

promoting access to White Rose research papers



Universities of Leeds, Sheffield and York
<http://eprints.whiterose.ac.uk/>

This is the author's pre-print version of an article published in **Advances in Ecological Research, 48**

White Rose Research Online URL for this paper:

<http://eprints.whiterose.ac.uk/id/eprint/76578>

Published article:

Ledger, ME, Milner, AM, Brown, LE, Edwards, FK, Hudson, LN and Woodward, G (2013) *Extreme Climatic Events Alter Aquatic Food Webs. A Synthesis of Evidence from a Mesocosm Drought Experiment*. *Advances in Ecological Research*, 48. 343 - 395. ISSN 0065-2504

<http://dx.doi.org/10.1016/B978-0-12-417199-2.00006...>

C0030 **Extreme Climatic Events Alter Aquatic Food Webs: A Synthesis of Evidence from a Mesocosm Drought Experiment**

Mark E. Ledger^{*1}, Lee E. Brown[†], François K. Edwards[‡], Lawrence N. Hudson[§], Alexander M. Milner^{*1}, Guy Woodward[§]

^{*}School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, United Kingdom

[†]School of Geography/water@leeds, University of Leeds, Leeds, United Kingdom

[‡]Centre for Ecology and Hydrology, Wallingford, United Kingdom

[§]Division of Ecology and Evolution, Imperial College London, Ascot, United Kingdom

[¶]Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska, USA

¹Corresponding author: e-mail address: m.e.ledger@bham.ac.uk

Au3

Contents

1. Introduction	2
1.1 Extreme events and climate change	2
1.2 Drought in river networks	3
1.3 Food webs in climate change research: From qualitative to quantitative approaches	5
1.4 Mesocosm experiments and climate change research	7
2. Methods	9
2.1 Stream mesocosms	9
2.2 Experimental design and application	13
2.3 Estimation of abundance, biomass and production of trophic elements	14
2.4 Food web construction: Binary webs	15
2.5 Food web construction: Quantitative webs	16
3. Results	18
3.1 Connectance webs	18
3.2 Drought impact on trophic elements	25
3.3 Quantified food webs	33
4. Discussion	42
4.1 Primary producers	42
4.2 Qualitative webs, size structure and species traits	43
4.3 Secondary production and quantified food webs	46
Acknowledgements	48

Appendix. Two-Way ANOVA Testing the Effect of Drought Treatment (Results Below) and Mesocosm Block ($P > 0.05$, Results Not Shown) on Secondary Production of Key Taxa 48

References 49

Abstract

Extreme climatic events are expected to increase in frequency and intensity under climate change. Climate models predict shifts in rainfall patterns that will exacerbate drought, with potentially devastating effects on freshwater ecosystems. Experimental approaches are now advocated to explore the impact of extreme events on natural systems: here, we synthesise research conducted in a stream mesocosms experiment to simulate the effect of prolonged drought on the structure and functioning of complex food webs in a 2-year manipulation of flow regimes. Drought triggered the losses of species and trophic interactions, especially among rare predators, leading to the partial collapse of the food webs. Drying caused marked taxonomic and functional turnover in algal primary producers, from encrusting greens to diatoms, whereas the total number of algal taxa in the food webs remained unchanged. The recurrent drying disturbances generated transient macroinvertebrate communities dominated by relatively few, *r*-selected, species and compensatory dynamics sustained total macroinvertebrate densities. However, the standing biomass and secondary production of the food webs were more than halved by the droughts. Consumer-resource biomass flux was also strongly suppressed by disturbance, yet several network-level properties (such as connectance and interaction diversity) were conserved, driven by consumer-resource fidelity and a reconfiguration of fluxes within the webs, as production shifted down the size spectrum towards the smaller species. Our research demonstrates that flow extremes could have far-reaching consequences for the structure and functioning of complex freshwater communities.

s0005



1. INTRODUCTION

s0010

1.1. Extreme events and climate change

p0385

Much of the effort related to understanding the effects of climate change has focused on incremental, gradual change in “average” conditions: far less consideration has been given to variation and increases in extreme events (Jentsch et al., 2007). Both types of change are, however, predicted under many climatic models, such that we are likely to see more stochastic extreme events overlain on a general warming trend in the future (IPCC, 2007). Unfortunately, extreme events are very difficult to study in natural systems because, by definition, they are very rare, and potentially unpredictable, occurrences. This is further compounded by the likelihood that what are

today's extremes will become more commonplace in the future, with increases in the intensity, frequency and duration of both droughts and floods beyond the normal envelope of contemporary conditions. Indeed, some may be so extreme that there is nothing in the historical record with which to compare them, and in such cases, we are entering uncharted waters that will require experimental manipulations and predictive models that can extrapolate beyond historical and contemporary conditions (Stewart et al., 2013).

