

Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages

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SUMMARY

1. It is axiomatic that unusually long dry periods (droughts) adversely affect aquatic biota. Recovery after drought is rapid by macroinvertebrates that possess strategies to survive drying or are highly mobile but other taxa take longer to recolonise depending on the timing, intensity, and duration of the dry phase.
2. Although drought acts as a sustained 'ramp' disturbance, impacts may be disproportionately severe when certain critical thresholds are exceeded. For example, ecological changes may be gradual while a riffle dries but cessation of flow causes abrupt loss of a specific habitat, alteration of physicochemical conditions in pools downstream, and fragmentation of the river ecosystem. Many ecological responses to drought within these habitats apparently depend on the timing and rapidity of hydrological transitions across these thresholds, exhibiting a 'stepped' response alternating between gradual change while a threshold is approached followed by a swift transition when a habitat disappears or is fragmented.
3. In two Australian intermittent streams, drought conditions eliminated or decimated several groups of macroinvertebrates, including atyid shrimps, stoneflies and free-living caddisflies. These taxa persisted during the early stages of the drought but did not recruit successfully the following year, despite a return to higher-than-baseflow conditions. This 'lag effect' in response to drought emphasises the value of long-term survey data. Although changes in faunal composition were inconsistent among sites, marked shifts in taxa richness, abundance and trophic organisation after the riffle habitat dried provide evidence for a stepped response.
4. Responses by macroinvertebrate assemblages to droughts of differing severity in English chalk streams were variable. The prolonged 1988–92 drought had a greater impact than shorter droughts in the early 1970s but recovery over the next 3 years was swift. Effects of the 1995 summer drought were buffered by sustained groundwater discharge from the previous winter. These droughts tended to reduce available riverine habitats, especially via siltation, but few taxa were eliminated because they could recolonise from perennial sections of the chalk streams.
5. In the contrasting environments of the intermittent streams studied in England and Australia, there are parallels in the rapid rates of recolonisation. However, recruitment by taxa that lack desiccation-resistant stages or have limited mobility is delayed. Currently, long-term data on these systems may be insufficient to indicate persistent effects of droughts or predict the impacts of excessive surface or groundwater abstraction or the increased frequency and duration of droughts expected with global climate change.

Keywords: chalk streams, disturbance, drought, intermittent streams, macroinvertebrates, sedimentation

Introduction

Aquatic biota, by definition, are characterised by adaptations to an existence in water. Therefore, one would predict that artificial or natural drying would stress or even eliminate these biota from aquatic environments. A second hypothesis is that the impact of drought on the biota in different aquatic environments varies, influenced by factors such as antecedent hydrological history (does the site dry regularly?), the timing and severity (duration and intensity) of the drying disturbance, and the presence of drought refuges. Finally, we would expect that human activities that alter the timing or increase the severity of drought would impact on most aquatic biota depending on the natural water regime of the specific environment. For example, is the biota of intermittent streams less vulnerable than that of perennial streams to species loss when 'artificial drought' is imposed through human activities?

Much of our knowledge about the effects of drought on aquatic ecosystems is phenomenological and usually opportunistic (Lake, 2000, 2003). Experimental manipulation at appropriately broad spatial scales for investigating the direct and indirect effects of drought on aquatic ecosystems is virtually impossible, as is the case with floods (Townsend, 1989). However, studies of the impacts of groundwater pumping, water diversions and dams has provided some insights (Wright & Berrie, 1987; Castella *et al.*, 1995; Ward & Stanford, 1995; Extence, Balbi & Chadd, 1999) but interpretation of these results is often hampered by the lack of adequate preimpact data or suitable reference sites. Not surprisingly, most phenomenological studies on the effects of natural drought suffer similar drawbacks, especially given the wide-ranging effects of drought that tend to compromise the value of adjacent reference systems for comparison.

As water budgets of all aquatic environments are linked by the hydrological cycle at various scales, droughts can have wide-ranging repercussions on various specific environments. For example, severe drought conditions in the catchment of the Thames estuary during 1989–92 reduced freshwater inflows and water quality sufficiently to decrease densities of several estuarine crustaceans [the crab *Carcinus maenas* (L.) and the amphipods *Crangon crangon* (L.) and *Gammarus* spp.] that form key components of the

Thames estuary food web (Attrill & Power, 2000). It is more likely that some of these changes in estuarine trophic dynamics cascade to adjacent marine ecosystems or even terrestrial food webs via changes in availability of prey for waterbirds feeding on mudflats or other intertidal zones (Attrill & Power, 2000).

Vertical linkages between surface habitats and the groundwater as well as lateral linkages with floodplains and riparian zones may also be disrupted by droughts and drying. Working in a sand-bed stream in the Sonoran Desert, Stanley & Valett (1992) demonstrated that drying severed hydrological exchange between surface and subsurface habitats, in turn affecting ecological processes occurring in the surface stream (Valett *et al.*, 1992). During drying, the assemblage composition of subsurface fauna (the hyporheos) in this stream also changed, partly due to the decreased influx of downwelling surface water (Boulton & Stanley, 1995). Changes in lateral connectivity during drying represent the logical counterpart of the flood pulse concept as applied to dryland rivers (Walker, Sheldon & Puckridge, 1995). Droughts alter the duration, frequency and extent of these river-floodplain linkages, and variation in macroinvertebrate assemblage composition in floodplain wetlands has been attributed to varying degrees of connectivity (e.g. Sheldon, Boulton & Puckridge, 2002). Even in tropical streams where annual flow conditions might be expected to be relatively consistent, severe droughts and low discharges can lead to leaf litter accumulation in riffles and pools, altering recruitment of long-lived decapod species (Covich, Crowl & Scatena, 2003) and illustrating drought effects on lateral riparian linkages in stream ecosystems.

As space precludes exploration of the repercussions of drought in a broad range of aquatic environments, this review is restricted to examining two contrasting, yet comparable, environments: temperate Australian intermittent streams and groundwater-fed perennial English chalk streams. It was necessary to choose two specific environments that at least shared some features (e.g. flowing water) so that ecological responses to drought could be isolated from responses to other parameters. The comparison focuses on the effects of drought on aquatic macroinvertebrates because this group is ubiquitous, exhibits a range of physiological and behavioural adaptations to drying, and plays a central ecological role in most aquatic ecosystems. The goals in this paper are to contrast the

effects of drought and degrees of recovery by macro-invertebrate assemblages in two contrasting but comparable environments and identify possible mechanisms by which the effects and subsequent recovery occur. Parallels and contrasts are synthesised in a schematic that illustrates the relationships among the effects of low flows during drought, the transitions among critical habitats, the role of drought refuges, and the various spatial and temporal contexts in which recovery after drought occurs in streams.

