

Ecological effects of perturbation by drought in flowing waters

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SUMMARY

1. Knowledge of the ecology of droughts in flowing waters is scattered and fragmentary, with much of the available information being gathered opportunistically. Studies on intermittent and arid-zone streams have provided most of the information.
2. Drought in streams may be viewed as a disturbance in which water inflow, river flow and water availability fall to extremely low levels for extended periods of time. As an ecological perturbation, there is the disturbance of drought and the responses of the biota to the drought.
3. Droughts can either be periodic, seasonal or supra-seasonal events. The types of disturbance for seasonal droughts are presses and for supra-seasonal droughts, ramps.
4. In droughts, hydrological connectivity is disrupted. Such disruption range from flow reduction to complete loss of surface water and connectivity. The longitudinal patterns along streams as to where flow ceases and drying up occurs differs between streams. Three patterns are outlined: 'downstream drying', 'headwater drying' and 'mid-reach drying'.
5. There are both direct and indirect effects of drought on stream ecosystems. Marked direct effects include loss of water, loss of habitat for aquatic organisms and loss of stream connectivity. Indirect effects include the deterioration of water quality, alteration of food resources, and changes in the strength and structure of interspecific interactions.
6. Droughts have marked effects on the densities and size- or age-structure of populations, on community composition and diversity, and on ecosystem processes.
7. Organisms can resist the effects of drought by the use of refugia. Survival in refugia may strongly influence the capacity of the biota to recover from droughts once they break.
8. Recovery by biota varies markedly between seasonal and supra-seasonal droughts. Faunal recovery from seasonal droughts follows predictable sequences, whilst recovery from supra-seasonal droughts varies from one case to another and may be marked by dense populations of transient species and the depletion of biota that normally occur in the streams.
9. The restoration of streams must include the provision of drought refugia and the inclusion of drought in the long-term flow regime.

Keywords: drought, impacts, perturbation, recovery, streams

Introduction

This paper describes the effects of drought as a disturbance in flowing waters and the responses of

the biota – principally invertebrates and fish – to drought. Information on the ecology of drought in flowing waters is both limited and scattered. The same situation applies to stagnant waters, whether they be phytotelmata (e.g. Bradshaw & Holzapfel, 1988), floodplain ponds (e.g. Corti, Kohler & Sparks, 1997) or lakes (e.g. Webster *et al.*, 1996). In general, data on the ecology of droughts in freshwater systems have been gathered serendipitously – the droughts

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occurred during studies being carried out with different research agenda (Boulton, 2003; Covich, Crowl & Scatena, 2003; Matthews & Marsh-Matthews, 2003).

Drought as an ecological perturbation

It is now generally accepted that perturbations in ecosystems consist of two sequential events: the disturbance when the disrupting forces are applied, and the responses by the affected biota to the disturbing forces (Glasby & Underwood, 1996; Lake, 2000) (Fig. 1). There are three types of disturbance: pulse, press and ramp. Pulse and press are well known (Bender, Case & Gilpin, 1984), whereas ramps have been defined as disturbances that increase in strength (and often spatial extent) with time (Lake, 2000).

What constitutes a drought in freshwater ecology is ill-defined. This situation is common, because outside ecology many types of droughts have been recognised: meteorological, hydrological, agricultural and economic. In freshwater systems, there appear to be two types of droughts: the predictable and periodic seasonal droughts, such as those that occur in the Mediterranean (e.g. Towns, 1985; Resh, Jackson & McElravy, 1990; Romani & Sabater, 1997; Gasith & Resh, 1999; Pires, Cowx & Coelho, 2000; Bravo *et al.*, 2001) and wet-dry tropical (e.g. Douglas, 1999; Rincon & Cressa, 2000; Medeiros & Maltchik, 2001; Douglas,

Townsend & Lake, 2003) climates, and the longer, rather unpredictable, aseasonal or supra-seasonal droughts marked by lingering decline in precipitation and water availability (Fig. 2) (Humphries & Baldwin, 2003). Seasonal droughts may be predictable presses, whilst supra-seasonal droughts are ramps marked by an extended decline in rainfall (Figs 1 and 2). Grigg (1996) refers to these droughts as 'creeping disasters'. Temporary streams may have regular seasonal droughts and longer supra-seasonal droughts (Boulton & Lake, 1992a; Gasith & Resh, 1999).