p0390 Extreme events can be characterised by their magnitude, timing and abruptness relative to the life cycles of the organisms. In riverine systems, changes in the magnitude and distribution of rainfall may exacerbate the global occurrence of extreme floods and droughts over both time and space. By the middle of the twenty-first century, annual average runoff is projected to increase by 10–40% at higher latitudes, and decrease by 10–30% over mid-latitudes (Kundzewicz et al., 2011; Milly et al., 2005). There is already clear evidence that the frequency and intensity of droughts are increasing (Kauffman and Vonck, 2011), particularly in the last decade (Espinoza et al., 2011). Some scenarios identify critical regions in Europe where the return period of 100-year droughts will decrease to between 10 and 50 years (Lehner et al., 2006). However, cyclical global climate circulation patterns must be overlain on directional shifts in weather; for example, the North Atlantic Oscillation (NAO) can increase the intensity of drought during high positive years (e.g. Vicente-Serrano et al., 2011), with unknown consequences for aquatic ecosystems. Au4 Au5

s0015 1.2. Drought in river networks

p0395 The socio-economic impacts of drought are well quantified in terms of water resources, agriculture and recreation, but less is known about their ecological effects (Lake, 2011). Droughts can occur both seasonally (i.e. short-term within-year water deficiencies) and supra-seasonally (i.e. multi-year water deficiencies), and tend to have the greatest impact where they arise unpredictably (e.g. Boulton, 2003). Drought is usually considered a “ramp” disturbance, increasing steadily in strength and spatial extent as habitat loss proceeds (e.g. Lake, 2008, 2011). Longitudinal connectivity may be lost as flow decreases, with the river bed becoming a mosaic of trickles, remnant pools and damp patches. Further drying may result in loss of free water within the hyporheic zone, thereby disrupting vertical connectivity. In severe droughts, all remnant pools and the hyporheic zone, if

present, may dry up completely. With increased drying, water quality deteriorates; typically, temperature and conductivity increase, dissolved oxygen declines and particulate organic matter accumulates (e.g. Lake, 2003; Ledger et al., 2012).

p0400 Stream biota have a low resistance (i.e. ability to withstand disturbance) but high resilience (i.e. ability to recover to a former state once the disturbance has past; Townsend and Hildrew, 1994) to drought (Bonada et al., 2007; Boulton, 2003; Fritz and Dodds, 2004; Lake, 2003). Resilience is substantially mediated by the use of refuges (Boulton, 2003; Dewson et al., 2007a; Lake, 2008; Poff et al., 2010). Invertebrate refuges consist of remnant pools, moist areas (e.g. under boulders) (Fenoglio et al., 2006), the hyporheic zone (Stubbington, 2012; Wood et al., 2010) or wetted reaches further downstream. Larger taxa are more susceptible to drought, particularly when drying sets in, due to their greater requirement for wetted habitat (Dewson et al., 2007a; Ledger et al., 2011). Non-drifting, low-motility invertebrates, like worms, molluscs and some crustaceans, have to use sedentary refuges (Dewson et al., 2007a), such as wet habitat under stones and woody detritus (Covich et al., 2003; Golladay et al., 2004), whereas other taxa drift to escape falling water levels (Lake, 2011). In running waters with hyporheic zones, invertebrates may bury themselves in the wet sediment (Young et al., 2011), though this may eventually dry out.