Critical stages during a drought

There appears no uniform definition of drought, even for hydrologists (Gordon, McMahon & Finlayson, 1992). For the papers in this Special Issue, drought has been defined as 'an unpredictable low-flow period, which is unusual in its duration, extent, severity or intensity' (Humphries & Baldwin, 2003), although the point was made that the term is difficult to define, not the least because of cultural connotations and regional specificity. McMahon & Finlayson (2003) contend that this cultural perception of drought renders its contemporary definition of limited utility for ecologists, and they suggest a search for a suitable ecological definition could be unproductive in comparison with 'low-flow' periods occurring in the hydrological regimes of specific study sites.

In the context of freshwater ecology, Lake (2003) makes the distinction between *seasonal* droughts (predictable drying as in Mediterranean or Wet-Dry tropical climes) and *supra-seasonal* droughts that are unpredictable, longer periods of drying and probably more closely fit most definitions of drought. This distinction is essential because the seasonal 'drought' is really just an extreme of the water regime of certain types of specific environments and probably not perceived by many biota as drought at all. However, in the Australian case study of 1982, a supra-seasonal drought was imposed on the seasonal droughts typical of the two study streams; so the distinction is useful because both are valid components of some streams' hydrological regimes.

The problems associated with defining drought may be partially resolved by recognising that all aquatic ecosystems will undergo unusually dry periods during their history but that most ecological interest will focus on 'critical stages' that occur in aquatic ecosystems during a drought. Therefore,

exploring the speed, magnitude and direction of ecological responses associated with these stages should provide valuable insights into the 'ecology' of drought. During a drought, critical stages are defined by thresholds of discharge or water level at which habitats become isolated or dry (Fig. 1). Beyond these thresholds, dramatic ecological transitions may occur as entire suites of macroinvertebrates are eliminated or favoured.

In a river or wetland, as drying or drawdown commences, fringing vegetation in the once-submerged littoral or riparian zone becomes isolated (Fig. 1), removing an important habitat for many aquatic macroinvertebrates that feed, shelter or emerge among the plants (Ormerod, Wade & Gee, 1987; Wright *et al.*, 1994). For instance, in six English chalk streams, marginal vegetation was favoured by most taxa that showed habitat preferences, and rare taxa occurred more often in this habitat (Harrison, 2000). Vegetation along the margins of streams provides attachment points for filter-feeding macroinvertebrates, refuge from current and fish predation, complex habitat structure and food for a variety of herbivores and detritivores, and exit points for emerging insects with aerial adult stages (Williams & Feltmate, 1992).

As the drought progresses, flow ceases in rivers, fragmenting the watercourse into pools. The loss of current eliminates many rheophilous taxa almost immediately (see case studies below), prevents drift as a means of recolonisation (Williams, 1977), and in many cases, water quality begins to deteriorate rapidly. Dissolved oxygen concentrations decline, water temperature rises, and most fish die shortly after (Larimore, Childers & Heckrotte, 1959). Changes in macroinvertebrate composition occur when sites become isolated from upstream reaches (Stanley *et al.*, 1994). However, in rivers with porous sand or gravel beds, pools often remain connected by subsurface flow through the hyporheic zone (Fig. 1).

The disappearance of surface water is the most critical stage for most aquatic macroinvertebrates, and occurs when the water table no longer breaks the surface or when the last water in a perched wetland evaporates (Fig. 1). At this phase, numerous dead and dying invertebrates provide food for terrestrial consumers in a pulsed transfer of carbon and energy between ecosystems (Boulton & Suter, 1986; Williams, 1987). Finally, declining water levels in the hyporheic

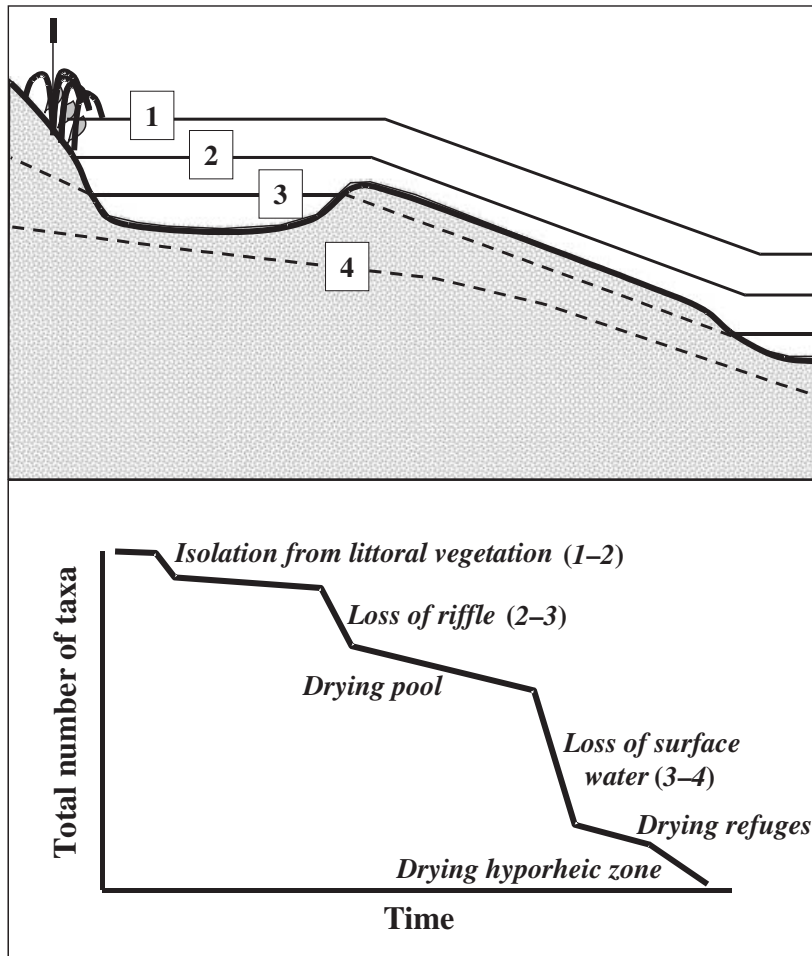


Fig. 1 Changes in macroinvertebrate assemblage composition in a 'stepped' fashion during transitions across threshold discharges or water levels. During drying, total numbers of taxa are posited to decline sharply when submerged or trailing littoral vegetation is isolated from the free water (1 to 2), then as flow ceases in the riffle (2 to 3), and when surface water disappears (3 to 4). Plausibly, further declines occur in the hyporheic zone as subsurface water levels fall.

zone may undergo phases during a 'subsurface drought'. Although we know that subsurface macroinvertebrate assemblages change during drawdown *within* the hyporheic zone (Boulton & Stanley, 1995; Clinton, Grimm & Fisher, 1996), the existence of critical hyporheic thresholds or transition zones has not been investigated. The hyporheic zone has been posited as a key refuge for surface macroinvertebrates during drought (see later), but perhaps extended periods of subsurface drying might eliminate some of these facultative refuges.