Drought as a perturbation consists of two parts: the disturbance (i.e. the impacts of the decline in water availability), and the biotic responses to the disturbance. The response may be viewed as covering two forms of response: resistance – the capacity of the biota to withstand the drought – and resilience, the capacity to recover from the drought (Lake, 2000) (Fig. 1). In terms of available data on responses to drought in flowing waters, more information is available on invertebrates and fish than on micro- and macro-algae, macrophytes and riparian plants (e.g. Yount & Niemi, 1990; Peterson, 1996; Matthews, 1998; Holmes, 1999).

Responses of the biota differ between seasonal and supra-seasonal droughts (Boulton & Lake, 1992a,b; Giller, 1996; Matthews, 1998). As seasonal droughts are predictable, the biota can be expected to have

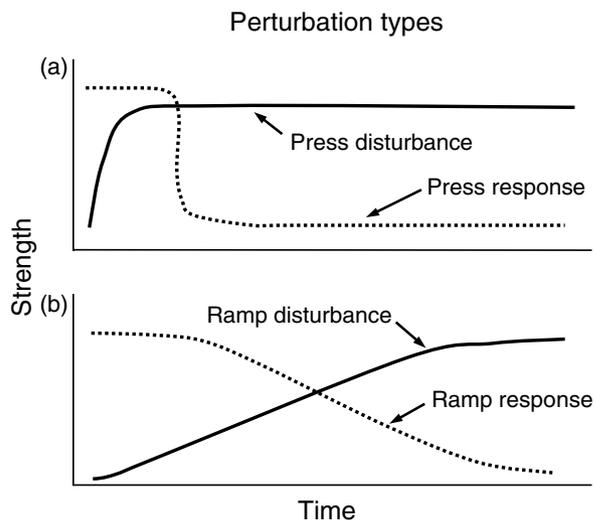


Fig. 1 Two perturbation types: (a) press disturbance and response of a seasonal drought; (b) ramp disturbance and ramp response of a supra-seasonal drought.

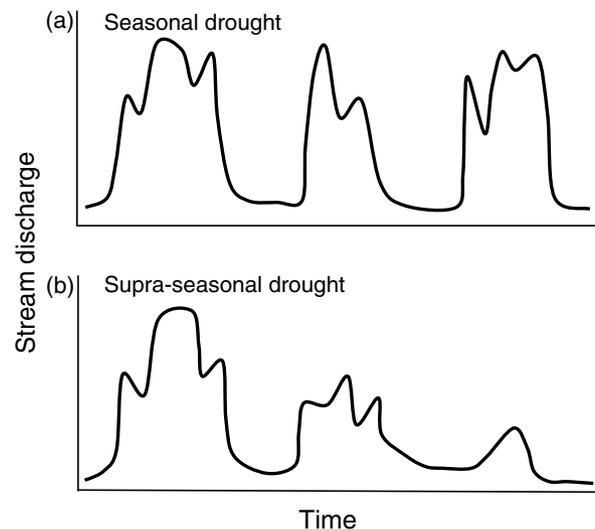


Fig. 2 The time courses of seasonal (a) and supra-seasonal (b) droughts. The seasonal drought is regular and predictable, whereas supra-seasonal drought arises from the failure of adequate precipitation over a number of seasons.

evolved adaptations, such as life-history scheduling and the adaptive use of refugia, to survive them (Yount & Niemi, 1990; Matthews, 1998; Humphries, King & Koehn, 1999). In general, it appears that the biotic response to seasonal droughts is characterized by a high resistance and a strong resilience (e.g. Resh *et al.*, 1990; Boulton & Lake, 1992a; Stanley *et al.*, 1994; Gasith & Resh, 1999; Pires *et al.*, 2000; Boulton, 2003; Medeiros & Maltchik, 2001; Douglas *et al.*, 2003). Supra-seasonal droughts are both unpredictable in timing and duration, and thus are more difficult for organisms to deal with through evolved adaptations. Overall, it appears that the biotic response to supra-seasonal droughts is characterized by a low to moderate resistance and a variable resilience (e.g. Ladle & Bass, 1981; Boulton & Lake, 1992a,b; Wood & Petts, 1994, 1999; Giller, 1996; Matthews, 1998; Wright & Symes, 1999; Wright *et al.*, 2001; Caruso, 2002; Boulton, 2003). Both resistance and resilience appear to be group-specific, if not species-specific. Not surprisingly, much more is known about biotic responses to seasonal than to supra-seasonal droughts.