p0405 There is thus usually a change in community composition as droughts progress which is often contingent upon the extent and rate habitat modification and/or loss (Everard, 1996). Rapid drying can act as a powerful environmental filter, reducing assemblages to a small subset of tolerant species. Taxa with preferences for low water velocities and fine sediment can dominate during drought periods, whereas rheophylic taxa (i.e. those that prefer to live in fast flowing water) such as filter-feeders are rapidly eliminated as flows decline, or confined to the few remaining riffle and cascading habitats (Dewson et al., 2007a). However, taxa with short life cycles may escape, or even exploit drought periods where their exposure to stressors is limited (Bonada et al., 2006, 2007; Dewson et al., 2007a). Species with a preference for shallow habitats such as riffles risk becoming stranded as water levels fall, especially those with limited motility (Gagnon et al., 2004; Golladay et al., 2004). Elevated nutrient concentrations and sedimentation favour taxa tolerant of low water quality and degraded habitat conditions (Boulton, 2003; Lake, 2011), suggesting that the vast volume of work done to identify functional traits for the biomonitoring of organic pollution could be adapted for assessing drought impacts (Friberg et al., 2011).

p0410 Drought also has the potential to alter ecosystem functioning and the supply of ecological goods and ecosystem services, such as carbon and nutrient cycling and fish production. Organic matter processing by microbes and detritivores may decline during severe drought (Schlief and Mutz, 2011), whereas primary production can at first increase greatly because of elevated temperature and nutrients, but then decline dramatically and even cease as drying intensifies (Ledger and Hildrew, 2001; Ledger et al., 2008; Suren et al., 2003; Wade et al., 2002). Direct impacts on the secondary production of invertebrates and fish depend on drought intensity, with greatest effects occurring where flow cessation occurs (Lake, 2011; Ledger et al., 2011; Matthews and Marsh-Matthews, 2003). Indirect impacts may also occur as a result of changes in primary production, with lower resource availability likely to suppress higher trophic levels (Hannesdóttir et al., 2013).

s0020 **1.3. Food webs in climate change research: From qualitative to quantitative approaches**

p0415 The impacts of climate change remain poorly understood at the higher multispecies levels of organisation (communities, food webs, ecosystems), especially for responses to components other than the direct effects of warming *per se*, such as atmospheric and hydrological changes in the environment (Stewart et al., 2013; Woodward et al., 2010), and to extreme events in particular. The history of food-web research in the context of environmental change, and its progression from qualitative binary approaches to the use of more sophisticated quantitative methods, has been covered elsewhere in recent reviews (e.g. Ings et al., 2009; Thompson et al., 2012). Nevertheless, a brief overview is instructive here, as much of the research conducted in our model mesocosm system mirrors these general trends (Stewart et al., 2013).

p0420 Qualitative binary metrics that were averaged across the whole network (e.g. linkage density, connectance, mean food chain length) were the main focus of the initial food-web work in this system (Brown et al., 2011). These were followed by measures that addressed other aspects of network substructure, such as degree distributions and small-world properties (e.g. Woodward et al., 2012). With respect to networks in general, several studies have suggested that they can be highly resilient to random removal of nodes, but more susceptible to directed removals of highly connected nodes (Callaway et al., 2000; Crucitti et al., 2004). However, it remains far from clear how such disturbances influence ecological network properties, largely because previous studies have worked on composite data from several

individual food webs (e.g. Dunne et al., 2002a; Krause et al., 2003; Townsend et al., 1998) and not produced replicate food webs from the one system but with different levels of disturbance. Furthermore, quantified information on biomass fluxes was generated to gain a more balanced view of the role of particular species and links within the context of the network, rather than weighting each equally (Ledger et al., 2013). At this step, there was a marked increase in the ecologically meaningful information that emerged. The initial finding that drought altered the webs structurally, by simplifying them due to the loss of certain nodes and links, was expanded upon with new insights into their functional dynamism. We observed that whilst drought suppressed secondary production of the system as a whole by about half an order of magnitude (Ledger et al., 2011), there was no shift in the overall distribution of biomass fluxes across the remaining species (Ledger et al., 2013). One obvious question that arises when exploring higher-level responses in multispecies systems is: are there any emergent effects that are not necessarily predicted from simple knowledge of the component species pairs, or is the food web simply the sum of its parts? There are several ways we aimed to address this, including trivariate approaches, where, for instance, the responses of the core community of species that are present under both ambient and perturbed conditions exhibit different allometric scaling relationships (see Woodward et al., 2012).