Saturated interstitial spaces below dried standing waters also constitute a refuge for some aquatic macroinvertebrates (Williams, 1987). In many wetland basins where drying is a relatively common event, desiccation-resistant stages of many crustaceans and some insects can persist in the sediments (Crome & Carpenter, 1988; Jenkins & Boulton, 1998), remaining viable for decades (Hairston *et al.*, 1995). Many insect taxa found in intermittent streams also have eggs or

juvenile stages that can survive drying (Boulton, 1989; Miller & Golladay, 1996).

Lake (2000, 2003) suggests that droughts act as 'ramp' disturbances with conditions steadily getting worse as droughts persist. The steady nature of the impact is debatable because the stepped model described in Fig. 1 implies that the response, rather than resembling a 'ramp' as figured in Lake (2000), may actually be more irregular as thresholds between critical stages are transcended. We need further empirical data to evaluate whether many of the ecological responses to 'ramp' disturbances such as drought are gradual ramps or actually take place as irregular steps, especially when habitat transitions during drying may result in swiftly unfavourable conditions for some taxa or a switch in the prevalent ecological process.

When assessing or predicting the impacts of drought on aquatic macroinvertebrates, we need to know the:

(i) contribution to diversity and ecological functioning made by the fauna in each critical habitat, and how these habitats are linked;

(ii) changes in composition and activity that occur when wetted critical habitats are fragmented or disappear (acknowledging that some of the changes may not be immediate);

(iii) availability of refuges for recolonisation of the critical habitats (given that some critical habitats may act as refuges); and,

(iv) importance of drought timing, duration, frequency and intensity, as well as the rapidity of drying in each critical habitat.

These parameters have ignored the other interactions that might be important, such as the changes in roles exerted by biological forces such as competitors and predators during drought or the fact that drought is not just simply loss of water but includes general changes in temperature, water quality, and even rates of nutrient cycling. Further, these statements are made without specifying timescales because they are equally true whether tracking the response to a single drought or the cumulative responses by aquatic biota to the 'drought history' in a particular aquatic environment.

The effects of drought on macroinvertebrates in two Australian intermittent streams

Water quality and macroinvertebrate densities in pools and riffles at four sites on two temperate, intermittent streams in Victoria, Australia, were sampled using sweep-nets and a box sampler (Boulton, 1985) during a drought in 1982 and the following wetter-than-average year. Both rivers drain dry sclerophyll forest and dry during summer, either annually (Werribee River) or 1 year in three (Lerderderg River) (Boulton & Lake, 1990). This drought was one of the most severe on record, and at one site (Spargo Creek) on the Werribee River, there was no surface water at all in 1982. Sampling was monthly during 1982, with additional trips in June, July, September and December. In March 1983, when pools at the study sites refilled, sampling occurred fortnightly until March 1984. During the dry period, possible over-summering refuges were explored, including dry sediments that were returned to the laboratory and reflooded (Boulton, 1989). Further details on the study areas, data analysis and results

are given in Boulton (1989) and Boulton & Lake (1990, 1992a–c).

As 1981 was a year of normal rainfall, pools persisted over the austral summer 1981–82 at all sites except Spargo Creek (Fig. 2, Boulton & Lake, 1990). In the pools, a typical lentic macroinvertebrate assemblage persisted, dominated by beetles (dytiscids), bugs (notonectids and corixids), dragonfly and chironomid larvae, atyid shrimps and case-building leptocerid caddisfly larvae (Boulton & Lake, 1992c). When sampling commenced in April 1982, water levels in the pools were below the fringing vegetation of *Lomandra* and trailing grasses but submerged woody debris existed at all sites.

Flow commenced in mid-June 1982 at the downstream site on the Werribee River and in mid-May at both sites on the Lerderderg River (Fig. 2). Early colonists in the riffle habitats included blackfly and chironomid (*Podonomopsis* spp.) larvae and the stonefly nymph *Illiesoperla*. With time, species richness in the riffle increased as a result of colonisation by mayfly nymphs, other species of stonefly nymphs, chironomids and other dipterans, riffle beetles (Elmidae), and various caddisflies including many free-living families such as hydrobiosids and ecnomids (Boulton & Lake, 1992b). However, taxa richness per sample declined by 30% in November 1982 as the riffle dried prematurely due to the drought (Fig. 2). Many individuals of some insects common in 1982 [e.g. the stonefly *Austrocerca tasmanica* (Tillyard) and some groups of rheophilous caddisflies] did not complete their life cycles, and a decline in recruitment was evident the following year (Boulton & Lake, 1992c).

In both streams, taxa richness rose steadily while flow persisted, primarily as a result of increasing diversity of chironomid and other diptera larvae, dragonflies, water mites, and lentic stoneflies and caddisflies. However when flow ceased, there was a sharp decline in average taxa richness, in some cases by over 50% (Fig. 2). These declines coincided with a fall in dissolved oxygen concentration, a slight rise in conductivity and water temperature (Boulton & Lake, 1990), and a switch in trophic dominance as relative proportions of invertebrate predators escalated. The cessation of flow and subsequent drying of the riffle habitat heralded marked and abrupt transitions in taxa richness, density and trophic organisation of macroinvertebrate assemblages in the pools (Fig. 2).

