and Watkins (2005) has also proposed this for the 2005 drought.

Droughts of the past and palaeolimnology

It is a rather bizarre finding that while accounts of the impacts of contemporary droughts on standing waters are relatively scarce, certainly in relation to those concerning flowing waters, signals from lake sediments, drowned trees and tree rings have produced a rich record of past droughts. By far, the major part of the studies on drought reconstruction has been done in the United States, in western USA. While there have been reconstructions back to the early Holocene (12,000 years before present BP) (e.g. Benson et al. 2002), for this draft review, I'll concentrate on the late Holocene (3,000 yrs BP till now).

Tree rings, a dendroclimatological signal, can date back 300 to 500 years, some even beyond that. Rings from trees that are exposed to moisture stress may provide a signal of past droughts (Fritts 1976, Stahle et al 1998, 2000, Woodhouse 2004). Thus, megadroughts of the past were detected (megadroughts being droughts that persist for longer than one or two decades (Woodhouse and Overpeck 1998). For example, tree-ring reconstruction allowed Stahle et al. (2000) to detect the severity, the persistence and spatial extent of the 16th century megadrought across western North America, especially in south-western USA and northern Mexico. In northern Mexico this megadrought extended from 1540 to 1598 (Stahle et al. 2000). When lake levels drop due to drought for long durations, trees may encroach down to the new shorelines. Such trees may then be inundated when the drought breaks. These trees—their stumps—can be then dated by C¹⁴ to yield times of inundation and time span of growth. Such stumps have been found in lakes in California and Nevada (e.g. Lake Tahoe, Lindstrom 1990, Mono Lake, Stine 1994). Stine (1994) concluded from the submerged trees, that California in mediaeval times was subjected to two megadroughts from 892 to 1112 and from 1209 to 1350AD in the "Mediaeval Warm Epoch".



Sediments can be sampled for indicators of wet and dry periods. Such indicators may either reflect changes in inputs to the lakes or changes to conditions within the lakes. Indeed the latter are valuable in revealing what may happen in lakes during drought as current data are somewhat lacking. Aging of sediments is usually done by C^{14} dating with controls such as Cs^{137} from nuclear testing. Indicators such as δO^{18} levels in sediments increase with drop in lake level, as do levels of total inorganic carbon (TIC) and magnetic susceptibility, the latter being due to inputs of ferromagnetite into the lake (Benson et al. 2002). Biological indicators include changes in diatom species composition that can be related to changes in salinity (conductivity) (e.g. Fritz et al. 1993) and to changes in the Mg/Ca ratio of ostracod shells (e.g. Fritz et al. 2000). Such methods have served to strengthen the findings from stump dating and dendrochronology that in the past 2000 years in central and western USA there have been long periods of drought, especially in mediaeval times and in the “Little Ice Age” of the 16th century (Stine 1994, Woodhouse and Overpeck 1998, Fritz et al. 2000, Benson et al. 2002, Yu et al. 2002, Woodhouse 2004). Similar results have been found from core sediments from east Africa (e.g. Verschuren et al. 2000, Alin and Cohen 2003). Analysis of a sediment core spanning 800 years from Ranu Lamongan, a lake in Java, Indonesia, has revealed two multi-decadal periods of drought from ~1275 to 1325 and from ~1450 to 1650, with the latter period being concurrent with the ‘Little Ice Age’ (Crausbay et al. 2006). However, there was little indication of the ‘Mediaeval Warm Period’.

Thus, it is clear that lake sediments can provide a good indication of the strength and duration of past droughts. It is also clear that megadroughts, such as those evident in the ‘Mediaeval Warm Period’ or the ‘Little Ice Age’, do occur and that the droughts of recent times are dwarfed by these megadroughts. However, the climatic forces that generate megadroughts remain quite unclear.



Droughts and freshwater systems

The literature on the ecological effects of drought on freshwater ecosystems and their biota is a very scattered one, with the exception of the special issue of “Freshwater Biology” edited by Humphries and Baldwin (2003). Basically, our understanding of the ecological effects of drought has come from two major sources. The serendipitous approach where drought unexpectedly occurs either when the intention of the study is quite different from that of observing drought, or when drought creates marked effects (e.g. fish kill, algal blooms) that are observed as a singular study. Such studies are generally short-term and may lack appropriate pre-drought data and recovery may not be tracked. A rarer, but much more valuable, approach comes from long-term studies—often derided as just “monitoring”. This approach comes when there is a committed long-term study in which drought occurs. Such studies, that provide key insights into the both short-term and long-term effects of drought, include those of the Northern Temperate Lakes Long-Term Ecological Research (e.g. Kratz et al. 1997), the 25-year study of fish in the Everglades wetlands (e.g. Trexler et al. 2005), and the 34-year study of a trout population in a stream of the English Lake District (Elliott 2006). These long-term studies reveal unexpected and lasting effects that a drought may have on a freshwater ecosystem and its denizens. Finally, there are a few experimental studies in the field of drought that while difficult to perform have made a valuable contribution (e.g. McGowan et al. 2005).

As mentioned before, hydrological drought sets in after meteorological and agricultural drought, but before groundwater drought. Thus, a water deficit, usually at a large scale, is generated in terms of the flows of lotic systems or volumes and water levels in lentic systems. We are referring here to natural systems as human interventions into freshwater systems and their catchments can exacerbate, or even generate drought. River regulation may also give rise to ‘anti-droughts’ in which irrigation releases from storages may mask the presence of regional drought (McMahon and Finlayson 2003). The water deficit from drought may cause streams to fall in level, shrink in length and cease to flow. Standing water bodies may shrink in volume and in surface area and may even dry out; a function of size and depth. Estuaries with diminished freshwater inputs may increase in salinity and salinity may extend into upriver sections usually freshwater.

Drought is a natural phenomenon and to very varying extents aquatic organisms have evolved means to survive droughts. If one considers the variety of ephemeral, episodic, intermittent and seasonal water body types (Williams 2006), it is clear that flooding and drying are normal events in many water bodies. Can the drying periods in these water bodies be classified as droughts? There are no clear guidelines for solving this problem, but systems that undergo regular periodicity in flow, or only have water occasionally, can be subjected to meteorological drought, in that their regions are in meteorological drought and the normal pattern of wet and dry conditions has been disrupted. Thus, Dahm et al. (2003) uses the PDSI and PHDI indices as measures of drought for their locality in their study of drought in New Mexico streams. For temporary wetlands a drought may mean the omission of wet periods for an abnormal period of time, and may result in the loss of biota and ecological functions that cannot persist for the extended abnormal period of dryness. In the case of temporary streams, such as the streams studied by Boulton and Lake (1992a, b), the streams had winter flows and summer dry periods, but the severe drought of 1982-83 greatly reduced the winter flows and extended the length of the summer dry periods, leading to subsequent losses of fauna when flow returned. For ephemeral systems, such as claypans and temporary ponds, there may be no detectable effect of drought on the aquatic biota. Much of the biota of such systems have desiccation-resistant propagules that may survive for very long times (decades) (Williams 2006).