p0425 Responses among individual taxa within the food web to low (or high) flows are well known for certain species or functional groups, as highlighted by the use of LIFE Scores in biomonitoring (Extence et al., 1999). However, these tend to focus on performance optima within the typical hydrological cycle and conditions, rather than extreme events in a given locale that may exceed the tolerance of the resident flora and fauna. Even less is known about how floods, and especially droughts, affect interactions between species or the structure and dynamics of entire food webs (Ledger et al., 2013; McLaughlin et al., 2013; Stewart et al., 2013). We can, however, now start to make some reasonable predictions based on established theory and the data collected to date, as to how the nodes, links and trophic network as a whole might respond. [Au8]

p0430 Perhaps one surprising consequence of both floods and droughts is an apparent tendency for biotic interactions to intensify, at least in the initial stages, as consumers and resources are concentrated into ever smaller refugia (cf. Lancaster, 1996; Ledger et al., 2013). This should (in theory) lead to increased network connectance and reduced stability of the food web, as predators exert stronger per capita effects on prey concentrating in refugia.

This burst of intense biotic interactions may be short-lived though, as physiological stress starts to increase over time and/or as the refugia continue to shrink, as larger taxa and those high in the food web tend to suffer disproportionately (Raffaelli, 2004): this may be due to reduced oxygen availability and increased metabolic demands (e.g. due to combined effects of warming, increased respiration and decomposition processes during droughts), and/or simply the physical inability to access refugia.

p0435 We should be able to extrapolate from here to predict what might happen in the food web, community or ecosystem as a whole. For example, in the immediate aftermath of an intense perturbation event, we might expect to see a short burst of intense and potentially destabilising predation followed by a more bottom-up dominated period, when *r*-selected species benefit from the subsequent loss of predators and the freeing-up of new habitat and food resources. This situation should eventually shift back to the pre-drought conditions as predator populations recover and top-down effects start to reassert themselves, and the rate at which this state is re-established represents the system's resilience. However, if the perturbations do not cease then we might expect the system to persist in a transient state, akin to arrested succession in highly disturbed, human-modified environments, such as heathland or fen. This is reflective of the intermediate disturbance hypothesis, whereby, at moderate levels of disturbance, top-down effects are offset by bottom-up effects, with neither one being able to completely dominate (e.g. Connell, 1978). Although the IDH was never proposed with an explicitly food web perspective in mind, the parallels are notable. Thus, we might expect droughts to be reflected by pulses of initially high mortality due to both density-dependent (i.e. intense competition or predation) and density-independent (e.g. mortality due to high temperature or desiccation) causes, followed by a relaxation of biotic control as predators run out of food and/or suffer disproportionately from increased metabolic demands and fragmentation of foraging patches. Subsequently, as the waters return (or the flood recedes), there is a dramatic increase in habitat and food availability for the survivors, which is likely to favour more *r*-selected species that are able to colonise and increase population sizes more rapidly than those towards the *K*-selected end of the gradient.

s0025 **1.4. Mesocosm experiments and climate change research**

p0440 Mesocosms are small experimental units that replicate aspects of the natural environment as closely as possible, thus typically allowing more ecological

realism than is the case for microcosms, and more replication/control than is possible in natural systems (e.g. Ledger et al., 2009). Mesocosms have been used widely by ecologists to gain a mechanistic understanding of ecosystem responses to a variety of variables based on the assumption that these systems can replicate the key responses of natural assemblages. Stream mesocosms have been used for investigating the response of biotic communities to flow events (e.g. Taulbee et al., 2009; Villeneuve et al., 2011), biotic interactions (e.g. Wellnitz and Poff, 2012) and effects of sediment and contaminants (e.g. Johnson et al., 2011). Research at the scale of mesocosms provides the ability to make direct comparisons of responses across replicated communities under different flow conditions and across at least one generation of the longest living organism. These intergenerational responses permit insights within and across food webs, where indirect effects may be prevalent (Ledger et al., 2013; Yodzis, 1988).