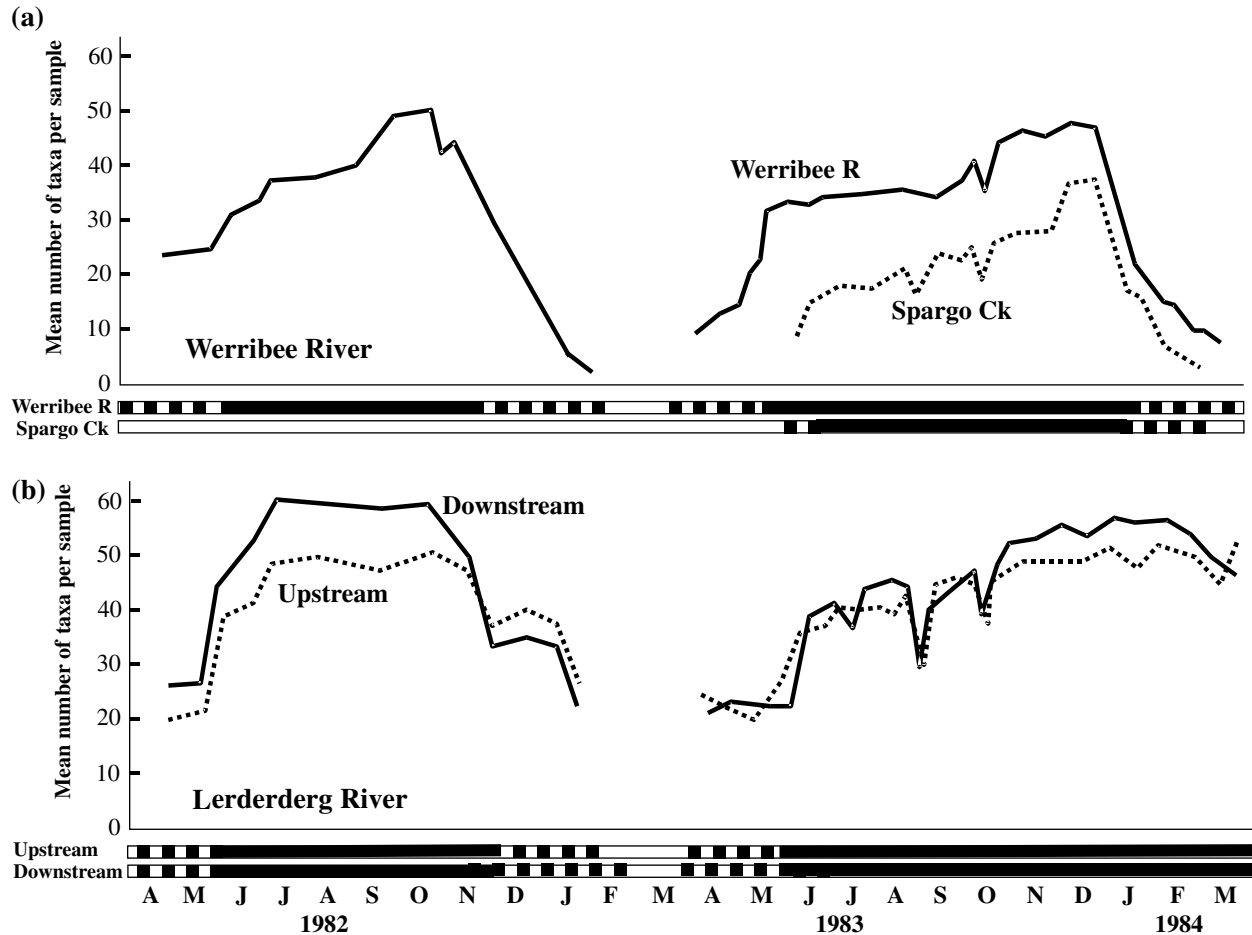


Fig. 2 Changes in mean taxa richness per sample at two sites along the Werribee River (a) (solid line = Werribee River; dotted line = Spargo Creek) and the Lerderberg River (b) (solid line = downstream site; dotted line = upstream site) during a drought (1982) followed by a wetter-than-average year (1983–84). Flow regime at each site is shown as an open bar for dry, a broken bar for pools only and a solid bar for flow.

Similar transitions have been observed during drying in other intermittent streams (e.g. Stanley *et al.*, 1994; Miller & Golladay, 1996).

Most macroinvertebrates appeared to survive the summer drought in nearby permanent pools along the rivers, highlighting the importance of these drought refuges. A few specialised taxa had desiccation-resistant stages and emerged from reflooded sediments, others survived under leaf-litter or stones, and a few persisted in crayfish burrows filled with water (Boulton, 1989). In 1983, after several 'false starts' when pools filled after heavy rain and then dried again, the pools filled and remained so from March until the resumption of flow in May at three sites and in June at Spargo Creek (Fig. 2). Again, the same sequence of recolonisation occurred, although some

taxa such as the amphipod *Afrochiltonia australis* (Sayce), the atyid shrimp *Paratya australiensis* Kemp, and some stoneflies, dragonflies and free-living caddisflies were either absent or much less common a year after the drought (Boulton & Lake, 1992c).

Faunal composition patterns were not consistent among sites and years (Boulton & Lake, 1992a,c). For example, at the site on the Werribee River where the river flowed in both years, the riffle fauna was similar in taxonomic composition both years whereas the pool composition in 1983 differed from that in 1982 because of extirpations or decreased densities of various taxa during the drought. As the riffle dries every year, perhaps the 'seasonal drought' regime imposes a high degree of predictability on the faunal composition of this habitat. Conversely, the riffle

fauna of the two sites on the Lerderderg River differed considerably during the drought year, especially while flow declined, but overlapped almost completely the following year. This difference during the drought may reflect a complex interaction between sediment particle size in the riffle and prevailing discharge. At one site, the riffle substratum is gravel whereas during the drought year, water trickled among boulders and cobbles at the upstream site. Low flows probably exaggerated these substratum differences because the next year, bankfull flow at both sites spanned the range of particle sizes, resulting in similar faunal composition (Boulton & Lake, 1992b).

Although several spates occurred during the sampling period, their effects on macroinvertebrate assemblage composition and taxa richness (Fig. 2) were short-lived and recovery to pre-flood composition was complete within 4 weeks (Boulton & Lake, 1992a). Conversely, drying completely reset the succession sequences at all sites. Nonetheless, after 2 years, there was little evidence of long-term impacts of the 1982 drought on at least two species of case-building leptocerid caddisfly sampled at the study sites in the Lerderderg River from 1982 to 1986 by St Clair (1993). Without long-term data sets for other taxa or data from nearby reference sites that were unaffected by the 1982 drought, it is impossible to demonstrate that the marked changes result from the transitions between critical stages and are not caused by other factors such as coincidental seasonal patterns or other cues. Nonetheless, overall faunal composition consistently changed when riffles ceased flow and again when surface water disappeared.

The effects of drought on macroinvertebrates in English chalk streams

Although the upper reaches of many English chalk streams are intermittent 'winterbournes', the lower sections are perennial and groundwater-fed, providing a contrasting environment to that of the Australian intermittent streams described above. The faunal composition of the intermittent winterbournes also differs markedly from that of the perennial sections (Casey & Ladle, 1976; Wright, 1984). This contrasts with the substantial overlap in macroinvertebrate assemblage composition evident in proximate permanent and intermittent streams in temperate Australia

(Boulton & Suter, 1986) where overall hydrological variability is much greater (Lake, 1995).

Many English chalk streams have been sampled intensively over the last three decades, prompted by concerns about the effects of droughts and water abstractions on groundwater recharge (Wright & Berrie, 1987; Agnew, Clifford & Haylett, 2000) and there are data on the impacts of the 1973, 1976, 1988–1992 and 1995 droughts on macroinvertebrates of the usually-perennial reaches. Chalk streams are especially susceptible to prolonged drought as about 80% of their annual discharge is derived from groundwater, and flow is strongly related to rainfall in the preceding months (Berrie, 1992). In their natural state, the lower reaches of chalk streams are typified by high levels of nutrients, relatively stable flow regimes, dense beds of macrophytes and diverse macroinvertebrate assemblages (Wright, 1992; Wood *et al.*, 1999). However, many chalk stream ecosystems are threatened by extended drying through river diversions and groundwater abstraction (Wright & Berrie, 1987; Castella *et al.*, 1995; Agnew *et al.*, 2000) and these impacts are exacerbated during droughts.

