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Drought and aquatic ecosystems: an introduction

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SUMMARY

1. This paper introduces, and summarises the key messages of, a series of papers that emanated from a symposium on the Role of Drought in the Ecology of Aquatic Systems, held in Australia in 2001.
2. Defining drought hydrologically is problematic because the return times, intensity, duration and long-term trends in low-flow periods are specific to regions and times. Droughts may instead be referred to as 'significant low-flow periods', many of which have been replaced by 'anti-drought' conditions in rivers as they are used increasingly as irrigation conduits.
3. Droughts can be divided into those that cause predictable, seasonal press disturbances and less predictable, protracted 'ramp' disturbances. However, while droughts may be 'ramp' disturbances, their effects on aquatic biota are most likely to be 'stepped' when geomorphological or hydrological thresholds are crossed, causing abrupt changes in biological community structure and ecosystem processes.
4. Physical, morphological, physiological or behavioural refugia confer resistance or resilience to riverine populations and communities that experience drought conditions. The physical and chemical parameters associated with refugia habitats and their formation, influence population parameters within, and interactions among, species and can have protracted reproductive consequences, even well after the cessation of the drought.
5. Fish, invertebrate and plant populations and assemblages seem to recover rapidly from drought. Most studies of the effects of drought, however, have arisen fortuitously and have involved relatively short temporal, and small spatial, scales. Innovative approaches, such as microsatellite DNA analyses, can reveal that the effects of drought may be profound and long-lasting, resulting in population bottlenecks and altering the course of the evolution of species.
6. During periods of drought, decreases in inputs of dissolved organic carbon, nitrogen and phosphorus may lead to carbon limitation to microbial metabolism, resulting in autotrophic production being favoured over heterotrophic production.
7. Long-term climate trends, as indicated by palaeoecological evidence, suggest that, at least for Australia, droughts are likely to occur more frequently in the future. Anthropogenic effects on climate are likely to exacerbate this.
8. It is important that drought is seen for what it is: a natural extreme of the flow continuum, with flooding at the other extreme. Thus, despite the potential for dramatic impacts on aquatic biota and the negative social connotations associated with such events, drought must be incorporated into river management plans.

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Introduction

Drought has often been cited as the most serious of natural disasters in terms of loss of life and its impact on agricultural production and economics (Wilhite, 2000). For this reason, drought has received much attention from government agencies around the world. However, drought is as much a natural feature of aquatic ecosystems in most regions of the world as is flooding (Davies & Walker, 1986; Gordon, McMahon & Finlayson, 1992; McMahon & Finlayson, 2003). Biota that inhabit hydrologically dynamic aquatic systems must possess morphological, physiological and/or behavioural adaptations to survive in such highly variable environments.

Whilst droughts and floods represent the extremes of the hydrological continuum and are clearly disturbances (Lake, 2000), they differ markedly in the physical and chemical stresses that they impose on resident biota and in relation to the return time, duration and spatial extent of their impact. Floods arise suddenly, and, while their severity is largely unpredictable, their return times and durations are often less so. The beginning of a drought, in contrast, is hard to define; often a drought can be identified as such only once it has been occurring for some time. However, sophisticated climatic models are now allowing much better warnings of when the next drought might be expected. The lack of predictive capabilities in the past is perhaps one reason that so few studies have focused on the ecological effects of drought (Giller, 1996; Poff *et al.*, 1997; Lake, 2000).

The importance and paucity of information on ecological effects of drought for aquatic ecosystems prompted us to organise a symposium on the Role of Drought in the Ecology of Aquatic Systems in Albury, Australia, in February 2001. It brought together nearly 100 participants from a dozen countries and included 40 papers that addressed issues related to low flow, drying, and their effects on ecosystem processes and patterns in biota of rivers and wetlands. This introductory paper presents some of the concepts associated with drought and low flows and introduces the papers that were selected to be incorporated into this special issue.