In the literature, and as defined by Lake (2003), there are seasonal hydrological droughts that are predictable and seasonal. These hydrological droughts or dry seasons are the outcome of seasonal climate variation, and as such are not really true droughts as they are not unusual or abnormal in terms of expected precipitation and hydrology. Such “seasonal droughts” occur in those areas with Mediterranean climate (e.g. Towns 1985, Resh et al. 1990, Gasith and Resh 1999, Bravo et al. 2001, Pinna and Basset 2004) and tropical and subtropical areas with marked wet and dry seasons (e.g. Kushlan 1976, Rincon and Cressa 2000, Douglas et al. 2003). The droughts detected by drought indicators (e.g. PHDI, cumulative water deficit) whilst normal are mostly unpredictable and straddle the seasons, thus being defined as supra-seasonal droughts by Lake (2003). It is these hydrological droughts that are the major concern of this report. Systems subject to seasonal drying periods may also be prone to drought due to the failure of their wet seasons.

The perturbation of drought: disturbance and response

As suggested by Bender et al. (1984), Glasby and Underwood (1996) and Lake (2000), the advent of a disturbance and the subsequent response constitute together a perturbation. Drought is a disturbance that has the potential to change if not damage both biota and ecological processes; but it should not be defined by the ecological responses to it, but rather by its abiotic properties (Lake 2000). Thus, as in earlier parts of this report, we have seen droughts defined in terms of their duration, their severity and their spatial extent. Droughts are notoriously hard to detect and their length (beginning and end) and severity can be defined by procedures, such as the rainfall deciles method or the PDSI for meteorological drought, or the PHDI and the low flow frequency threshold for hydrological drought. The mapping of these indices can produce maps showing changes in the spatial extent of drought in current (e.g. the US Drought Monitor: Svoboda 2000) and past time periods (e.g. Cook et al. 1999).

As a drought sets in surface runoff declines, interflow declines and the water table may decline diminishing the groundwater inputs to water bodies (Dahm et al. 2003). Due to accompanying high temperatures, and often high winds, loss of water from evaporation and transpiration may increase. Thus, as a disturbance, drought’s primary force is the steady loss of water from the landscape and waterscape. In view of this, Lake (2000, 2003) defined drought as a ramp disturbance to distinguish it from pulse disturbance, such as floods, or press disturbance, such as constant flow volume from river regulation. Droughts may also end as a steady ramp decreasing in strength, or rapidly as a pulse as in the case of a La Niña event closely following an El Niño event (Whetton 1997). As water is lost, the area inundated in both lentic and lotic systems decreases, resulting in a steady loss of habitat. However, there may be abrupt changes in habitat loss, step changes rather than graded changes (Boulton 2003). A clear example of this may happen as a stream dries up with the rapid loss of longitudinal connectivity as riffles dry up, converting a continuous flowing stream into a series of pools (Stanley et al. 1997, Boulton 2003). As a lake dries up, there may be a step change as the water level recedes from the normal shoreline with riparian and emergent vegetation. Thus, physically, as drying occurs there may be step changes, steps that in turn create step changes in the biota as when a riffle dries, the fauna of flowing water is lost (Boulton 2003). In general, large systems in their natural condition, such as deep large lakes and big rivers, may not show such step changes. It all depends on the duration and severity of the drought as illustrated by the shoreline changes of North American lakes that suffered megadroughts, or the pooling of large dryland rivers, such as the Murray in the Federation drought of 1895-1903 (Keating 1992) and the 1911-16 drought (Sinclair 2001).

In disturbance ecology, there is general agreement that biota may react to disturbances in two ways; either by resistance or by resilience (Webster et al. 1983, White and Pickett 1985). Resistance refers to the capacity of the biota to withstand and persist through a disturbance

and resilience refers to the capacity of the biota to suffer loss but effectively recover from the impacts of the disturbance. For many biota, dealing with disturbance entails a combination of resistance and resilience. In the case of the disturbance of floods in streams, many studies have reported that the biota tend to have low resistance, but a very effective resilience (Lake 2000). Biota in dealing with the impacts of drought may show a range of responses to drought. For example, in the marshes of southern Florida, the Everglades, droughts occur and pools with low water quality become small isolated patches, sometimes resulting in fish kills (e.g. Kushlan 1974). Two species of the same genus *Fundulus* in these marshes react differently to drought. The golden topminnow (*Fundulus chrysotus*) shows resistance to the low water quality conditions of the “drydown” persisting in low numbers, whereas adults of the marsh killifish (*Fundulus confluentus*) spawn along the peripheries of the pools as they dry up and their eggs are then left on dry ground (Kushlan 1973). With rewetting the eggs hatch (Harrington 1959)—a mechanism of resilience. In many cases, species may show in drought both considerable levels of resistance and resilience, for example, also in the Everglades, the eastern mosquitofish *Gambusia holbrooki*, can tolerate the poor conditions in drying pools and when high water levels return, it rapidly disperses into newly inundated habitat, reproduces and rapidly builds up high population numbers (Ruetz et al. 2005).

The use of refugia in drought

As drought sets in, organisms may seek ways to survive and thus seek and use refugia. Refugia have been defined as “habitats or environmental factors that convey spatial and temporal resistance and/or resilience to biotic communities impacted by biophysical disturbances” (Sedell et al. 1990). Note that it is individuals of species that use refugia, not communities *in toto*, as selection shapes the adaptations at the population level with species. Lancaster and Belyea (1997) usefully expanded the definition of refugia by including attributes of the life histories of biota that reduce the impacts of disturbance. Magoulick and Kobza (2003) justifiably contend that refugium/ia is a relative term and should be defined for specified biota, particular species, in each particular spatial-temporal context. Although refugia have been substantially conceived as a means of evading physico-chemical disturbance, refugia are also important in evading adverse biotic interactions (Magoulick and Kobza 2003). For example, Kobza et al. (2003) report that small-bodied fish seek refuge during drought in rather shallow solution holes that do not harbour large-bodied predators that reside in deep solution holes.

Dependent on the type of water body and the composition of the biota, there can be a considerable variety of refugia available, at least seven (Boulton et al. 1992, Williams 2006). These include active dispersal and subsequent re-invasion (Williams and Hynes 1977), migrating to moist leaf litter (Boulton 1989), moving to the moisture under rocks or logs (Boulton 1989), surviving in remaining pools (Magoulick and Kobza 2003), migrating into the hyporheic zone or digging into the bed of the water body (Smith 1931, Clinton et al. 1996), and dwelling as “pholeteros” (Lake 1977) in the burrow water of crayfish (Boulton 1989).

The availability, the sizes and the spatial distribution of refugia during drought clearly have a powerful influence not just on drought survival, but on the nature and rate of subsequent recovery after the drought breaks (Magoulick and Kobza 2003). Whilst there is evidence to support the strong positive influence of refugia in surviving drought, evidence to support the positive influence of refugia in patterns of drought recovery is fragmentary. The long-term study of fish populations in wetlands of the Florida Everglades is one study producing evidence for the key role that refugia have in drought survival and subsequent recovery (e.g. Kobza et al. 2004, Trexler et al. 2005, Ruetz et al. 2005).