Ladle & Bass (1981) sampled a normally perennial section of Waterston Stream that ceased flow from August 1973 to January 1974, and reported dramatic changes in faunal composition. Some taxa such as the amphipod *Gammarus pulex* (L.), the predominant crustacean in English chalk streams, were virtually eliminated whereas others such as the mayfly *Ephemera ignita* Poda apparently gained a substantial advantage. The influence of the timing of the drought on faunal composition was evident from the availability of recolonists such as eggs, aerial adults or desiccation-resistant stages. Macrophyte cover also changed. *Apium nodiflorum* (L.) gained a competitive advantage over *Ranunculus calcareus* (Butcher) through its tolerance of drying. Given the reliance by many macroinvertebrates upon submerged aquatic vegetation for food and shelter (Williams & Feltmate, 1992), these changes may mediate some of the shifts in faunal composition.

In the perennial section of another chalk stream sampled during the 1976 drought, Wright & Berrie (1987) reported that excessive siltation and inhibited growth of *Ranunculus* limited macroinvertebrate habitat quality and availability, resulting in a decline in the abundance of some benthic taxa such as blackflies and baetid mayflies. However, the overall

density of aquatic invertebrates increased and the total number of taxa resembled those recorded in previous years. Ecological effects of the drought seemed most severe in the upper perennial reach where the impact of siltation on aquatic macrophytes and invertebrates persisted into autumn, 1977 (Wright & Berrie, 1987) but recovery was complete by the following year (Wright & Symes, 1999).

The extended drought of 1988–92 dried many historically perennial reaches of several groundwater-fed English streams. Wood & Petts (1994, 1999) monitored the effects of this drought on macroinvertebrates in the Little Stour near Canterbury. Usually perennial, this stream dried out in sections up to 2 km long. Sweep-net samples were taken annually in late summer from 1992 to 1995 to track recovery after the drought (Fig. 3). Total numbers of taxa and mean densities of individuals per sample increased steadily (Fig. 4), reflecting the increase in surface flows and habitat availability and the flushing of silt (Wood & Petts, 1999).

Physical habitat diversity appears to govern the sensitivity of the macroinvertebrate assemblages to drought stress, as is evident from the above-mentioned that identify the contributions of macrophyte habitat complexity and siltation to taxa diversity in chalk streams. Wood & Petts (1994, 1999) also noted longitudinal variation in ecological response to drought by macroinvertebrates because the relatively uniform, deep, and slow-flowing lowland section was less sensitive to hydrological variation than the upper, geomorphologically more diverse section.

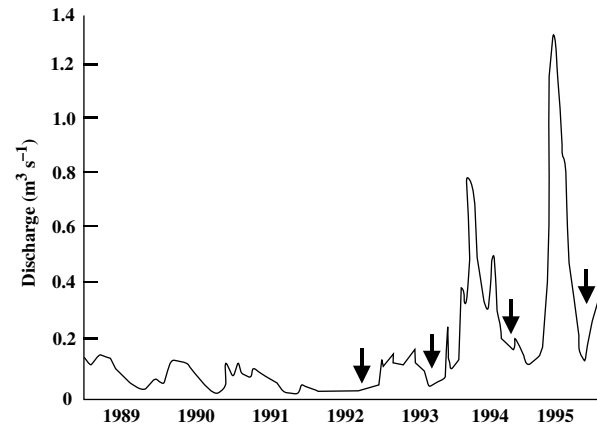


Fig. 3 Average weekly flow (1989–95) at Seaton, midway along the Little Stour River, England. Arrows mark the sampling dates: 17 Aug. 1992, 8 Sept. 1993, 7 Sept. 1994 and 6 Sept. 1995. Modified from Wood & Petts (1999).

In 1995, a severe deficit in summer rainfall had no detectable impact on macroinvertebrate composition in the Little Stour, indicating the significance of winter groundwater recharge in sustaining summer flows (Wood, 1998; Wood & Petts, 1999). In this sense, groundwater recharge buffers aquatic environments from short droughts. Such short-term buffering capacity indicates the importance of a long-term view when identifying groundwater-dependent ecosystems (GDEs) (NCC, 1999), some of which may only depend on groundwater during rare droughts.

Wood (1998) suggests that there are two different types of drought in Great Britain that can be distinguished in terms of their effect on river flow

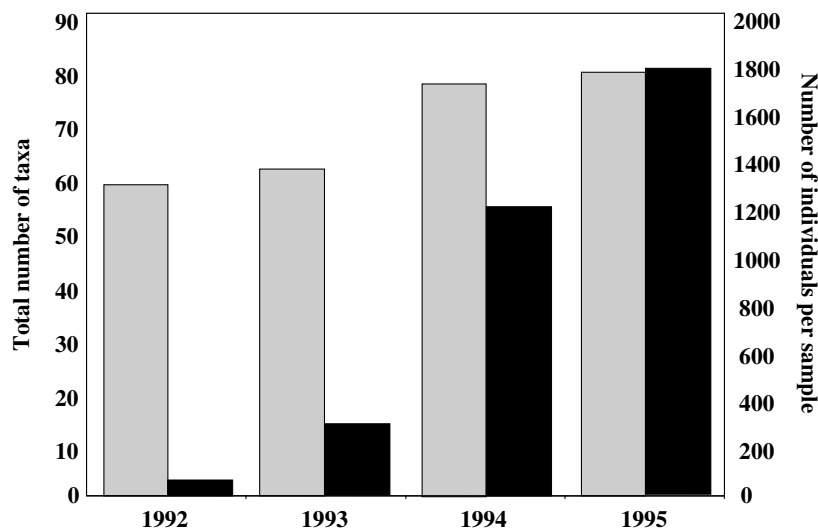


Fig. 4 Changes in the total number of taxa (grey fill) and the number of individuals per sample (black fill) in the Little Stour River, England.

and aquatic biota. 'Surface water droughts' are largely confined to spring, summer and/or autumn of a single year, and have greatest impact on streams where groundwater is only a minor component of flow. 'Groundwater droughts' usually develop following a surface water drought but include one or more dry winters, and have greatest impact on catchments where baseflows are largely fed by groundwater. These latter droughts are rare but capable of causing severe degradation of riverine habitats because of a reduction in wetted channel area, altered water chemistry and deposition of fine sediment (Wood, 1998; Wood, Agnew & Petts, 2000).