Aquatic ecosystems and drought

Of the studies that have dealt with the effects of drought in aquatic ecosystems, there is general avoidance of, or little consistency with, definitions of drought (e.g. Larimore, Childers & Heckrotte, 1959; Deacon, 1961; Extence, 1981; Ladle & Bass, 1981; Griswold, Edwards & Woods, 1982; Cowx, Young & Hellawell, 1984; Gordon *et al.*, 1992; Smock *et al.*, 1994; Wilhite, 2000; Matthews & Marsh-Matthews, 2003). The inability of workers to agree on how drought should be defined is largely because drought is so specific to regions and climatic zones. Hydrological drought (as distinct from meteorological, agricultural or sociological drought) is '…associated with the effects of periods of precipitation shortfall on surface or subsurface supply… rather than with precipitation shortfalls…' (Wilhite, 2000, p. 11). However, the frequency and duration of the 'precipitation shortfall' – as translated into surface or subsurface supply – are the key parameters that define a hydrological event, and these will vary from one dry period and from one region to the next (Wilhite, 2000). Analysis of low-flow frequency curves generally show a break point, as flow declines, and this point has been used to indicate the start of a drought period (Gordon *et al.*, 1992). For European systems, this break point has been given by the Institute of Hydrology (1980) as approximately 65% probability of exceedance, whilst in the south-eastern region of Australia, a value of approximately 80% is considered more appropriate (Gordon *et al.*, 1992).

It is unlikely that a robust definition of hydrological drought will emerge that will satisfy everyone. Yet 'drought' remains a compelling term, even for ecologists, because of its implied cultural meanings and the mental images it creates. For this reason, we will continue to use drought in this introduction and associated papers as a general term for an unpredictable low-flow period, which is unusual in its duration, extent, severity or intensity. We suggest, however, that those who work on drought in the future, describe their particular 'drought' in hydrological terms, so that others can judge the severity of the low flow period. These descriptions might include the location of the reach in the catchment (e.g. first order upland or seventh order lowland stream), the nature of the stream in regard to its hydrological regime and occurrence of zero flows (e.g. perennial stream with low or high annual variability, ephemeral stream with regular periods of zero flow, and arid zone stream with extended and variable periods of zero flow) (McMahon & Finlayson, 2003), a description of how this low-flow period compares with the long-term flow record (e.g. recurrence interval, and this low flow versus the seasonally specific median daily flow) and rate of decline in flow.

McMahon & Finlayson (2003) agree with our difficulties in defining drought and suggest that drought *per se* cannot be defined except from a cultural viewpoint and thus is of little utility for ecologists. They identify the need, not for a definition (the search for which they suggest can often be unproductive), but for an understanding of where 'low-flow' periods sit in the hydrological regime of streams. They perceive 'droughts' as 'significant low-flow periods', which can be described in terms of recurrence intervals, duration and trends brought about by large-scale climatic mechanisms, but which are distinct for different stream types. Furthermore, as indigenous aquatic biota from dry regions, such as much of Australia, would have adaptations to naturally occurring periods of low flow, McMahon & Finlayson (2003) argue that the real problem in a cultural context is not drought but 'anti-drought': the imposition of augmented flows in regulated rivers at times when naturally the rivers would experience low or no flow. This idea builds on what scientists have been stating for many years about the effects of altered seasonality of flows, and thus the removal of natural low-flow periods (e.g. Davies & Walker, 1986). However, McMahon & Finlayson (2003) present hydrological analyses quantifying not only the loss of the low-flow period, but also anthropogenic alterations to a range of hydrological parameters that can affect physical, chemical and biological attributes of aquatic ecosystems.