Traits and adaptations to drought

Linked with the use of refugia is the nature of adaptations or traits that organisms have evolved to deal with the stresses of drought. Such adaptations may involve life history attributes, morphology, physiology, and behaviour. At first glance, it appears that freshwater ecologists dealing with disturbance have concentrated on traits evolved to deal with floods rather than droughts (Lytle and Poff 2004). However, for particular biota such as plants, invertebrates such as crustaceans, and fish, there appears to be a rich variety of traits, many refugial in nature, to deal with drought (Brock et al. 2003, Lytle and Poff 2004, Williams 2006).

In temporary wetlands and streams, the biota are adapted to deal with drying and thus dealing with drought may not be a problem. Desiccation-resistant propagules, be they eggs or seeds, are a common form of drought resistance. Such dormant eggs and seeds can persist for long dry periods albeit with some loss of viability (De Stasio 1989, Hairston 1996, Leck and Brock 2000, Brock et al. 2003). Eggs may hatch immediately with the return of water (e.g. eggs of *Fundulus confluentus* Harrington 1959) or be dormant or diapause eggs with staggered hatching. As summarised by Brock et al. (2003), communities, with biota dealing with drought through egg and seed banks, “recover after the disturbance of drying by means of their specific patterns of dormancy, dormancy breakage, hatching, germination, establishment and reproduction”.

As wetlands and streams dry, obligate aquatic animals, notably fish become confined to pools that may develop severe water quality problems, such as low oxygen levels, high water temperatures, high levels of chemicals such as polyphenols, and an increased intensity of biotic interactions—predation and competition (Magoulick and Kobza 2003, Matthews and Marsh-Matthews 2003). Freshwater bivalves differ greatly in their capacity to survive emersion such as in droughts. Traits of emersion-tolerant species include the uptake of aerial oxygen, careful control of valve movement, and the use of calcium to buffer haemolymph acidosis (Byrne and McMahon 1994, Gagnon et al. 2004). Fish living in drought-prone environments, especially in the tropics, have developed a range of adaptations, including metabolic torpor (Emery 1978), tolerance of low oxygen levels (Matthews 1987), air-breathing from the surface (Smith 1931, Kramer 1987) and spines and armour to resist predation (Power 1984). Many fish appear to be adapted to seek out and migrate to refugial pools as a drought develops and longitudinal connectivity is threatened (Magoulick and Kobza 2003).

It is quite obvious that the identification, mechanisms and evolution of traits of freshwater biota to deal with drying and drought is incomplete at present. Our knowledge of the biota of temporary waters has recently been very effectively reviewed by Williams (2006), and many of his findings are applicable to drought. This possibility is limited as drought is not only an abnormal phenomenon, but it also has very strong impacts on perennial systems and their biota.



Drought in standing waters—ponds, wetlands and lakes

As precipitation goes below the expected levels and drought sets in, surface runoff disappears, inflow from streams declines and the water table may start to drop. Droughts as failures in rainfall are usually accompanied by high temperatures, and possibly high winds, so that evaporation and transpiration may increase sharply. Water bodies such as ponds and shallow wetlands may rapidly dry out completely, or as in the case of the Everglades become a mosaic of dry pools and deeper pools with water (e.g. Kobza et al. 2004, Chick et al. 2004).

In the wetlands of southern Florida there are marked wet and dry seasons with periodic droughts imposed on this seasonal pattern. With drought, fish kills in wetland pools may occur (e.g. Kushlan 1974, Kobza et al. 2004). These drought—long “drydowns”—appear to govern fish distribution at the large scale, with large bodied predators, such as bass and gar, only occurring in good numbers at deep wetland sites that persist through drought (Chick et al. 2004). Small bodied fish tended to occur in shallow sites that may dry out with drought. Some of these fish, such as eastern mosquitofish and flagfish, recover rapidly via dispersal from drying and rapid reproduction (Baber et al. 2002, Ruetz et al. 2005), whereas other species, such as bluefin killifish, least killifish and golden topminnow, take time to recover from drought; a lag, but they still occur largely at shallow sites. Thus drought, in creating a mosaic of sites of various depths and lengths of “hydroperiods”, as a regional force has a key role in determining fish abundance and distribution in these Florida wetlands (Baber et al. 2002, Trexler et al. 2005, Ruetz et al. 2005). This pattern may be sharpened by the influence of predation, as large predators such as gar and *Amia* can tolerate the low water quality of deep sites in drought and prey upon the small bodied fish (Kobza et al. 2004, Chick et al. 2004).

Floodplain wetlands, especially in the tropics, undergo seasonal wet-dry cycles also with the occasional drought imposed on this pattern (Welcomme 1979, 1986, Merron et al. 1993, Lae 1995, Swales et al. 1999). In the water bodies of such wetlands—pools, billabongs, oxbow lakes—water quality in terms of high temperature, very low oxygen levels and high nutrients generating algal blooms (e.g. Swales et al. 1999) may cause fish kills, especially in shallow pools, or physiologically tax the fish fauna. Many fish in pools that persist possess adaptations to deal with the stress of stagnation. Such adaptations include the ability to undertake physiological torpor, the ability to aestivate, and the ability to breathe air from the water surface (Kramer and McClure 1982, Kramer 1987, Lae 1995, Magoulick and Kobza 2003). Drought greatly reduced the diversity and biomass of the fish fauna of the Phongolo floodplain, in Zululand, South Africa, with the biomass of lakes with low water quality being dominated by the cichlid, *Oreochromis mossambicus*, a species with a very wide range of physiological tolerance and which does not require rainfall or flooding to breed (Merron et al. 1993).

Temporary standing waters contain biota that are adapted to survive through dry periods (Williams 2006), and may be exposed to regular seasonal drying events and supra-seasonal droughts. In the case of the latter, there appears to be very little information on the degree to which the biota of regularly-drying pools and wetlands survive the rigours of an extended drought. Hershey et al. (1999) studied the invertebrate assemblages of prairie wetlands in Minnesota, USA, that were subject to a severe drought (PHDI ~7). They found that different invertebrate groups responded to drought in different ways, Mollusca (gastropods and bivalves) increased, whereas insects were less abundant and less diverse and took several years to recover. In the zooplankton, both rotifer and cladoceran abundance declined, but recovered fairly rapidly, whereas copepods and ostracods appeared to be unaffected by the drought. Wissinger and Gallagher (1999) in an experimental study compared temporary (autumnal) and



permanent ponds and found that recovery from drought was much more strongly driven by the hatching of pre-drought fauna from drought-resistant stages in the autumnal ponds than in the permanent ponds, whereas both types of ponds had about equal levels of re-colonisation from immigration by winged insects. After a year, the autumnal pools had about 90% of the pre-drought fauna compared with about 77% for the permanent ponds. From these studies, it does appear that the fauna of shallow wetlands normally subject to drying do have the capacity to survive in and recover from the impacts of severe drought. However, the capacity to persist may be taxed by either droughts of long duration or if the drought-resistant biota is depleted by false starts, filling events that do not persist long enough to allow reproduction.