Parallels, contrasts and management issues

In all the above-mentioned case studies, drought caused dramatic changes in faunal composition, especially when surface water disappeared. Unfortunately, published temporal data from the chalk stream studies are insufficient to assess the faunal changes occurring during the actual transition period (critical threshold) when flow ceased and pools became fragmented habitats. Another parallel is the rapid recovery to predrought composition, even in usually perennial streams. In all cases, the crucial role of drought refuges was evident, and this is highlighted in other studies of recovery by macroinvertebrates from drought and drying in other streams (e.g. Hynes, 1958; Larimore *et al.*, 1959; Miller & Golladay, 1996; Ledger & Hildrew, 2001; Shivoga, 2001).

Related to the role of refuges is the physical complexity of the stream bed. Not only can macroinvertebrates avoid desiccation by sheltering below cobbles, in debris, or among exposed macrophytes (Williams & Hynes, 1977; Boulton, 1989; Ledger & Hildrew, 2001), but some also appear capable of penetrating the interstices of the hyporheic zone and occupy this refuge as facultative inhabitants (Clifford, 1966; Boulton, 2000). If the timing of the drought coincides with the seasonal presence of small instars, moist habitats in the sediments are especially beneficial for these groups (Ledger & Hildrew, 2001). However, this interstitial refuge may be unavailable in streams with homogeneous substrata such as sand or where siltation has filled the interstices. For example, Smock *et al.* (1994) found the hyporheic zone of a sand-bed stream in South Carolina was not a refuge from drying because anoxic conditions existed

3–5 cm below the surface. Few surface benthic taxa in a Sonoran Desert stream used the hyporheic zone as a refuge during drying (Boulton & Stanley, 1995).

Although siltation during low flows is an issue in the ecological response to drought in the chalk streams (Wright & Berrie, 1987; Wood & Armitage, 1999; Wood *et al.*, 2000), it did not appear relevant in the two Australian intermittent streams. This probably reflects differences in land-use, geology and catchment stability more than hydrological regime. However, this aspect of siltation provides an interesting insight into the fine-scale effects of a large-scale phenomenon such as drought that generates differential microhabitats, thus altering the overall macroinvertebrate composition. Variations in assemblage composition may not necessarily reflect tolerance to drying but simply be responses to the availability of different habitats. In many cases, low flows and drying exacerbate the impacts of other stressors such as organic pollution, siltation and toxicants (Williams & Hynes, 1977; Caruso, 2002; Hall, Bergthold & Sites, 2003), resulting in a complex ecological response to drought that may not be consistent from year to year within a specific environment.

The effect of drought on benthic macroinvertebrate assemblage composition during the following year or sometimes longer is a key issue because assessments of the influences of drying *during* the drought year may only reveal part of the impact and miss longer term and perhaps more profound differences. This was evident from the case study on Australian intermittent streams and has been reported elsewhere. For example, in a Welsh stream (Afon Dulas), the severe drought of 1976 altered the subsequent assemblage composition markedly after densities of invertebrates were reduced by about 60% (Cowx, Young & Hellawell, 1984). For the major insect species occurring in the Afon Dulas, the drought overlapped with the normal period of hatching, and markedly reduced the abundance of these insects in 1977. Interestingly, densities of other taxa such as chironomids and simuliids rose sharply (Cowx *et al.*, 1984). Feminella (1996), in a comparison of benthic macroinvertebrate responses to varying flows in six Alabama streams, found year-to-year variance in assemblage composition to be as great as differences among streams of contrasting permanence. He reported that the antecedent hydrological conditions associated with riffle permanence largely governed

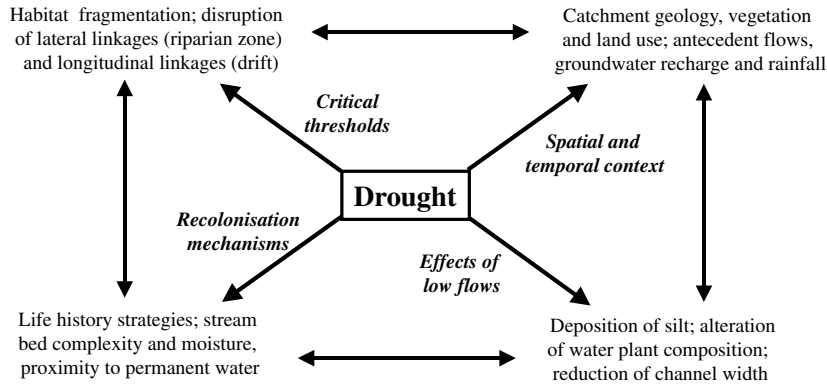


Fig. 5 The relationship among low flows, critical thresholds, recolonisation mechanisms and the spatio-temporal context in the drought dynamics of aquatic macroinvertebrates.

macroinvertebrate assemblage structure, apparently due to their influences on survival and recruitment of subsequent generations as found in the Australian intermittent streams.

In most of the chalk streams, maximum groundwater abstraction usually coincides with natural periods of low flow (Agnew *et al.*, 2000) but in the Australian case study, water abstraction was not an issue as the catchment of the study sites is forested. Nonetheless, many other Australian streams suffer prolonged periods of low or zero flow through 'artificial droughts' caused by surface water diversion and abstraction or groundwater extraction on so-called 'unregulated streams', and this topic is becoming a research priority for water management agencies in Australia (Kingsford, 2000). It is crucial to recognise the hydrological links between groundwater and river flows in many systems (Wood *et al.*, 2000), and this dependency becomes especially evident when drought alters baseflow conditions in small streams (Caruso, 2002). Recent policy development in Australia (NCC, 1999) acknowledges the importance of GDEs, specifically targeting river baseflow as one 'ecosystem type' along with some elements of terrestrial vegetation, aquifers and cave ecosystems, and wetlands.

Conclusions

Drought exerts its myriad influences upon macroinvertebrate assemblages in various aquatic environments via hydrological alterations whose effects depend on the spatial and temporal context (i.e. antecedent conditions of rainfall, catchment land-use and geology, Fig. 5). Low flows enhance siltation, change the composition of aquatic vegetation, alter

channel shape and affect water chemistry. As drought progresses, receding water levels transcend thresholds between critical habitats (Fig. 1), creating new environmental conditions for aquatic macroinvertebrates. These transitions and the resultant changes in macroinvertebrate assemblage composition are most marked when flow ceases and when surface water disappears. Postdrought recolonisation depends on the availability of refuges (related to physical habitat complexity, proximity to permanent water and macroinvertebrate life histories), the degree of habitat fragmentation and the changes wrought by low flows or drying (Fig. 5). All of these influences are related closely, and effects are expected to vary among specific aquatic environments, across habitats and over time.