Lake (2003) broadens the definition of drought and distinguishes between what he calls 'seasonal drought', which occurs in some aquatic systems every year as a period of low flow, and 'supra-seasonal drought', which conforms to the conventional idea of drought occurring less frequently, usually on the scale of decades. He considers that seasonal droughts tend to act as press disturbances, but because of the longer time-scale involved, supra-seasonal droughts act more like 'ramps'. The effects of this ramp disturbance, by definition, increase with time, and may elicit concomitant ramp-like responses in organisms. Lake (2003) argues that organisms that experience either type of drought will need to have adaptations to a lack or scarcity of water, although these adaptations may not fully protect them from the stresses imposed by drought. However, some groups will be affected to a greater extent than others, depending on the nature of their adaptations and on the severity of the drought. Boulton (2003) agrees that supra-seasonal droughts act as 'ramp' disturbances, but disagrees in how these disturbances progressively impact upon aquatic biota. As a drought progresses and various geomorphological/hydrological thresholds are crossed, he contends that responses may be 'stepped' rather than ramped, and presents data on changes in macroinvertebrate community structure in several streams during drought to support his argument. Boulton (2003) also considers Lake's (2000, 2003) seasonal droughts as predictable and relatively benign for biota that have had a long period to develop appropriate adaptations; quite different from the less predictable, protracted periods of low flow that severely curtail distributions and abundances of many aquatic organisms.

Effects of drought on aquatic biota

If the low-flow period is severe enough to cause drying of parts of a river bed, then the resident biota will experience some unique challenges. Refuges retaining water become essential for the maintenance of most populations. This is the subject of the review by Magoulick & Kobza (2003). Rates of mortality, birth and migration, as well as interactions among components of the biota that have retreated to refugia, are affected by the nature of the refuge; spatial extent of the refuges, the rate of drying, and the ambient physical and chemical conditions. The study by Covich, Crowl & Scatena (2003) provides a good example of the effects of the contraction of stream pools, resulting from protracted low flows, on shrimp populations in a small neotropical stream. The abundance of two species of shrimp increased in upstream pools of the stream during a particularly dry period and the species showed different reproductive responses once the drought ended.

An alternative strategy for coping with drying events is the production of a long-lived bank of propagules (eggs, seeds or spores) that are resistant to desiccation. Brock *et al.* (2003) compare and contrast the germination of seeds from seed banks and the hatching of zooplankton from resting eggs collected from floodplain soils, to examine the resilience of different components of aquatic communities to dry periods of varying durations. They show that species-rich communities can rapidly develop from this bank of propagules following inundation. Indeed, they suggest that, while a dry phase may be considered a disturbance for many aquatic ecosystems, it should not necessarily be considered a catastrophic event.

It is also important to note that low-flow periods can affect the biogeochemical processes underlying ecosystem functioning (Baldwin & Mitchell, 2000). Although not well studied, there is evidence that periods of drying will affect the way both nutrients and energy are transformed both during and following extended periods of drought (Baldwin & Mitchell, 2000; Dahm *et al.*, 2003). For example, Dahm *et al.* (2003) report a decrease in dissolved organic carbon as well as in phosphorus and nitrogen inputs to an ephemeral stream during drought, and suggest that a decrease in microbial activity may ensue, leading to a shift from predominantly heterotrophic to autotrophic processes.

Approaches to studying drought in aquatic ecosystems

Many studies of the ecological effects of drought have arisen fortuitously, like several of the studies described above, with research being conducted on a population or community in an area that just happened to experience a period of extended low flow (Boulton, 2003; Matthews & Marsh-Matthews, 2003). This is understandable, considering the difficulties in the past in predicting the onset of drought. However, this descriptive, opportunistic approach is unlikely to disentangle the relative effects of the spatial from the temporal extent of low flows and of these from the pattern of drying of the river bed. It is also difficult to investigate questions such as: 'How does the density of organisms in drought refuges or the presence of predators affect resistance of populations or assemblages?' Nor are serendipitous studies likely to cover the range of temporal and spatial scales needed to understand the effects of drought (Matthews & Marsh-Matthews, 2003), although meta-analyses may prove useful.