In water bodies deep enough to persist in drought, the water levels steadily drop exposing the littoral zone, its sediments and its macrophytes to drying. Such water-level recessions may cause the oxidation and mineralisation of organic phosphates (De Groot and Van Wijck 1993), resulting in the release of phosphate when the drought breaks. Nitrogen as nitrate may accumulate in the sediments, and both denitrification and ammonification (from organic N) may occur in the deeper anoxic sediments (de Groot and Van Wijck 1993, McGowan et al. 2005). In an experimental study of a winter drought in Canada, McGowan et al. (2005) found that with the drought breaking, there were increased ammonium-N concentrations in the lake's water, but no significant changes in other chemical attributes ($\text{PO}_4\text{-P}$, $\text{NO}_3\text{-N}$, total dissolved nitrogen, total dissolved carbon).

As the levels of the water bodies decline exposing the littoral zones, immobile biota, such as attached algae and macrophytes (Brock et al. 2003, Furey et al. 2006), and fauna, such as molluscs and oligochaetes, may be stranded and killed by the drought. It seems that the damage incurred by drought on the littoral fauna is dependent on the overall regime of water level changes. Furey et al. (2006) compared the littoral invertebrate fauna of a reservoir (with numerous level changes) with that of a nearby stable lake, and found that the fauna of the drawdown exposure zone of the reservoir was greater in density and biomass than that of the stable lake. They suggest that the reservoir shore fauna with r-selected survival strategies is well adapted to drawdowns, such as occur in droughts. In megadroughts water level decreases may be quite considerable as shown in palaeolimnological studies.

In the water column of lakes, turbidity may increase due to mobilisation of previously inundated sediments, conductivity and salinity may rise, surface temperatures may rise and stratification may increase in strength and duration (Nowlin et al. 2004). In acid lakes in Florida during drought, James (1991) observed that anoxic hypolimnia developed in lakes with high dissolved organic carbon (DOC) levels and bacterial levels. With the breaking of the drought DOC levels rose whereas bacterial levels dropped, possibly because of inhibitory effects of DOC, including polyphenols, at the high concentrations. As palaeolimnological studies have shown, changes in lakes, such as the rise in salinity, induce changes in diatom composition and the zooplankton, notably ostracods. In such studies the abiotic changes are considerable. In the recent study of McGowan et al. (2005), there were no marked differences in phytoplankton and zooplankton (copepods) between the control and experimental drought lake, but a major change in macrophyte assemblage structure occurred. The pre-drought assemblage was dominated by *Ceratophyllum demersum* and after the drought, not only was the macrophyte assemblage much more abundant, but it was dominated by *Potamogeton pectinatus* (McGowan et al. 2005). Thus, drought as a disturbance can create a new community state that may be stable. However, overall it is very evident from literature searches that there is a rather thin literature on the effects of drought on standing water bodies, especially lakes.



Lakes and indirect effects of drought

Droughts may create indirect effects on ecosystems. Landscape position of lakes may influence their response to drought. In northern Wisconsin at the Northern Temperate Lakes Long-Term Ecological Research Site, lakes differ dependent in their elevation in the landscape (Webster et al. 1996, Kratz et al. 1997). Lakes high in the landscape and high in their position in the hydrological flowpath were found to receive most of their water from precipitation rather than groundwater. Lakes, low in the landscape receive a considerable proportion of their inputs from groundwater. When drought occurs, an elevated lake loses its precipitation input, but maintains its groundwater outflow, while a low lake continues to receive its groundwater inputs. This pattern of flows in the landscape results in the elevated lakes losing ions, notably calcium and magnesium, whilst the low lakes increase their content of calcium and magnesium (Webster et al. 1996). As low calcium concentrations may limit the distribution of animals, such as crustaceans and molluscs, which have a high calcium requirement, their distribution in the elevated lakes may be limited (Capelli and Magnuson 1983, Kratz et al. 1997).

In eastern North America many lakes and streams were, and many still are, damaged by acid rain created by fossil fuel combustion and smelters. Since SO_2 emissions have declined from the 1970s onward, many lakes have shown a recovery, but for some it is slower than expected (Dillon et al. 1997). A possible cause for the slow recovery appears to be related to drought linked to El Niño events in conjunction with the influence of the North Atlantic Oscillation (Dillon et al. 2003). Sulphur from acid rain accumulates in the anoxic soils of the lake catchments and when drought occurs with the drying of the soil, this sulphur is re-oxidized. When autumn comes with rain, this sulphur is mobilised and flows into the lakes causing a significant drop in pH (Dillon et al. 1997, Dillon and Evans 2001). This event in turn may set back the recovery of both phytoplankton and rotifer assemblages with the damaging effect lasting for seven years in the case of the phytoplankton (Arnott et al. 2001). In addition, the re-acidification stimulated the emergence of zooplankton from the egg bank residing in the sediments (Arnott and Yan 2002), an emergence that depletes the egg bank and in the long run may deplete the zooplankton assemblage of the lake.



Drought and flowing waters

Flowing waters may be subject to seasonal and supra-seasonal droughts (Lake 2003), with supra-seasonal drought being the major concern of this report, given that seasonal drought is usually part of a normal seasonal cycle. As outlined above, hydrological drought in reducing flow volumes and water levels can be defined and quantified using a range of indicators, such as cumulative water deficit and duration and volumes of low flows below a threshold set from long-term data sets.

The nature of drought in flowing waters

Natural droughts arise from protracted periods of low or no rainfall, little or no surface runoff and a receding water table. The rate of water loss from the channel and thus the severity of drought onset vary greatly dependent on many factors including rainfall patterns, groundwater levels, and nature of the streambed (bedrock versus deep sand) (Dahm et al. 2003). Water levels in the channel drop and surface water recedes from the normal littoral margins and from the riparian zone (Stanley et al. 1997), weakening lateral connectivity. This sets in train the process of loss of habitat quantity and quality. With receding water depths, there comes a time when longitudinal fragmentation starts to occur, and this will tend to take place in shallow areas of the stream such as riffles and runs (Stanley et al. 1997)—a step-change as envisaged by Boulton (2003). Pools form and if deep they may persist, whereas shallow pools in riffles, runs or sand bars have a limited persistence. In systems with deep sediments, such as in sand-bed streams, hyporheic flow may persist (Stanley et al. 1997, P.S. Lake personal observation). Persistence of pools may also occur through the input of groundwater from springs and deep aquifers (Dahm et al. 2003).

The above events are likely to occur with drought in small to medium-sized streams. Drought, of course, can affect large rivers and in this case longitudinal connectivity is usually maintained and it is lateral connectivity, which is very substantially dependent on flooding, which is compromised (e.g. Welcomme 1986, Merron et al. 1993, Lae 1995). On floodplains without seasonal flooding, wetlands and lagoons may dry or their water quality may decline with high temperatures and low oxygen levels to such an extent as to cause fish kills. On the floodplain without flooding, the water table may decline to such levels that riparian trees, such as river red gums of the Murray River floodplain, may become stressed and die (Murray-Darling Basin Commission 2004). Large rivers in drought may decline in depth. Reibsame et al. (1991) report that in the summer of 1988 in the severe 1987-89 drought, due to rapid loss of depth in the Mississippi, Missouri and Ohio Rivers, barge traffic was reduced by 50%. There may be declines in water quality, with high temperatures and high nutrient levels, but the channel-dwelling biota may be relatively unaffected. For example, in the Latrobe River, Victoria, in the sharp 1982-83 drought, Chessman and Robinson (1987) detected declines in water quality, but could not detect changes in the macroinvertebrate fauna of the river channel. Droughts as low flow phenomena in large lowland rivers may exert effects on fauna, notably fish, when low water levels create “habitat bottlenecks” (Wolter and Menzel 2005). Population densities of juvenile fish, such as pike and pikeperch, were found to decline with drought; an effect which persisted for several years after adequate river flow returned (Wolter and Menzel 2005).