p0445 Mesocosm experiments are especially important for studying extreme Au7 events, as surveys will be unable to replicate them: even those that are still within the current historical envelope (e.g. 1-in-10-year or 1-in-100-year floods) are rarely captured by survey data, and if they are it is often after the event, with little or no meaningful prior data (but see McLaughlin et al., 2013). There are clear parallels with the challenges faced by ecologists studying invasive species and extreme events: in both cases, it is very difficult to predict when and where they will arrive, and the changes they bring may result in novel communities or ecosystems, whose characteristics are unknown. Correlational survey data are rare because of this inherent unpredictability of extreme events. Conversely, because we need to understand how complex multispecies systems respond across different organisational levels, short-term laboratory experiments have limited realism. Field-based mesocosm experiments therefore represent an optimal approach to study this aspect of climate change and ultimately to parameterise predictive models. Too frequently, there are no adequate controls or pre-disturbance data for comparison in survey data. To understand fully the ecosystem responses to extreme events in general, controlled manipulations are needed (Jentsch et al., 2007), including mesocosm experiments to explore community and functional responses to climate change (Benton et al., 2007). Mesocosms have some key advantages over laboratory-based microcosm studies, despite the latter typically providing more extensive replication and control. Although rare, studies of food webs using an experimental approach are vital for untangling causative relationships between changing environmental conditions and food-web structure and dynamics (Ledger et al., 2013).

p0450 The limitations and potential shortcomings of the mesocosm approach that need to be borne in mind are mostly related to the logistical constraints that mean they are restricted to limited spatiotemporal scales and levels of biological complexity (Harris et al., 2007; Ledger et al., 2009; Stewart et al., 2013). Although the ability to replicate treatments is a clear advantage of mesocosms, their ecological realism to whole freshwater systems has also been questioned (Petersen and Englund, 1995; Schindler, 1998). Ledger et al. (2009) assessed the water quality and community composition of four replicate stream mesocosms, reporting that acceptable levels of realism may be attained in large outdoor systems close to a source of colonists. Subsequent studies have also shown that these outdoor mesocosms can contain complex food webs with structural properties consistent with natural systems (Brown et al., 2011; Ledger et al., 2011).

p0455 In this chapter, we synthesise the results of an experiment conducted to test the effect of extreme drought on riverine communities. We used a series of large stream mesocosms to manipulate flows, exposing biota to drying disturbances repeatedly over 2 years. We tested two hypotheses: (1) that drought disturbance would generate turnover in community structure and biomass production, with small *r*-selected species replacing larger, longer-lived taxa with more *K*-selected traits and (2) that dietary generalists would benefit over specialists, modifying network properties and biomass flux.

s0030

2. METHODS

s0035

2.1. Stream mesocosms

p0460 Research was conducted over 24 months (March 2000–February 2002) in outdoor stream mesocosms fed by a chalk stream at the Freshwater Biological Association River Laboratory, UK (50°40'48"N, 2°11'06"W; Fig. 1). Each mesocosm was a linear channel (width 0.33 m, length 12 m, depth 0.30 m) receiving water and suspended particles (including algae, detritus and invertebrates) through a 110-mm diameter pipe (6 m length) from the feeder stream. Two of the mesocosms in each block were used in this study, with data from the third mesocosm reported elsewhere (Ledger et al., 2008, 2012). Water flow was controlled by a valve at the closed upper end of each channel. Water flowed freely from mesocosms under gravity, via an open outlet positioned 10 cm above a drainage channel, preventing any potential transfer of biota among the mesocosms. Each channel was filled to 20-cm depth with clean substrate dominated by chert gravel (volumetric proportions