The alternative to chance encounters with drought is to simulate drought conditions in the laboratory or in mesocosms or use drying gradients to explore community response to drying (Brock *et al.*, 2003). Clearly, however, mesocosm experiments suffer the limitation that their scale dictates and cannot expect to mimic the widespread effects of a true drought. Another possibility is to explore the ecological effects of drought using methods that track historical developments, such as microsatellite DNA analyses in fish (e.g. Douglas, Brunner & Douglas, 2003) or analyses of sediment cores and charcoal (Kershaw, Moss & van der Kaars, 2003). Such approaches potentially allow an examination of how far and for how long the effects of drought resonate through ecosystems over much greater spatial and temporal scales than would normally be possible (Matthews & Marsh-Matthews, 2003). For example, Douglas *et al.* (2003) make a striking case for how drought in the Colorado River devastated a fish species, and essentially altered the course of its evolution. The broader message of their study is that when examining the effects of drought on aquatic biota, we must not simply look for proximate causes, such as the presence of a dam, for current species distributions or gene frequencies, but also consider the much longer time scales relevant to evolution. The likelihood of drought conditions has indeed changed over long periods. Kershaw *et al.* (2003), for example, present evidence to suggest that Australia has tended to experience a drier and more variable climate over the last 350 000 years, and they predict that the continent will also become drier in the future, irrespective of human-induced activities.

Future directions

During the symposium it became clear that our current understanding of the role of drought in aquatic ecosystems is rudimentary. As the climatic and hydrologic patterns in many ecosystems are changing (Arnell *et al.*, 1996), both in the short- and long-term, many fundamental questions relating to drought are still unanswered. For example:

1. Is drought necessary for the maintenance of populations and whole communities in some ecosystems and what are the consequences, as is increas-

ingly common, when droughts are removed from systems that naturally experience them?

2. Does drought aid or hinder the spread of introduced species and how does drought influence the interaction between native and introduced species?

3. Can drought be a fatal blow for endangered species, leading to local or total extinctions?

4. Might drought be critical to promote speciation under other conditions?

5. How do periods of extended drying influence the microbially mediated cycling of carbon and nutrients in these environments?

6. If return frequencies of droughts decrease or the duration of dry periods increase with climate change, how will humans deal with the competing demands between environmental sustainability and exploitation of water resources?

7. Can human-induced water quality problems, such as eutrophication, which are exacerbated by drought, be a greater threat to aquatic biota than simply the effects of low flow?

8. What roles do past and present catchment management practices play in ameliorating or exacerbating the effects of drought; for example, does siltation, as a result of land clearing, reduce the availability of hyporheic refuges for riverine macroinvertebrates (Boulton, 2003)?

When considering these questions, it is important to recognise that low flow in a river is not the only physical variable of importance during a drought, although it is the most obvious one in most instances. Variables that are usually associated with drought conditions, such as higher than average air temperatures, low humidity and increased wind activity (Wilhite, 2000), can individually, or in combination, increase water temperatures and/or evaporation and so accelerate drying of aquatic systems and exacerbate the stresses experienced by aquatic biota. Considering the role of other variables besides low flow is particularly important in light of some of the predictions made under the auspices of global climate change (Arnell *et al.*, 1996).

Finally, the current narrow perception of drought as an undesirable disturbance is ripe for a change, so that droughts, like floods, are considered an integral part of the flow regime of a river. Consequently, management plans must not simply attempt to eradicate drought from the aquatic environment, but recognise that drought can be an important event in the natural long-term flow regime of a river and that its removal may hence have harmful ecological consequences. An ethos of promoting constancy (e.g. successful bird breeding every year or consistently large populations of legal-sized fish) still pervades much of the conservation debate and natural resource management, especially fisheries and waterbird management. This idea tends to encourage the perception that events like drought, and the 'devastation' they cause, are antipathetic to good management. Clearly, this view does not do justice to the potential significance of drought for shaping and maintaining many aquatic communities and ecosystems.

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