Many studies of drought, being unplanned, are at the small site scale, and it should be realised that a full understanding of the nature and impacts of drought may be gained from taking a landscape or scape approach at the reach, or even river spatial extent (e.g. Fausch et al. 2002, Gomi et al. 2002, Dodds et al. 2004, Stanley et al. 2004). Given that droughts are prolonged events, then they should be quite amenable to study at the large scale. Such an approach has, however, rarely been undertaken.



At the large spatial extent, it appears that there are at least three longitudinal patterns of drying that may occur in streams as opposed to large rivers (Lake 2003), with some exceptions such as the Murray River in 1895-1903 (Keating 1992) and the 1911-16 drought (Sinclair 2001). Many streams originate in headwaters as springs, which may persist in drought whilst drying and fragmentation may occur downstream (e.g. Erman and Erman 1995). Such upstream sections may act as refugia. More commonly, the headwaters and upstream sections dry with drought and the downstream reaches persist as pools or low flow streams (e.g. Larimore et al. 1959, Covich et al. 2003, Dodds et al. 2004, Westwood et al. 2006). In other situations, such as in the Granite Creeks, Victoria, Australia, both headwaters and downstream reaches may persist in drought and drying occurs in the heavily sedimented mid reaches (Bond and Lake 2005). The spatial pattern of channel drying, in substantially determining the geometry of the refugia, will have a strong influence on subsequent recovery (Magoulick and Kobza 2003, Stanley et al. 2004, Fritz and Dodds 2004), though this possibility remains unexplored.

Ecological effects of drought in flowing waters

Studies on seasonal droughts or seasonal dry periods are far more common than those of supra-season droughts of longer duration and less predictability. The early effects of drying seem similar for both seasonal and supra-seasonal droughts, but the extended effects of supra-seasonal droughts are more severe, less predictable and more lasting in terms of lag effects.

As low flow sets in, fine particulate material and sediments settle out on the stream bottom (Wright 1992, Hakala and Hartman 2004). The cessation of flow, or very low flow, disrupts the longitudinal transport of nutrients and organic matter down the stream, which in turn may lower nutrient and dissolved carbon levels in pools (Dahm et al. 2003). The creation of lentic conditions may be particularly evident in unshaded pools where algae may bloom (Freeman et al. 1994, Dahm et al. 2003) and such blooms may create oxygen stress in the pools (Matthews 1998). Cessation of flow serves to deplete or eliminate fauna, such as filterers including simuliids, hydropsychid caddis and bivalves, and grazers (e.g. Harrison 1966, Boulton and Lake 1992a, Golladay et al. 2004) that rely on water currents for the provision of resources, especially food. In pools with time, high temperatures can be produced, conductivity steadily rises (e.g. Caruso 2002) and in some instances in deep pools, stratification may be set up. The amount of habitat space and the quality of habitat, as lotic habitat, steadily declines (e.g. Elliott 2006). The pattern of habitat drying at the landscape level remains undescribed and awaits investigation (Stanley et al. 2004). Lateral connectivity is weakened and prey subsidies (Baxter et al. 2005, Ballinger and Lake 2006) may decline due to aquatic habitat contraction from the stream margins and low arthropod densities in the riparian zone.

As flow drops to low levels, cyanobacteria and micro-algae on solid surfaces may be exposed to the air and become desiccated, but not necessarily dead (Romani and Sabater 1997, Stanley et al. 1997, Robson and Matthews 2004). The development of resistance of algae appears to depend upon the rate of drying, with rapid drying not allowing resistant mechanisms to develop (Stanley et al. 2004). Filamentous algae, such as *Cladophora*, appear to rapidly expire with drying (Stanley et al. 2004). With time some species of macrophytes may die with lasting effects on subsequent assemblage structure when the drought breaks (Ladle and Bass 1981, Holmes 1999, Westwood et al. 2006). Major changes in the aquatic plant assemblage structure and availability both during and after drought undoubtedly alter the ecology of both invertebrate and fish assemblages (Boulton 2003).

As streams dry up, especially when this occurs rapidly, animals from insects to fish can become stranded or become entrapped in shallow pools that may subsequently dry up producing fish kills (Tramer 1977, Mundahl 1990, Lake 2003, Matthews and Marsh-Matthews 2003). Mussels,

being sedentary, that dwell in riffles can suffer high mortality, whereas those dwelling in deep pools survive droughts with little mortality (Golladay et al. 2004). In shallow sections of drought-affected rivers, mussels may also survive in the holes generated downstream of coarse wood (Gagnon et al. 2004). Hyporheic zones may contract away from the drying channel surface, a contraction that can give rise to increased faunal abundance and diversity in the deeper parts of the zone (Boulton and Stanley 1995, Clinton et al. 1996). Mobile invertebrates (e.g. Stanley et al. 1994, Covich et al. 2003) and fish may move into pools (e.g. Magoulick 2000, Magalhães et al. 2002), or as the drought develops emigrate either upstream or downstream into refugia (Elliott 2000, Magoulick and Kobza 2003, Matthews and Marsh-Matthews 2003). Presumably, the directions of migration are related to the landscape configuration of drying. In pools, both invertebrates (e.g. Stanley et al. 1994, Miller and Golladay 1996) and fish (Magoulick and Kobza 2003) may be concentrated and high densities may be expected to increase the intensity of intra- and interspecific interactions, such as predation and competition.

In extended droughts the deficit of rainfall can result in unseasonal low flows or cessation of flow in small streams and tributaries of major rivers. In temperate climates, this may mean that recruitment of fish, such as salmonids that use small gravel streams for breeding, is limited. In Wales Cowx et al. (1984) found that drought reduced salmon (*Salmo salar*) spawning in a small stream, Elliott (2006) found that drought reduced sea trout (*Salmo trutta*) recruitment in a small English stream, and in north-eastern Tasmania Davies et al. (1988) found that drought reduced recruitment of both brown (*Salmo trutta*) and rainbow (*Oncorhynchus mykiss*) trout in small headwater streams. In small, forested streams in West Virginia USA, Hakala and Hartman (2004) found that drought reduced the body condition of brook trout (*Salvelinus fontinalis*) and increased siltation of spawning gravels, both factors that reduced trout populations during and after the drought. Similarly, both Davies et al. (1988) and Elliott (2006) found the drop in recruitment had a lag effect on the trout populations after the drought.