Drought and hydrological connectivity

With the onset of drought there is a sequential decline in precipitation, run off, soil moisture, groundwater levels and stream flow (Changnon, 1987; Grigg, 1996; Dahm *et al.*, 2003). Natural flowing waters have three axes of hydrological connectivity (Ward, 1989; Pringle, 2001). Water and dissolved and particulate matter move longitudinally from upstream to downstream. Biota move longitudinally in both directions. The stream is connected laterally and hydrologically with its riparian zone. In constrained upland streams, this connection is continuous whereas in lowland rivers, the riparian zone is the flood plain, and the surface water connection is periodic. Surface water is connected vertically with the hyporheic zone and groundwater.

Droughts in streams disrupt hydrological connectivity. Conversely, floods amplify hydrological connectivity. With the onset of drought, falling water levels reduce the amount of habitat available for most aquatic biota, exposing the marginal areas (Stanley, Fisher & Grimm, 1997), breaking surface water contact between the stream and its riparian zone, and reducing the hydraulic heterogeneity of flow. With falling water levels, lentic habitats may increase in

extent and new types of habitats may be created, that favour some species, both residents and invaders. As drying proceeds, the threshold of cessation of surface flow is reached, although hyporheic flow may persist (Stanley *et al.*, 1997; Matthews, 1998, Boulton, 2003). For example, in a severe drought in Sycamore Creek, Arizona, a 12 km section of stream with continuous flow was reduced to 4 km of disconnected sections (Stanley *et al.*, 1997). Shallow sections, such as riffles and runs, are the first to disappear and these sections of the stream can become a series of fragmented pools (Boulton & Lake, 1990; Stanley *et al.*, 1997; Matthews, 1998; Magoulick & Kobza, 2003). Many of these pools are short-lived. In deeper stream sections with relatively impervious bottom substrata, pools may persist. In constrained sections with impervious substrata, pools may persist, but in unconstrained stream sections with highly pervious bottom substrata, pools may not endure, although hyporheic flow may continue (Stanley *et al.*, 1997). Flow cessation means that fine sediments settle out (Everard, 1996; Wright & Symes, 1999), detritus and nutrients no longer move in surface flow, and wastes and toxic materials are not diluted and exported. Many aquatic biota cannot move and become trapped and concentrated in lingering pools (Boulton *et al.*, 1992b; Stanley *et al.*, 1994; Matthews, 1998; Covich *et al.*, 2003; Magoulick & Kobza, 2003; Matthews & Marsh-Matthews, 2003). Stream connectivity becomes differentially disrupted by the cessation of upstream–downstream longitudinal links, and the weakening of lateral links between the stream channel and riparian zone (this includes the flood plain) and vertical links between the surface, hyporheic zone and groundwater. Finally, in a very severe drought, whole sections of streams may lose any trace of surface water and hydrological connectivity can be completely lost (Phase 4 of Matthews, 1998).

With reduced flow from inflowing rivers, estuaries can become disconnected from the sea and become lagoons, with low water quality (Gasith & Resh, 1999; Mackay & Cyrus, 2001). Estuaries with reduced flow can develop poor water quality that can deplete populations of estuarine biota (Attrill & Power, 2000).

At the scale of a whole stream, there appear to be at least three longitudinal patterns of drying up (Fig. 3). Many streams originate from permanent springs and if a drought occurs in such a stream type, the headwater sections may contain water, but downstream the stream channel becomes dry (Fig. 3a). The

springs may serve as refugia for biota (Cooling & Boulton, 1993; Erman & Erman, 1995). In other streams, the headwaters dry and as the stream channel increases in size downstream, surface water remains in pools (Larimore, Childers & Heckrotte, 1959; Tramer, 1977) (Fig. 3b). Refugia and sources of colonists lie downstream (Magoulick & Kobza, 2003). In other instances, such as Castle Creek near Euroa, Victoria, Australia, the stream in drought has upstream perennial springs and at a considerable distance

downstream it has pools, but no surface flow in between (P.S. Lake, personal observation) (Fig. 3c). Similarly, during drought in Sycamore Creek, Arizona, constrained sections may contain water in pools but unconstrained sections dry, although subsurface hyporheic flow may persist (Stanley *et al.*, 1997).