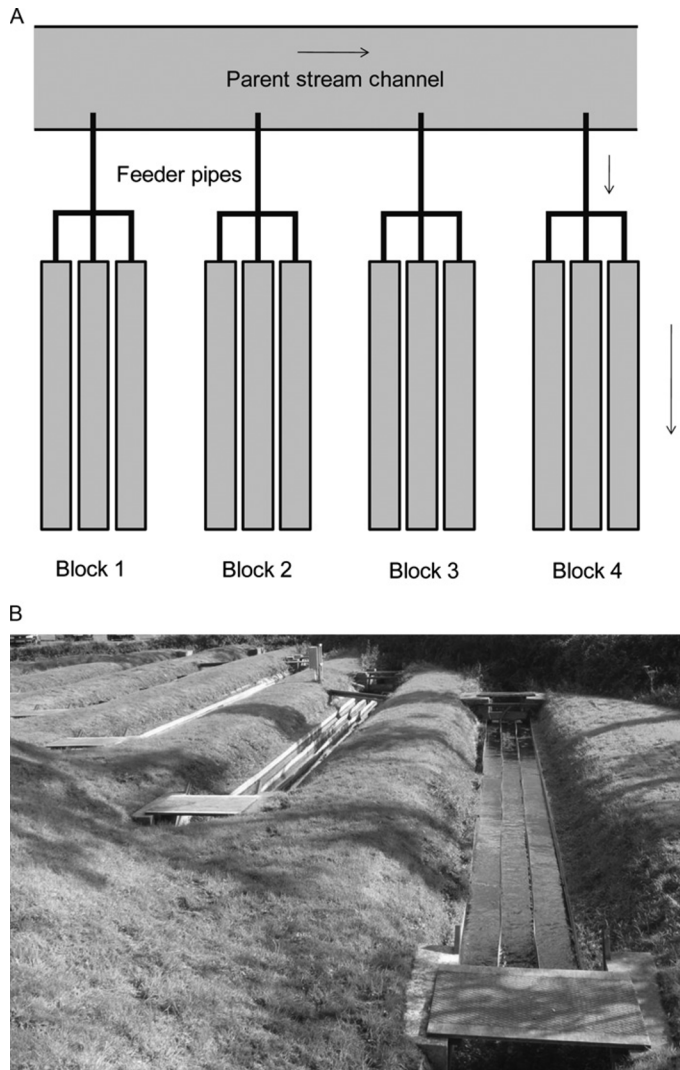


Figure 1 Schematic representation (A) and photographic image (B) of the stream mesocosm facility at the Freshwater Biological Association River Laboratory, Dorset, UK. Four blocks of three stream mesocosms (each channel 12 m length \times 0.3 m width) were fed water through pipes (6 m length) from the parent stream. Water flow (direction indicated by arrows) into each mesocosm was controlled by a valve. Each block contained a control channel and a disturbed channel, with the third channel in each block used in allied research not reported here. (For colour version of this figure, the reader is referred to the online version of this chapter.)

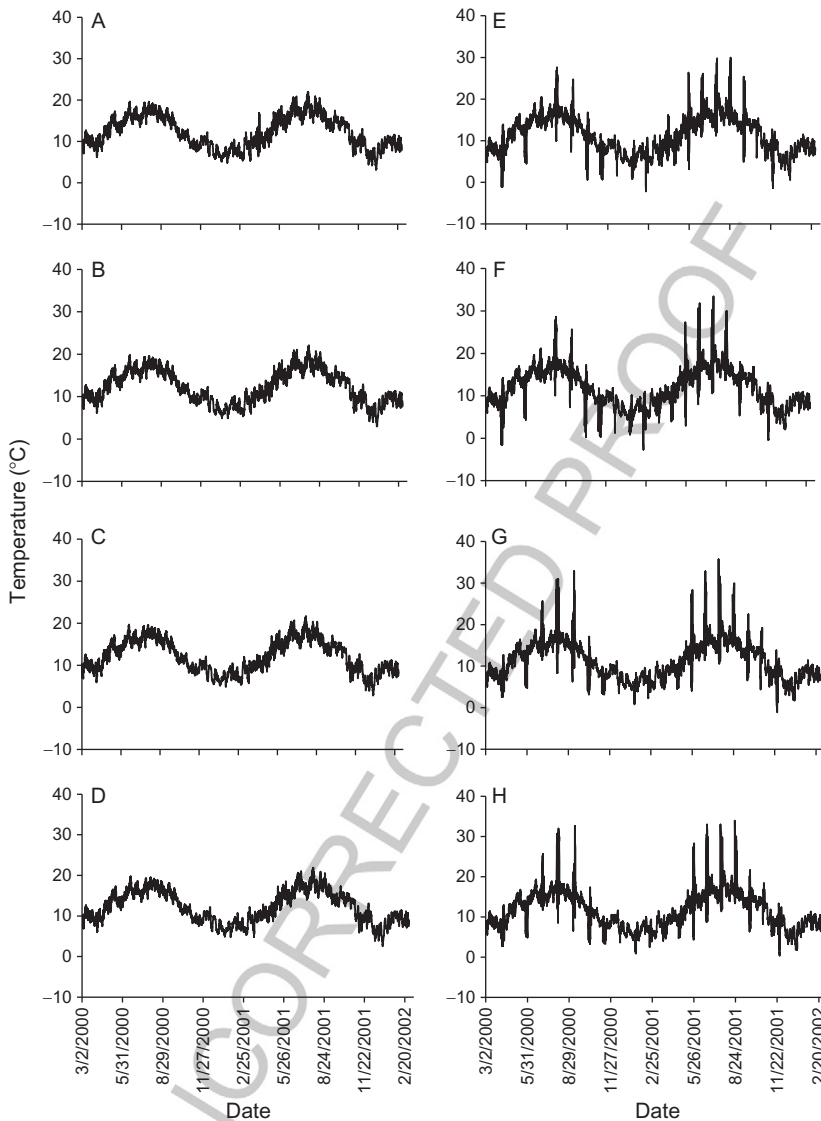
of particle sizes, 85% 11–25 mm, 5% 2–11 mm, 5% 0.35–2 mm, 5% < 0.35 mm), matching the source stream (Harris et al., 2007). Whilst the mesocosms did not have extensive hyporheic zones, conditions were consistent with that observed in many headwater streams, where the majority of macrofauna are confined to surface sediments and shallow oxygenated interstices (Trimmer et al., 2010), and substrata provided physical refugia for suitably adapted species during drying disturbances (Harris, 2006).