Refugia between generations include the production of desiccation-resistant eggs (e.g. Boulton 1989, Paltridge et al. 1997) and spores (e.g. Dunphy et al. 2001). With drought, fish may migrate to stream sections with water and with the breaking of the drought, juveniles from the surviving adults, can recolonise newly inundated stream sections (Matthews 1998, Labbe and Fausch 2000, Magoulick and Koba 2003, Magalhães et al. 2002, Bond and Lake 2005). Refugia within generations can involve changes in habitat or within-habitat tolerance. Changes in habitat is exemplified by the movement of surface-dwelling invertebrates into the hyporheic zone as drying occurs (e.g. Clinton et al. 1996) or into the water of crayfish burrows—the pholeteros (Lake 1977, Boulton 1989). This migration is dependent on the condition of the hyporheic zone; in the study by Smock et al. (1994) with drought the hyporheic zone became anoxic and was not a refuge. Refugium use within habitat is shown by insects, especially beetles, and by crayfish that may remain under stones and logs without free water, but with high humidities (Boulton 1989, Boulton et al. 1992).

Pools with accumulated detritus, warm temperatures, high levels of dissolved organic matter and low oxygen levels create inhospitable conditions that may kill fish and invertebrates (Lake 2003). In regions such as south-eastern Australia, leaf fall from eucalypts into the streams is maximal in summer (Boulton 1991, Lake 1995). During drought, this input of leaves (course particulate organic matter, or CPOM) produces large amounts of dissolved organic carbon, predominantly polyphenols (O'Connell et al. 2000) that in turn, through bacterial metabolism, can produce very low levels of dissolved oxygen. These conditions may be expected to be taxing for fish and yet some fish, such as the western carp gudgeon (*Hyseleotris klunzingeri*) and pygmy perch (*Nannoperca australis*), show a remarkable tolerance of high levels of DOC levels and very low oxygen levels (McMaster and Bond 2006). This lends support to the idea that drought acting as a strong selection force may give rise to a distinct assemblage of highly

tolerant animals, especially fish (Magoulick and Kobza 2003, Matthews and Marsh-Matthews 2003).

Biotic interactions and drought

With pool formation the density and diversity of predators may increase (Boulton 2003, Lake 2003). These predators may be fully aquatic species (e.g. odonatan nymphs, fish), mobile semi-aquatic species (e.g. adult dytiscid beetles and hemipterans) and fully terrestrial animals (e.g. birds, reptiles, mammals). Lentic predators, notably beetles and hemipterans, can invade the pools in great numbers and may subsequently disappear to nearby lentic pools when flow returns. Predation of and by fish may be a major factor deciding at the pool level population survival when the drought breaks (Magoulick and Kobza 2003). In Spain, fish in the pools of a dry stream may have to contend with the rather unselective predation of otters (Magalhaes et al. 2002). The fauna trapped in drying pools may be prey for a galaxy of fauna including ants, carabid beetles, goannas and foxes. Droughts, as indicated above, may strengthen interspecific interactions, notably predation.

Competition may also be expected to increase as habitat space and resources decrease, but this remains relatively unstudied. Covich et al. (2003) in a Puerto Rican stream affected by drought noted that limited habitat space and depleted resources resulted in strong competition between shrimp individuals resulting in substantially reduced reproductive outputs. In a wonderful long-term study (34 years) of the population structure and density of sea trout (*Salmo trutta*) in a small Lake District stream (Black Brows Beck), Elliott (2006) found that during drought the habitat space available for the fish was reduced and this resulted in low spawning success, as indicated by egg numbers. This low spawning continued its effect into the subsequent 1+ and 2+ trout, and trout stressed by the drought retreated to deep parts of the stream. However, another fish species, the bullhead (*Cottus gobio*) had increased survival and densities in response to the drought. Elliott (2006) suggested that with the habitat loss of the drought, the bullhead were able to occupy shallow habitat from which they had previously been excluded by competition from trout.

Drought may also alter the success of invasion. In a small stream in south-eastern Australia under normal flow conditions the stream channel was totally dominated by the invasive brown trout. The native galaxiid, the mountain trout (*Galaxias olidus*), prey for brown trout, was confined to small headwater pools. During a severe drought, the poor water quality in the stream with the polyphenol phenomenon (referred to above), killed brown trout. Galaxiids tolerated these poor water conditions and with the drought breaking, juvenile galaxiids recolonised the trout-free drought-affected sections of the stream (Closs and Lake 1995).

Fish, when confined to pools by drought and in elevated densities, can become infected by parasites or pathogens. Medeiros and Maltchik (1999) in a small Brazilian stream observed that drying of the stream and pool formation gave rise to increased infestation of fish by the copepod parasite *Lernaea cyprinacea*; from low levels (0-11%) when the stream flowed, to levels of ~22% of fish when the stream ceased flowing. One species *Astyanax bimaculatus* was heavily parasitised, up to 64% (Medeiros and Maltchik 1999). This increase in parasite or pathogen transmission and infestation not only occurs in fish in drought when they are concentrated in specific patches, but also occurs in hosts of arboviruses, such as mosquitoes and water birds (e.g. Shaman et al. 2004, 2005).

Drought and ecosystem processes in streams

Droughts alter ecosystem processes, however, as both Lake (2003) and Dahm et al. (2003) indicate, the effects of droughts on ecosystem processes have been neglected. Large amounts



of particulate organic matter (POM) can accumulate on the bed of drought-stricken streams, especially in Australia with a summer leaf-fall (Boulton 1991). Decomposition of this dry POM is slow, much slower than aquatic decomposition (Boulton 1991, Maamri et al. 1997, Pinna et al. 2004). Detritus decomposition is slower in small low-order streams that dry than in large streams that have water through seasonal summer drought (Pinna and Basset 2004). Accumulated POM in pools may produce high levels of DOC–polyphenols. The DOC in turn may favour bacterial metabolism, giving rise to hypoxia (McMaster and Bond 2006).

In Sycamore Creek, an Arizonan desert stream, nitrogen is a limiting element. Nitrogen availability is severely disrupted by drying with some pools receiving high levels of nitrogen from fixation (Grimm and Petrone 1997) and hyporheic upwelling (Dent et al. 2001). Given the localised supply of nitrogen to pools, a mosaic of pools at the landscape scale can be generated with quite different communities and production (Stanley et al. 1997, 2004).

In drought, deep groundwater inputs may be the major source of water to streams (Dahm et al. 2003). This input low in dissolved organic carbon, nitrogen and phosphorus may serve to favour autotrophic production as opposed to heterotrophic production, and thus change the major source of energy for the food web (Dahm et al. 2003). However, in some systems, such as the Australian streams (McMaster and Boulton 2006), with high DOC levels in the water column and an abundance of benthic CPOM, the pools may be heterotrophic rather than autotrophic, though this may change with time. Groundwater inputs are patchy in distribution and thus, once more, pools may vary greatly and a mosaic of patchiness is generated.

Recovery from drought

In streams subjected to regular seasonal drought, both resistance and resilience appear to be relatively high, whereas in long supra-seasonal droughts, resistance may steadily decline and resilience is highly variable, with, in some instances, long lags in recovery particularly after drought in perennial streams.

With rewetting of the stream channel, pools may form prior to the arrival of flow (Stanley et al. 2004). Such pools in the small streams of the wet–dry tropics may have relatively high temperatures, conductivities and nutrient levels and harbour a distinctly non-insect fauna, consisting of crustaceans, oligochaetes and nematodes (Douglas et al. 2003). At this time there is the damaging hazard of “false starts” (Boulton 2003) when the pools briefly fill and then dry. Droughts may also break with floods (Whetton 1997) in which case the change is severe with the floods removing the CPOM in the channel and scouring and depositing sediments on the streambed. The form of water return is important for consequent recovery.