Impacts of drought on stream biota and ecological processes

Droughts can have direct and indirect impacts on stream biota. Direct impacts are those caused by loss of water and flow, and habitat reduction and reconfiguration, whereas indirect impacts are those associated with changes in phenomena such as interspecific interactions, especially predation and competition, and the nature of food resources.

Direct effects centre on loss of water, habitat and dispersal routes. As the stream size shrinks and habitat availability decreases (Resh, 1992; Everard, 1996; Matthews, 1998), animals (e.g. snails, mussels, caddis and pyralid larvae) become stranded (Extence, 1981; Stanley *et al.*, 1994) or trapped in dried-up habitats, such as riffles, and die (e.g. Iversen *et al.*, 1978; Ladle & Bass, 1981; Smock *et al.*, 1994; Stanley *et al.*, 1994; Golladay *et al.*, 2002). In a drought affecting the Flint River, USA, riffle-dwelling mussels were the most severely affected with a mortality level of 53% (Golladay *et al.*, 2002). Shallow layers of the hyporheic zones can dry up, greatly reducing faunal diversity and abundance, whereas deeper layers with water may show an increase in abundance in fauna (Boulton, Valett & Fisher, 1992a; Boulton & Stanley, 1995; Clinton, Grimm & Fisher, 1996). With fragmentation, biota become concentrated in pools and such pools may harbour very high densities of invertebrates (e.g. Canton *et al.*, 1984; Boulton & Lake, 1992c; Stanley *et al.*, 1994; Miller & Golladay, 1996) and of fish (e.g. Paloumpis, 1958; Larimore *et al.*, 1959; Tramer, 1977; Matthews, 1998; Labbe & Fausch, 2000; Matthews & Marsh-Matthews, 2003). Different isolated pools may harbour different assemblages of biota and with time, such pools can diverge from each other in their community structure (Power, Matthews & Stewart, 1985; Meyerhoff & Lind, 1987; Stanley *et al.*, 1997).

As water flow and volumes decrease, water temperatures may start to rise and can become lethal for aquatic biota such as fish (Matthews, 1998). Simulta-

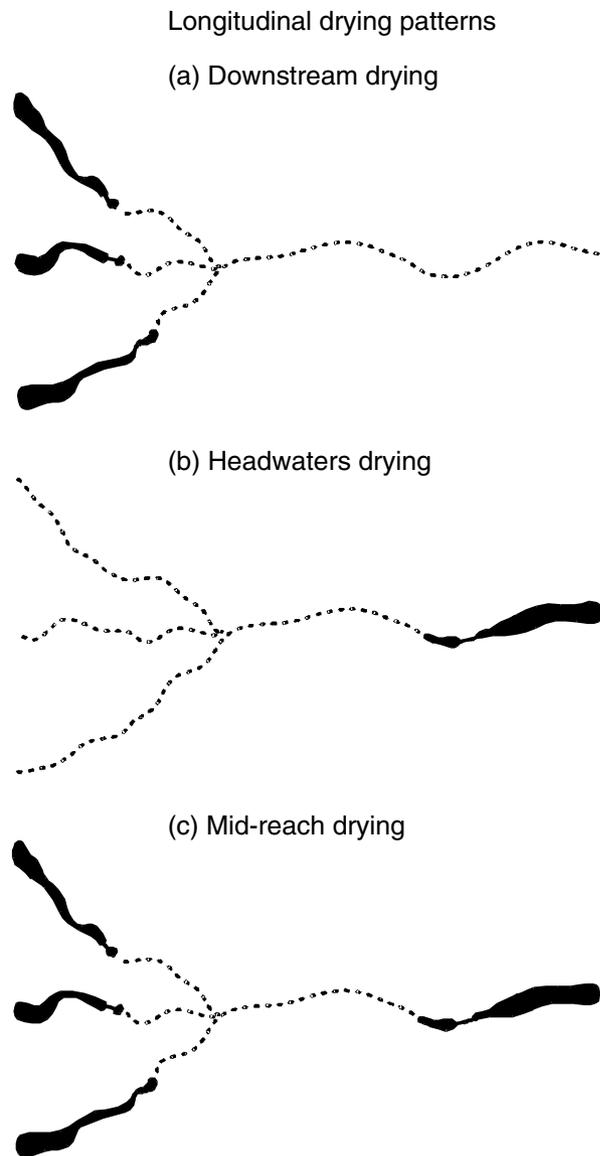


Fig. 3 Three patterns of channel drying during a drought: (a) downstream drying, (b) headwaters drying and (c) mid-reach drying.