Successful water managers recognise the likelihood of droughts in all aquatic ecosystems, and seek ways to protect these systems from excessive water deprivation resulting from human extractions. Some of these management options could entail alterations in the timing and extent of water diversions (Rader & Belish, 1999; Kingsford, 2000), pumping policies to maintain river flows above levels that cause siltation and macrophyte loss (Wright & Berrie, 1987), and explicit recognition of the link between groundwater extraction and surface flows in many rivers (NCC, 1999; Agnew *et al.*, 2000). Many GDEs may only be groundwater-dependent during occasional droughts but this does not make them any less vulnerable. There is also an urgent need for effective methods for river flow indexing that adequately account for drought (Extence *et al.*, 1999).

It is reassuring to note the apparent rapid recovery after drought in most aquatic environments where recolonisation from refuges is unimpeded, and habitat

recovery (e.g. desiltation and renewal of connections among critical habitats) occurs (Ledger & Hildrew, 2001; Shivoga, 2001; Caruso, 2002). This swift recovery probably reflects the long evolutionary history of drought in most aquatic environments. However, most of our data are relatively shortterm and opportunistic. Few surveys have been designed specifically to ensure that the effects of drought can be separated from other variables and that adequate preimpact data exist. Increasing human demand for water against a backdrop of global climate change, increasing aridity (Grimm *et al.*, 1997), and chronic surface and groundwater pollution in many parts of the world underlines our need to understand the mechanisms and processes of natural droughts and ameliorate the effects of artificial droughts. Conversely, we should acknowledge the role of natural droughts in maintaining a temporal mosaic of habitats and diversity in aquatic environments and ensure that we do not over-react by removing this natural flow variability (Boulton *et al.*, 2000).

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References

Agnew C.T., Clifford N.J. & Haylett S. (2000) Identifying and alleviating low flows in regulated rivers: the case of the Rivers Bulbourne and Gade, Hertfordshire, UK. *Regulated Rivers: Research & Management* **16**, 245–266.

- Attrill M.J. & Power M. (2000) Effects on invertebrate populations of drought-induced changes in estuarine water quality. *Marine Ecology Progress Series* **203**, 133–143.
- Berrie A.D. (1992) The chalk-stream environment. *Hydrobiologia* **248**, 3–9.
- Boulton A.J. (1985) A sampling device that quantitatively collects benthos in flowing or standing waters. *Hydrobiologia* **127**, 31–39.
- Boulton A.J. (1989) Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. *Transactions of the Royal Society of South Australia* **113**, 23–34.
- Boulton A.J. (2000) The functional role of the hyporheos. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **27**, 51–63.
- Boulton A.J. & Lake P.S. (1990) The ecology of two intermittent streams in Victoria, Australia. I. Multivariate analyses of physicochemical features. *Freshwater Biology* **24**, 123–141.
- Boulton A.J. & Lake P.S. (1992a) The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers, and years. *Freshwater Biology* **27**, 99–121.
- Boulton A.J. & Lake P.S. (1992b) The macroinvertebrate assemblages in pools and riffles in two intermittent streams (Werribee and Lerderderg Rivers, southern central Victoria). *Occasional Papers of the Museum of Victoria* **5**, 55–71.
- Boulton A.J. & Lake P.S. (1992c) The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. *Freshwater Biology* **27**, 123–138.
- Boulton A.J. & Stanley E.H. (1995) Hyporheic processes during flooding and drying in a Sonoran Desert stream. II. Faunal dynamics. *Archiv für Hydrobiologie* **134**, 27–52.
- Boulton A.J. & Suter P.J. (1986) Ecology of temporary streams – an Australian perspective. In: *Limnology in Australia* (Eds P. De Deckker & W.D. Williams), pp. 313–327. CSIRO/Dr W. Junk, Melbourne/Dordrecht.
- Boulton A.J., Sheldon F., Thoms M.C. & Stanley E.H. (2000) Problems and constraints in managing rivers with variable flow regimes. In: *Global Perspectives on River Conservation: Science, Policy and Practice* (Eds P.J. Boon, B.R. Davies & G.E. Petts), pp. 411–426. John Wiley and Sons, London.
- Caruso B.S. (2002) Temporal and spatial patterns of extreme low flows and effects on stream ecosystems in Otago, New Zealand. *Journal of Hydrology* **257**, 115–133.
- Casey H. & Ladle M. (1976) The chemistry and biology of the South Winterbourne, Dorset, England. *Freshwater Biology* **6**, 1–12.