With channel rewetting, algal and cyanobacterial colonisation of surfaces may occur rapidly either from resuscitation of dormant cells or by colonisation by upstream propagules (Romani and Sabater 1997, Ledger and Hildrew 2001, Robson and Matthews 2004, Stanley et al. 2004), with the result that primary production rapidly recovers from drought and may provide food for early invertebrate colonisers.

Drought reduces macrophyte diversity and density in streams. With the return of flow after a “severe” drought (1973–1974), Ladle and Bass (1981) observed a rapid recovery of macrophyte cover, but a major change in the aquatic plant community structure. In a later “severe” drought in the UK (1989–1992), Holmes (1999) found in one stream (Chitterne Brook) a complete lack of aquatic plants, and in another stream (the Ver) the dry channel was invaded by non-aquatic plants. However, in both cases with the return of flow, the recovery period was “no more than two years”.



The colonisation of dry but subsequently inundated stream sections by invertebrates is variable and appears to be dependent on a variety of factors such as the severity of the drought (e.g. Boulton and Lake 1992b, Paltridge et al. 1997, Wood and Armitage 2004), whether the stream is normally perennial or intermittent (Stanley et al. 1994, Miller and Golladay 1996, Feminella 1996), the presence of and distance from populations in refugia (Larimore et al. 1959, Wood and Petts 1999, Ledger and Hildrew 2001, Boulton 2003, Fritz and Dodds 2004), whether desiccation-tolerant refugia were used (Boulton 1989, Boulton and Lake 1992b, Stanley et al. 1994, Paltridge et al. 1997) and whether there are lag effects from past droughts (Boulton 2003). Means of recolonisation vary from system to system with downstream movement from upstream refugia being important (e.g. Fritz and Dodds 2004, Paltridge et al. 1997, Boulton 2003) along with emergence, especially of Crustacea, from desiccation resistant eggs (e.g. Douglas et al. 2003). In some systems insect colonisation may be mainly through flying adults laying eggs (e.g. Harrison 1966). In pools persisting through drought, a lentic fauna may develop and, thus a major change in recovery with flow returning is the elimination or displacement of the lentic fauna and its replacement by a lotic biota.

The recovery of invertebrates in intermittent streams from seasonal drought appears to follow a predictable pattern of assemblage development provided that there are no lag effects from past supra-seasonal droughts (Boulton and Lake 1992a,b, Boulton 2003). Early colonists are groups with short life cycles, such as chironomids and simuliids (Harrison 1966, Fritz and Dodds 2004). Species richness steadily increases as longer-lived collectors and grazers (Ephemeroptera, Trichoptera) build up with the predators arriving as species richness levels off, prior to declining with the recurrence of seasonal drying (Boulton and Lake 1992, Boulton 2003). Thus, there is a strong indication of adaptations, such as in life histories, to drought, but this area remains largely unstudied (Lytle and Poff 2004).

In perennial British streams (e.g. Cowx et al. 1984, Morrison 1990, Wood and Petts 1999, Wright et al. 2004), streams of mid-western USA (Larimore et al. 1959, Fritz and Dodds 2004) and New Zealand (Caruso 2002) recovery from severe supra-seasonal drought is quite rapid with only a few uncommon taxa not returning. However, recovery from supra-seasonal drought, even in streams subjected to seasonal drought, can be somewhat unpredictable due to the deletion of species by the drought and to the arrival of new or uncommon species. For example, Hynes (1958) reported the loss of species of mayflies and stoneflies in the recovery from drought in a small Welsh stream, and both Ladle and Bass (1981) and Wood and Armitage (2004) observed a great decline of the hitherto very abundant amphipod *Gammarus pulex* in drought and a very slow recovery. Drought by drastically reducing the abundances of species and creating potential new habitat space may create the conditions to favour new or uncommon species. For example, in a small acid stream, Ledger and Hildrew (2001) found that recovery after drought in terms of abundance was rapid, but the community structure was quite different from the pre-drought configuration and for a time was dominated by a tanypod chironomids, that were uncommon prior to the drought. It was only with the return of high flows that the community came to resemble that existing prior to the drought. Thus, it is evident that supra-seasonal droughts may leave lingering signals in community structure. This lag effect is quite evident in fish population structure (e.g. Wolter and Menzel 2005, Elliott 2006).

Drought as a result of either extremely low flow or a cessation of flow creates a mosaic of patches, mainly pools, in which fish populations persist (e.g. Labbe and Fausch 2000, Magoulick and Kobza 2003, Elliott 2000, 2006). Pools may differ greatly in their species composition and population structure (e.g. Magalhaes et al. 2002). With the breaking of the drought there is a remixing and after seasonal droughts the recovery of fish assemblages is relatively rapid (Matthews 1998, Matthews and Marsh-Matthews 2003). Recovery from severe supra-seasonal droughts is variable. In some instances such as described by Larimore et al. (1959), recovery

was rapid—a matter of months. In other instances, recovery was slow and incomplete (e.g. Deacon 1961, Matthews and Marsh-Matthews 2003 (Brier Creek 2000), with the drought resulting in long lag effects. In a recent severe and drought episode (2001-2004) in south-east Australia affecting a small lowland stream, native fish recovered but an exotic species (carp) was eliminated (N.Bond, pers.comm.). Needless to say, due to lack of studies we have a rather sparse understanding of how drought affects the assemblage structure of stream fish. To understand the dynamics of fish before and through drought, it is necessary to operate at the spatial scales at which the fish react to the drought and to commit to long-term studies. This is why the long-term studies by investigators, such as Elliott (2000, 2006) in England and Chick et al. (2004) and Trexler et al. (2005) in Florida, are so valuable and informative. In an evolutionary context, fish have clearly adapted to seasonal drought and possibly to supra-seasonal drought, though the efficacy of the adaptations will depend on the duration and severity of the drought. Drought, especially supra-seasonal drought, by acting as a harsh filter (Poff 1997) may be, especially in regions with marked seasonality or with semi-arid conditions, substantially determining the species composition of the freshwater fish fauna.

Droughts are feared by human beings because of the damage they inflict upon humans and upon economic activities. However, it should be borne in mind that droughts are a natural phenomenon and that many species of biota, both terrestrial and aquatic, have evolved many different adaptations to contend with drought. Unlike floods, droughts do not change the geomorphology of rivers and their floodplains, but like floods they may serve as environmental filters to eliminate or reduce some biota and create opportunities for others. In this way, as re-setting or scene changing events, droughts may be vital for the long-term persistence of natural lotic ecosystems (Everard 1996, Humphries and Baldwin 2003).