neously, especially in pools, deoxygenation may occur, threatening biota (Tramer, 1977; Stanley *et al.*, 1997; Labbe & Fausch, 2000; Mol *et al.*, 2000; Golladay *et al.*, 2002). With flow reduction, FPOM transport may decline (Cuffney & Wallace, 1989) and as flow ceases, transport of detritus and fine sediments stops, giving rise to accumulations of DOM, POM and sediments in pools (Townes, 1985; Boulton & Lake, 1990, 1992c; Everard, 1996; Wright & Symes, 1999). Conductivity and nutrients may also increase (Stanley *et al.*, 1997; Caruso, 2002, P.S. Lake, personal observation). If pools are shaded and POM accumulates, the water in the pools may become dark brown with DOM leached from leaves. Leachates, from leaves, may cause deoxygenation and contain toxic materials (Townes, 1985, 1991; Boulton & Lake, 1990, 1992c; Chergui *et al.*, 1997). As streams dry and the surface water shrinks to unshaded pools, the build-up of nutrients, high temperatures and solar radiation can precipitate blooms of algae (Freeman *et al.*, 1994; Dahm *et al.*, 2003). The algae may create large diel changes in oxygen concentration (Matthews, 1998). Thus, there are the direct effects of loss of water and indirect effects, generated by the loss of water volume, that affect water quality and resource availability that in turn affect the biota.

The direct and indirect impacts of drought can greatly reduce population densities, species richness and alter life-history schedules, species composition, patterns of abundance, type and strength of biotic interactions (predation and competition), food resources, trophic structure and ecosystem processes. As these effects have been partly dealt with in other reviews (e.g. Matthews, 1998; Gasith & Resh, 1999; Lake, 2000; Boulton 2003; Matthews & Marsh-Matthews, 2003), I will illustrate them with a few salient examples.

Although changes in population structure have been poorly documented there are however, some interesting examples. A severe drought in California in 1977 eliminated a population of the caddisfly, *Gumaga nigricula* (McL.) (Resh, 1992). Before the drought, this population had multiple cohorts, but after the drought only a single cohort occurred. After the drought broke, it took 10 years for the original population structure to be restored. Fish population structure can also be changed by drought, reducing spawning and recruitment. Cowx, Young & Hellawell (1984) found that drought greatly reduced

recruitment of salmon (*Salmo salar* L.) in a Welsh river, and Davies, Sloane & Andrew (1988), working in a Tasmanian stream system, noted that in drought years, recruitment by trout (*S. trutta* L. and *Oncorhynchus mykiss* Walbaum) from small headwater streams was severely limited. Fish (Larimore *et al.*, 1959; Tramer, 1977; Griswold, Edwards & Woods, 1982; Closs & Lake, 1995) and invertebrate (Hynes, 1958; Kamler & Riedel, 1960; Iversen *et al.*, 1978; Extence, 1981; Ladle & Bass, 1981; Morrison, 1990; Boulton & Lake, 1992a; Smock *et al.*, 1994; Stanley *et al.*, 1994; Wood & Petts, 1994, 1999; Wright *et al.*, 2001; Boulton, 2003; Golladay *et al.*, 2002; Matthews & Marsh-Matthews, 2003) populations may be eliminated or greatly reduced during droughts.

With the alteration in habitat structure and availability associated with water loss, major changes in trophic structure can occur. With reduced flow and the loss of riffles, periphyton used by grazers disappears and detritus movement down the stream stops (Boulton & Lake, 1992a,b). Thus, filterer and grazer density may be greatly reduced (Canton *et al.*, 1984; Boulton & Lake, 1992a,b) and collector numbers may increase in the pools (Maamri, Chergui & Pattee, 1997). However, Boulton (1991) and Maamri *et al.* (1997) have also found that in drying streams, scrapers rather than shredders were more important in litter breakdown. In stagnant pools with accumulated detritus, deoxygenation and the build-up of toxic leachates may occur (Townes, 1985, 1991; Boulton & Lake, 1990, 1992b) and kill all but a few tolerant species of fish and invertebrates (Larimore *et al.*, 1959; Tramer, 1977; Townes, 1991; Closs & Lake, 1995). With the formation of pools, predator densities may increase (Boulton & Lake, 1992a,b; Stanley *et al.*, 1994; Matthews, 1998). The predators are drawn from three groups: the full aquatics (e.g. odonatan nymphs, fish), the mobile semi-aquatics (e.g. dytiscid beetles, hemipterans), and fully terrestrial predators (e.g. birds). In the dry sections of the stream, terrestrial scavengers, for example, ants, beetles and foxes, may feed on the dead and dying stream fauna. The loss of freshwater prey because of drought in streams may lead to a decline in their predators. For example, loss of fish in Mediterranean streams because of drought can be linked with declines in otter populations (Olmo, Lopez-Martin & Palazon, 2001).