p0465 Physicochemical conditions were highly congruent among the mesocosms (Table 1; Harris et al., 2007). During the main study period, water temperature (mean 12.2 °C) varied seasonally, with summer maxima

t0005 **Table 1** Physicochemistry (outside dewatering periods) demonstrating mesocosm replicability among controls (C1–C4) and drought-impacted (D1–D4) channels

	Control				Drought			
	C1	C2	C3	C4	D1	D2	D3	D4
Conductivity ($\mu\text{S cm}^{-1}$)								
Mean	458.9	457.6	460.2	462.1	459.0	460.4	460.6	461.0
Range	179.0	181.0	176.0	175.0	177.0	179.0	177.0	179.0
Discharge (L s^{-1})								
Mean	4.0	4.8	4.3	4.9	4.9	4.3	4.8	4.3
Range	4.3	6.4	5.9	5.5	8.5	7.0	5.9	4.7
pH								
Mean	8.1	8.1	8.1	8.1	8.1	8.1	8.1	8.1
Range	1.0	1.0	1.0	1.0	1.0	1.0	1.1	1.0
Water temperature ($^{\circ}\text{C}$)								
Mean	13.2	13.2	13.2	13.3	13.2	13.2	13.2	13.2
Range	12.0	12.0	12.1	12.0	12.0	12.0	12.0	12.1
Nitrate (mg L^{-1})								
Endpoint	6.8	6.9	6.9	7.0	6.9	7.0	6.9	7.0
SRP ($\mu\text{g L}^{-1}$)								
Endpoint	59.2	54.3	55.5	59.2	58.0	54.8	56.0	54.1

Determinants were measured approximately monthly, excepting nitrate and soluble reactive phosphorus (SRP) which were both sampled once that the end of the experiment.



f0010 **Figure 2** Temperature profiles of mesocosm replicates subject to continuous (A–D) and intermittent (E–H) flow.

(18.7 °C in June 2000) and winter minima (6.0 °C in December 2001) (Fig. 2). Inflowing water was nutrient rich (mean PO_4 : 56.4 $\mu\text{g L}^{-1}$; NO_3 : 5.62 mg L^{-1} from March 2000 to February 2002) with alkaline pH (mean 8.1) and high conductivity (mean 460 $\mu\text{S cm}^{-1}$) (Harris et al.,

2007), consistent with water quality in local chalk rivers (Bowes et al., 2005; Casey, 1975; Ledger et al., 2009). Outside the experimentally simulated dewatering periods, discharge in the mesocosms was stable (cross-treatment mean 4.5 L s^{-1}), with mean water velocity (at two-thirds depth) and depth over the gravel of 0.20 m s^{-1} and 81 mm, respectively, and water residence times were short (mean 66 s) (Harris, 2006). Biota (algae and macroinvertebrates) in the mesocosms were taxonomically diverse and similar in composition to nearby streams (Ledger et al., 2009).