Drought and estuaries

Most rivers eventually go to sea and in many situations where this occurs there are estuaries. Droughts can have a strong impact on estuaries and their biota. With a reduction in freshwater inputs to estuaries, the normal salinity gradient can be truncated, elevated salinity can extend up the estuaries and poor water quality may develop due to a drop in freshwater inputs, tidal flushing and exchange with the sea (Attrill et al. 1996, Livingston et al. 1997, Attrill and Power 2000a, Grange et al. 2000, Peirson et al. 2001). Small estuaries may be disconnected from the sea (Gasith and Resh 1999, Mackay and Cyrus 2001). With the reduction of freshwater inputs and the advance upstream of high salinity, there can be marked declines in abundance and seaward distribution of upper-estuarine freshwater biota (Attrill et al. 1996), whereas the abundance of marine animals, such as crabs and shrimps, may increase in abundance within the estuary (Attrill and Power 2000b). With the drought-induced decrease in the freshwater inputs of nutrients phytoplankton and zooplankton may decline (Grange et al. 2000). In a south Florida estuary, Livingston et al. (1997) found that with drought, turbidity of the estuary greatly declined allowing greater light penetration into the water increasing primary productivity. This pulse of high productivity served to increase the biomass of herbivores, omnivores, primary and secondary carnivores, but not tertiary carnivores. The tertiary carnivores, many of which were basically freshwater fish were probably excluded from the estuary because of the high and stable salinity (Livingston et al. 1997). In summary, it is clear that droughts by greatly lowering the freshwater inputs of estuaries can induce major changes in the biota and in the trophic structure of estuaries.

As for some freshwater biota, droughts may favour some species. For example, in an estuary of south-western Victoria, winter floods which result in low salinity in the estuary greatly deplete populations of the bivalve *Soletellina alba*. However, drought by eliminating the winter floods greatly reduces the seasonal mortality of these bivalves (Matthews 2006). In droughts with elevated water temperatures and limited circulation in estuaries, algal blooms may occur. For example, in estuaries of eastern USA extended drought conditions are linked to brown tide blooms, such as by the chrysophyte *Aureococcus anophagefferens* (Gastrich et al. 2004).

Human alterations of aquatic ecosystems and drought

Human activities throughout the world have degraded the condition of flowing waters by imposing a wide range of disturbances, predominantly unnatural, on streams and rivers. For example, sediment movement, a natural phenomenon in streams, may be greatly increased by land clearance and subsequent unwise farming and create severe and extensive sedimentation in the stream channel with major effects on the biota and ecological processes (Wood and Armitage 1996). Unnatural disturbances, in many cases range from various forms of pollution, to major and abrupt changes in temperature, to inputs of synthetic chemicals such as pesticides and endocrine disrupters.

Human activities on catchments can exacerbate droughts. By creating a large number of storage dams on catchments, runoff into streams can be greatly reduced. Such reductions may render downslope streams more drought-prone by reducing their total flow volumes (Brock et al 1999, Savadamuthu 2002). Land clearance and subsequent drying, reductions in soil carbon, increased surface albedo and compaction of soils may give rise to catchments that have increased surface runoff, but less groundwater recharge, reducing the capacity of groundwater to maintain streams during drought. The move of agriculture in many parts of the world into marginal lands with cultivation of crops, such as wheat, that involves land clearing and ploughing may actually increase the severity of drought (Glantz 1994, 2000). Land clearance by reducing tree cover may also serve to reduce rainfall. In south-western Western



Australia, it appears that loss of tree cover by very extensive land clearing has served to reduce surface roughness that in turn leads to less precipitation due to increased horizontal wind velocities and lowered vertical velocities (Pitman et al. 2004).

Human activities have greatly changed the nature and strength of hydrological disturbances. River regulation by dams has been a dominant force changing floods. Dams with reservoirs may greatly reduce the frequency and strength of small to medium high flow events, such that only large severe floods (e.g. one in a 100-year floods) may move down stream channels and inundate floodplains. In many cases, dams serve to store water that is then diverted away from the river, which in turn leads to a great reduction in flow below the dam. Such reductions can be drastic, for example Jindabyne Dam on the Snowy River in south-east Australia only releases one per cent of annual mean flow (now increased to three per cent, from 2006). Such low flows in wide channels create conditions akin to perpetual drought, often accompanied by low water quality. River regulation invariably reduces the lateral connectivity between rivers and their floodplains, so that the lack of floods becomes a severe disturbance in itself—a long-term press disturbance, a form of localised and unnatural drought. River channelisation along with levee construction also serves to sever lateral connectivity, creating drought conditions for floodplain wetlands and lagoons. River regulation combined with high water extraction, such as occurs along the Murray River or Snowy River in Australia, not only prevents floods from flooding the floodplains, but also prevents floods from reaching the estuary, giving rise to constant high salinities and disruption of fish migrations and breeding. Reduced inputs of freshwater into estuaries can cause changes akin to those of drought and greatly alter the estuarine biota and damage fisheries, as exemplified by the present condition of the Coorong estuary below the Murray River barrages in South Australia.

Seasonal low flow events and droughts occur naturally in many rivers. In many regulated rivers in dry periods, water is released from upstream dams to supply water to downstream irrigators. Such flows result in high flows, often of cold hypolimnetic water, in the river at the time when normally the flow would be low and the water warm. This removal of normally expected low flow periods from regulated rivers gives rise to what McMahon and Finlayson (2003) have termed “anti-droughts”.

When rivers have low flows and go into drought, reducing water availability, the human demands for water extraction from streams invariably rise. The loss of water from the stream, by both legal and illegal means, may greatly exacerbate the effects of drought by accelerating its onset and increasing its severity and duration by the extraction of water from streams and pools that left unmolested may have persisted though the drought. Groundwater extraction, by lowering water tables, may be expected to exacerbate drought in streams, though clear evidence for this contention appears to be mixed (Wright and Berrie 1987, Agnew et al. 2000). Loss of water by extraction combined with high nutrient levels from sewage and non-point agricultural sources can lead to the development of low water quality and algal and cyanobacterial blooms

For droughts the damaging effects of human activities may be heightened by the reduction of available refugia. Such processes as channelisation may result in the loss of habitat heterogeneity, such as pools, that may serve as refugia. Barriers, be they road fords or large dams, can prevent migration upstream or downstream to refugia by mobile biota as drought sets in. Furthermore, recovery from floods and droughts may be greatly impeded by barriers restricting migration from refugia back to newly inundated habitats. Sadly, many changes implemented on rivers have simply not considered the provision of and access to refugia by biota dealing with flow-generated disturbances (Bond and Lake 2005).



A very large-scale disturbance slowly becoming evident is the greenhouse effect, generated by the release into the atmosphere of greenhouse gases, principally carbon dioxide and methane, that will steadily give rise to elevated temperatures and consequent climate change. Elevated temperatures and changes in evaporation and precipitation will alter water availability at the regional scale and is expected to increase the frequency and severity of extreme events such as floods and droughts (Poff et al. 2002, Pittock 2003). The elevated temperatures of recent droughts appear to indicate that global warming is starting to influence the severity of droughts in Australia (Karoly et al. 2003, Nicholls 2004, Watkins 2005).

Finally, it does appear that Australians are becoming increasingly aware that drought is a natural part of living in Australia, and that we must start to modify our domestic, agricultural and industrial activities to more effectively deal with drought. Perhaps we have broken our ties with the “Hydro-illogical” cycle (Wilhite 1992) and are now prepared to adjust our activities pro-actively before drought sets in rather than view drought as an unusual phenomenon that generates reactive measures, many of which are counteractive to dealing with drought in the long term. Rather than “drought proofing” related to resisting drought, we need to be considering drought managing measures that engender resilience in dealing with drought.



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