There are undoubtedly changes in ecosystem processes with drought. In streams, up till now, the

emphasis in studies of the effects of disturbance on ecosystem processes have mostly concerned floods. However, there are some studies during seasonal droughts on nutrient dynamics and decomposition.

Streams in drought can retain large amounts of POM in the dry channel that may be exported downstream with storms (e.g. Cuffney & Wallace, 1989) or when the drought breaks (Boulton & Lake, 1992c). Decomposition of leaves in the dry channel occurs at a very slow rate in comparison with submerged leaves (Gurtz & Tate, 1988; Boulton, 1991; Maamri *et al.*, 1997). The breakdown of leaves, with the return of stream flow, is notable for the relative scarcity of shredders in comparison with the high densities of scrapers and collectors (Boulton, 1991; Maamri *et al.*, 1997). Dry leaves have very low bacterial, fungal and microbial activity levels, and with submersion the abundances of bacteria and aquatic hyphomycetes and of levels of microbial activity rapidly rise (Boulton, 1991; Maamri *et al.*, 1998, 1999). Thus drought, at least seasonal drought, greatly inhibits detritus decomposition.

In Sycamore Creek, a Sonoran Desert stream, nitrogen is a limiting element (Grimm & Fisher, 1986). Dissolved inorganic nitrogen may be supplied from the catchment by floods (Grimm, 1994), but during summer drying, nitrogen is supplied from hyporheic upwellings and nitrogen fixation (Grimm, 1994; Grimm & Petrone, 1997). With drying and low flow, patches of blue-green algae may increase and attendant high levels of nitrogen fixation may become the major nitrogen source for the stream (Grimm & Petrone, 1997). In drying streams, the hyporheic zone can undergo major changes in spatial configuration, producing major alterations in the biogeochemical processes carried out in this zone. Hyporheic upwellings supply nitrogen to surface waters, and with flow cessation, 'source' pools with upwellings can have relatively high nitrogen (and phosphorus) concentrations (Dent, Grimm & Fisher, 2001). However, deep layers of the hyporheic zone (phreatic) and parafluvial habitats can become hypoxic and nitrate concentrations decline, such that parts of the hyporheic zone instead of being sites of oxidation become sites of reduction (Stanley & Boulton, 1995; Fisher *et al.*, 1998). In pools with increased nutrients, higher temperatures and more light, high levels of primary production from dense growths of attached algae may develop (Stanley *et al.*, 1997) that may be grazed by

herbivorous fish and tadpoles (Peterson & Boulton, 1999). Overall in drought, production declines, but isolated pools may become temporary hotspots of production.

In their 'telescoping ecosystem model' for streams, Fisher *et al.* (1998) proposed that disturbances such as floods would increase the 'processing length' (length of stream subsystem required to process imported nutrients). However, with droughts, the stream becomes progressively fragmented, with processing lengths for different nutrients increasing or decreasing and being strongly dependent on local conditions and morphology (e.g. pools, dry stream bed). Very little is known about the post-drought effects that products of biogeochemical processes, carried out in drought, have on stream ecosystem metabolism.

Drought refugia

A key component to resistance and resilience, and hence overall survival of fauna in a drought, is the use of refugia (Magoulick & Kobza, 2003). This may be passive, such as the retreat of fish down a stream as the headwaters dry, or active such as the possession of desiccation-resistant life stages. It would be expected that the fauna of intermittent streams with seasonal droughts have acquired, through evolution, a range of adaptations, such as life-history schedules, physiological mechanisms and behaviours (Williams, 1996; Magoulick & Kobza, 2003) that provide refugia. Thus, the fauna of such intermittent streams would be expected to be both more resistant and more resilient to supra-seasonal drought than the fauna of perennial streams in any one region.