- Castella E., Bickerton M., Armitage P.D. & Petts G.E. (1995) The effects of water abstractions on invertebrate communities in U.K. streams. *Hydrobiologia* **308**, 167–182.
- Clifford H.F. (1966) The ecology of invertebrates in an intermittent stream. *Investigations of Indiana Lakes and Streams* **7**, 57–98.
- Clinton S.M., Grimm N.B. & Fisher S.G. (1996) Response of a hyporheic invertebrate assemblage to drying disturbance in a desert stream. *Journal of the North American Benthological Society* **15**, 700–712.
- Covich A.P., Crowl T.A. & Scatena F.N. (2003) Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology* **48**, 1199–1206.
- Cowx I.G., Young W.O. & Hellawell J.M. (1984) The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biology* **14**, 165–177.
- Crome F.H.J. & Carpenter S.M. (1988) Plankton community cycling and recovery after drought - dynamics in a basin on a flood plain. *Hydrobiologia* **164**, 193–211.
- Extence C.A., Balbi D.M. & Chadd R.P. (1999) River flow indexing using British benthic macroinvertebrates: A framework for setting hydroecological objectives. *Regulated Rivers: Research & Management* **15**, 543–574.
- Feminella J.W. (1996) Comparison of benthic macroinvertebrate assemblages in small streams along a gradient of flow permanence. *Journal of the North American Benthological Society* **15**, 651–669.
- Gordon N.D., McMahon T.A. & Finlayson B.L. (1992) *Stream Hydrology: An Introduction for Ecologists*. John Wiley and Sons, Chichester.
- Grimm N.B., Chacon A., Dahm C.N., Hostetler S.W., Lind O.T., Starkweather P.L. & Wurtsbaugh W.W. (1997) Sensitivity of aquatic ecosystems to climatic and anthropogenic changes: The Basin and Range, American Southwest and Mexico. *Hydrological Processes* **11**, 1023–1041.
- Hairston N.G. Jr, Van Brunt R.A., Kearns C.M. & Engstrom D.R. (1995) Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* **76**, 1706–1711.
- Hall D.L., Bergthold B.S. & Sites R.W. (2003) The influence of adjacent land uses on macroinvertebrate communities of prairie streams in Missouri. *Journal of Freshwater Ecology* **18**, 55–68.
- Harrison S.S.C. (2000) The importance of aquatic margins to invertebrates in English chalk streams. *Archiv für Hydrobiologie* **149**, 213–240.
- Humphries P & Baldwin D.S. (2003) Drought and aquatic ecosystems: an introduction. *Freshwater Biology*, **48**, 1141–1146.
- Hynes H.B.N. (1958) The effect of drought on the fauna of a small mountain stream in Wales. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **13**, 826–833.
- Jenkins K.M. & Boulton A.J. (1998) Community dynamics of invertebrates emerging from reflooded lake sediments: flood pulse and aeolian influences. *International Journal of Ecological and Environmental Science* **24**, 179–192.
- Kingsford R.T. (2000) Protecting rivers in arid regions or pumping them dry? *Hydrobiologia* **427**, 1–11.
- Ladle M. & Bass J.A. (1981) The ecology of a small chalk stream and its responses to drying during drought conditions. *Archiv für Hydrobiologie* **90**, 448–466.
- Lake P.S. (1995) Of floods and droughts: River and stream ecosystems of Australia. In: *River and Stream Ecosystems* (Eds C.E. Cushing, K.W. Cummins & G.W. Minshall), pp. 659–694. Elsevier, Amsterdam.
- Lake P.S. (2000) Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* **19**, 573–592.
- Lake P.S. (2003) Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology* **48**, 1161–1172.
- Larimore R.W., Childers W.F. & Heckrotte C. (1959) Destruction and re-establishment of stream fish and invertebrates affected by drought. *Transactions of the American Fisheries Society* **88**, 261–285.
- Ledger M.E. & Hildrew A.G. (2001) Recolonization by the benthos of an acid stream following a drought. *Archiv für Hydrobiologie* **152**, 1–17.
- McMahon T.A. & Finlayson B.L. (2003) Droughts and anti-droughts: the low-flow hydrology of Australian rivers. *Freshwater Biology*, **48**, 1147–1160.
- Miller A.M. & Golladay S.W. (1996) Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. *Journal of the North American Benthological Society* **15**, 670–689.
- NCC (1999) *Desktop Methodology to Identify Groundwater Dependent Ecosystems*. Nature Conservation Council of New South Wales, Sydney.
- Ormerod S.J., Wade K.R. & Gee A.S. (1987) Macro-floral assemblages in upland Welsh streams in relation to acidity and their importance to invertebrates. *Freshwater Biology* **18**, 545–557.
- Rader R.B. & Belish T.J. (1999) Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research & Management* **15**, 553–563.
- Sheldon F., Boulton A.J. & Puckridge J.T. (2002) Conservation value of variable connectivity: aquatic invertebrate assemblages of channel and floodplain habitats of a central Australian arid-zone river, Cooper Creek. *Biological Conservation* **103**, 13–31.

- Shivoga W.A. (2001) The influence of hydrology on the structure of invertebrate communities in two streams flowing into Lake Nakuru, Kenya. *Hydrobiologia* **458**, 121–130.
- Smock L.A., Smith L.C., Jones J.B. & Hooper S.M. (1994) Effects of drought and a hurricane on a coastal headwater stream. *Archiv für Hydrobiologie* **131**, 25–38.
- St Clair R.M. (1993) Life histories of six species of Leptoceridae (Insecta: Trichoptera) in Victoria. *Australian Journal of Marine and Freshwater Research* **44**, 363–379.
- Stanley E.H. & Valett H.M. (1992) Interactions between drying and the hyporheic zone. In: *Troubled Waters of the Greenhouse Earth* (Eds P. Firth & S.G. Fisher), pp. 234–249. Springer-Verlag, New York.
- Stanley E.H., Buschman D.L., Boulton A.J., Grimm N.B. & Fisher S.G. (1994) Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist* **131**, 288–300.
- Townsend C.R. (1989) The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* **8**, 36–50.
- Valett H.M., Fisher S.G., Grimm N.B., Stanley E.H. & Boulton A.J. (1992) Hyporheic-surface water exchange: implications for the structure and functioning of desert stream ecosystems. In: *Proceedings of the First International Conference on Groundwater Ecology* (Eds J.A. Stanford & J.J. Simons), pp. 395–405. American Water Resources Association, Bethesda, Maryland.
- Walker K.F., Sheldon F. & Puckridge J.T. (1995) A perspective on dryland river ecosystems. *Regulated Rivers: Research and Management* **11**, 85–104.
- Ward J.V. & Stanford J.A. (1995) The serial discontinuity concept: extending the model to floodplain rivers. *Regulated Rivers: Research and Management* **10**, 159–168.
- Williams D.D. (1977) Movements of benthos during the recolonization of temporary streams. *Oikos* **29**, 306–312.
- Williams D.D. (1987) *The Ecology of Temporary Waters*. Timber Press, Portland, Oregon.
- Williams D.D. & Feltmate B.W. (1992) *Aquatic Insects*. C.A.B. International, Wallingford, Oxon, UK.
- Williams D.D. & Hynes H.B.N. (1977) The ecology of temporary streams. II. General remarks on temporary streams. *Internationale Revue der gesamten Hydrobiologie* **62**, 53–61.
- Wood P.J. (1998) The ecological impact of the 1995–1996 drought on a small groundwater-fed stream. In: *Hydrology in a Changing Environment*. Volume 1. (Eds H. Wheaton & C. Kirby), pp. 303–311. John Wiley and Sons, Chichester.
- Wood P.J. & Armitage P.D. (1999) Sediment deposition in a small lowland stream – management implications. *Regulated Rivers: Research & Management* **15**, 199–210.
- Wood P.J. & Petts G.E. (1994) Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research & Management* **9**, 303–316.
- Wood P.J. & Petts G.E. (1999) The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes* **13**, 387–399.
- Wood P.J., Armitage P.D., Cannan C.E. & Petts G.E. (1999) Instream mesohabitat diversity in three groundwater streams under baseflow conditions. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**, 265–278.
- Wood P.J., Agnew M.D. & Petts G.E. (2000) Flow variations and macroinvertebrate community responses in a small groundwater-dominated stream in south-east England. *Hydrological Processes* **14**, 3133–3147.
- Wright J.F. (1984) The chironomid larvae of a small chalk stream in Berkshire, England. *Ecological Entomology* **9**, 231–238.
- Wright J.F. (1992) Spatial and temporal occurrence of invertebrates in a chalk stream, Berkshire, England. *Hydrobiologia* **248**, 11–30.
- Wright J.F. & Berrie A.D. (1987) Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research & Management* **1**, 145–160.
- Wright J.F. & Symes K.L. (1999) A nine-year study of the macroinvertebrate fauna of a chalk stream. *Hydrological Processes* **13**, 371–385.
- Wright J.F., Blackburn J.H., Clarke R.T. & Furse M.T. (1994) Macroinvertebrate-habitat associations in lowland rivers and their relevance to conservation. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **25**, 1515–1518.

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