There are two major classes of refugium-use strategies, those that occur between generations and those that occur within generations (Lancaster & Belyea, 1997). For refugium use between generations, the strategies involve complex life cycles or changes in habitat use. An example of the strategy of complex life cycles is given by two species of leptocerid caddisflies [*Leptorussa darlingtoni* (Banks) and *Lectrides varians* Mosely] that lay terrestrial eggs (Townsend, 1983). A clear example of the second type of strategy – changes in habitat between generations – is given by fish that retreat in a drought and with the breaking of the drought recolonise the stream with juveniles (Larimore *et al.*, 1959; Stanley *et al.*, 1997; Matthews, 1998;

Gasith & Resh, 1999; Labbe & Fausch, 2000). This phenomenon occurred after a recent drought in Castle Creek, Victoria, Australia, where drought-affected sections were recolonized by juveniles of the fish, *Galaxias olidus* Günther (N. Bond, personal communication).

Refugium-use strategies within generations involve either changes in habitat or within-habitat refugium use. Refugium use through changing habitat is exemplified by the movement of insect larvae from surface waters into the hyporheic zone with drought (e.g. Williams & Hynes, 1974; Cooling & Boulton, 1993), although the use of the hyporheic zone as a drought refuge seems to vary greatly from case to case (e.g. Gagneur & Chaoui-Boudghane, 1991; Boulton & Stanley, 1995; Clinton *et al.*, 1996; Del Rosario & Resh, 2000). Refugium use by surviving within habitat is exemplified by insect larvae and adults (especially beetles) that may persist in micro-habitats without free water but with high humidities (e.g. Boulton, 1989; Boulton *et al.*, 1992c).

All these refugium-use strategies may be used by animals during drought. The studies of Boulton (1989) and Boulton *et al.* (1992c) of over-summering strategies of macroinvertebrates undergoing seasonal drought suggest that the most common strategies are refugium use between generations through complex life cycles and refugium use within generations and within habitat. However, no comparative study has been made of refugium-use strategies in streams exposed to supra-seasonal drought, or has any study examined the relative survival of fauna using different types of refugia during a lengthy drought.

Drought and interspecific interactions

Droughts, like floods, may alter interspecific interactions. Predation levels increase as the stream channel dries. Competition for diminishing resources probably also intensifies, although it has not been documented.

Drought in the Lerderderg River, Victoria, created water quality conditions that killed introduced trout in upstream pools and left reduced populations in pools downstream (Closs & Lake, 1995). The native fish, *Galaxias olidus*, normally does not occur with trout as a result of predation and competition (Fletcher, 1986). However, the galaxiids appear to be better adapted to drought conditions. With the breaking of the drought, their range was extended into trout-free sections and

their populations increased greatly. During drought, fish may be confined to pools containing predatory fish and consequently their numbers can decline greatly (Power *et al.*, 1985). The threatened Arkansas darter (*Etheostoma cragini* Gilbert) can tolerate drought in upstream pools free of northern pike (*Esox lucius* L.), an introduced predator, but in downstream pools, that the pike can tolerate, darters are greatly reduced by predation (Labbe & Fausch, 2000). In the Granite Creeks, Victoria, during the recent drought in areas affected by sand slugs – extensive channel-filling sand deposits – (*sensu* Davis & Finlayson, 2000), surface water was reduced to very small pools with depleted oxygen levels, high temperatures and high levels of DOM (N. Bond, B. David & A. Glaister, personal communication). Under these conditions, the exotic common carp (*Cyprinus carpio* L.) populations were eliminated, whilst the native galaxiids (*G. olidus*) and southern pygmy perch (*Nannoperca australis* Günther) survived.

Interactions between riparian plants are affected by hydrological disturbance. For example, in the southwestern USA, the invading riparian plant, *Tamarix ramosissima* (Ledebour) is better adapted to drought conditions than native species, such as *Populus deltoides* Marshall, and thus invasion is facilitated by drought (Busch & Smith, 1995). However, after floods, seedlings of the native *P. deltoides* may outcompete those of *T. ramosissima* (Sher, Marshall & Gilbert, 2000). By reducing floods and accentuating droughts, river regulation may thus facilitate the invasion of exotic species.

Recovery from drought

The patterns of recovery or resilience differ markedly between seasonal drought and supra-seasonal drought. Recovery can be measured with a number of different variables; e.g. species richness, population densities and species composition. Faunal recovery (using species composition) to predrought or predicted successional assemblages after the breaking of seasonal drought is relatively rapid, with a distinct and predictable sequence of biota (e.g. Boulton & Lake, 1992b,c; Miller & Golladay, 1996; Gasith & Resh, 1999; Pires *et al.*, 2000; Rincon & Cressa, 2000; Bravo *et al.*, 2001; Medeiros & Maltchik, 2001; Douglas *et al.*, 2003). Recolonization by fauna from refugia is important in this recovery.

On the contrary, recovery from a supra-seasonal drought appears to vary considerably. In some cases recovery is rapid. For example, recovery in British chalk streams after extreme droughts was relatively rapid (within months) with only a few taxa missing (Wood & Petts, 1994, 1999; Wright & Symes, 1999, Wright *et al.*, 2001). Relatively rapid (within a year) recovery of invertebrates has also been reported in mid-western USA streams (Larimore *et al.*, 1959; Griswold *et al.*, 1982; Canton *et al.*, 1984), Welsh streams (Cowx *et al.*, 1984), Scottish streams (Morrison, 1990) and New Zealand streams (Caruso, 2002).

However, rapid recovery is not universal. Two processes may influence recovery. The first is succession, whereby recovery occurs through sequential changes in species composition. Some investigators (e.g. Harrison, 1966; Iversen *et al.*, 1978; Ladle & Bass, 1981) have reported that in recovery there may be a phase of early dominant colonizers (e.g. simuliids, chironomids) that increase in density and then decline, as species with longer life cycles increase in numbers. In the coastal freshwater stream studied by Smock *et al.* (1994) the early invaders were marine crustaceans. Secondly, drought may eliminate species that are not readily restored. For example, Hynes (1958, 1961) reported the loss of some species of stoneflies and mayflies for at least a year from a Welsh stream after the 1955 drought. Iversen *et al.* (1978) and Ladle & Bass (1981) reported the virtual elimination of the hitherto abundant amphipod, *Gammarus pulex* L., after drought. The consequent loss in abundant species may cause major changes in community structure and a marked lag in recovery (Boulton & Lake, 1992b; Boulton *et al.*, 1992b; Resh, 1992).

Drought and restoration

Many streams and rivers have been degraded by loss of habitat, loss of flow and changes in flow regime. In streams subjected to habitat simplification, the loss of habitat may not only reduce diversity under normal circumstances but may greatly reduce the availability of refugia. Thus, the resilience of the stream's biota to drought may be greatly diminished. In stream restoration, restoring resistance and resilience to disturbances, such as drought, is a critical target.

Many streams have been dammed and many of these dams are water diversionary structures. Below such structures, streams may be locked into perma-

nent drought. Thus, a critical step in environmental flow setting is to ensure that the restored flow regime does not contain extended periods of extreme low flow or no flow. Other streams, such as many in the southern part of the Murray–Darling basin, Australia, are used to supply irrigation flow and this means that they have high flows in summer and low flows in winter. Droughts or extended periods of low flow in summer are natural phenomena and as for other disturbances, serve as a major force in maintaining biodiversity (Everard, 1996). For fish, low flow periods may be a time at which successful recruitment occurs for some species (Humphries *et al.*, 1999) and droughts can also selectively deplete populations of invaders (e.g. Closs & Lake, 1995). Thus, for the restoration of streams used for irrigation water delivery, it would be desirable, if not necessary, for the maintenance of biodiversity to implement low flows at the natural time of the year.

Conclusions

Our understanding of the effects of drought on the ecology of flowing waters is limited. Most knowledge has come from studies of the effects of predictable seasonal droughts rather than of supra-seasonal droughts. At the levels of populations and communities, some generalizations about the biotic responses to the disturbance of drought may be made, but for ecosystem processes more studies need to be carried out. With streams subject to seasonal droughts, both descriptive and experimental studies can be planned and carried out. For the impacts of supra-seasonal droughts, it is obvious that long-term data sets need to be compiled to allow assessment of the impacts of such droughts (e.g. Wright *et al.*, 2001). With global climate change likely to increase the intensity and frequency of droughts (Arnell *et al.*, 1996), a comprehensive understanding of the effects of drought on streams and their biota becomes a basic requirement to forecast effects and to aid resource management.

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