s0040 **2.2. Experimental design and application**

p0470 Unfiltered water from the source stream was diverted into the mesocosms to initiate colonisation and community development (February–March 2000). Macroinvertebrate colonisation was either passive, in drift from the source stream, and/or by adult oviposition (Ledger et al., 2009). Following this colonisation period, an intermittent flow regime of substratum drying and wetting (repeating cycles of mean 6 dry days [i.e. flow cessation] followed by mean 27 wet days) was applied to one mesocosm in each block, mimicking supra-seasonal drought that causes repeated patchy dewatering of river bed sediments over prolonged periods (see Ledger et al., 2013). These events are expected to become more frequent globally under most of the Intergovernmental Panel on Climate Change (IPCC) future scenarios (Beniston et al., 2007; IPCC, 2007). Drought disturbances were applied by slowly closing inflow ducts and allowing water to drain from the channels, causing patchy drying over several days. During dewatering, surface flows ceased and drying of exposed substrata occurred in patches, whereas the interstices beneath the bed surface remained wet, and small pools persisted at intervals along the length of the dewatered channels, providing refugia for suitably adapted species (Harris, 2006). Surfaces of exposed substrata dried at natural ambient rates, such that the stress experienced by organisms stranded in the mesocosms was consistent with those in adjacent drying stream reaches (Harris, 2006; Ledger et al., 2008). In the control mesocosms, flows were continuous throughout the experiment. The hydrologic and thermal conditions were highly replicable among the mesocosms, with drought treatments consisting of greater extremes of flow variation and temperature than controls (Table 2). A blocked experimental design (Zar, 1999) was used in which each treatment was replicated four times, with each block of channels containing a drought treatment and a control (4 blocks \times 2 treatments = 8 channels in total).

10010 **Table 2** Descriptors of flow and thermal regimes in undisturbed control (C1–C4) and drought-disturbed (D1–D4) stream mesocosms

	Control				Drought			
	C1	C2	C3	C4	D1	D2	D3	D4
Flow ($L s^{-1}$)								
Mean	4.0	4.8	4.4	4.9	2.4	2.1	2.4	2.1
Maximum	6.0	8.1	7.5	7.2	6.3	6.0	6.7	4.7
Minimum	1.7	1.7	1.7	1.7	0	0	0	0
Range	4.3	6.4	5.9	5.5	6.3	6.0	6.7	4.7
Temperature ($^{\circ}C$)								
Mean	12.1	12.2	12.0	12.1	11.0	11.6	11.0	11.3
Maximum	21.9	22.1	21.7	21.9	30.0	33.5	35.7	34.0
Minimum	3.1	3.0	2.8	2.6	-2.2	-2.7	-1.1	0.4
Range	18.8	19.1	18.9	19.3	32.2	36.2	36.8	33.6

Temperature profiles in drought-disturbed channels include heating/cooling at the substratum surface during dewatering episodes.

s0045 **2.3. Estimation of abundance, biomass and production of trophic elements**

p0475 Estimates of invertebrate abundance and biomass were made from samples (Surber sampler $0.025 m^2$, 300- μm mesh, $n=3$ per channel) collected monthly from each mesocosm between March 2000 and February 2002, immediately (1 h) before disturbances were applied to the drought treatment. On each occasion, three Surber samples ($0.0225 m^2$, 300- μm mesh aperture) were taken from each replicate mesocosm, to provide sufficiently precise estimates whilst limiting the extent of destructive sampling (Harris, 2006). Macroinvertebrates were sorted from debris, identified to the lowest practicable taxonomic unit (usually species) and counted. Data from each of the three samples were pooled to provide a single estimate of biomass ($mg m^{-2}$) for each mesocosm on each sampling occasion (i.e. channels, not sample units, were replicates). For secondary production ($mg m^{-2} year^{-1}$) estimation, macroinvertebrate body lengths (all individuals sampled, $n=63,092$) were measured to the nearest 0.1 mm using an ocular graticule and dissecting microscope (Burrell and Ledger, 2003; Ledger and Winterbourn, 2000). Individual biomass (mg dry weight) was calculated for

all invertebrate specimens using published length–mass regressions (see Edwards et al., 2009).

p0480 Secondary production ($\text{mg m}^{-2} \text{year}^{-1}$) of all invertebrates was calculated using the size–frequency method (Hynes and Coleman, 1968), excepting rare taxa $<1\%$ total numbers where production was estimated by multiplying mean annual biomass by an annual P/B value of the most closely related taxon (see Ledger et al., 2011, 2013). Production was estimated for each replicate control and treatment channel. Production for the first year and the second year of the experiment was averaged and incorporated into biomass flux estimates as mean annual secondary production. At the end of the experiment, we collected the entire macroinvertebrate assemblage in each mesocosm, using samples to construct food webs by direct observation of feeding links and determined biomass of basal resources (detritus and algae) as the ash-free dry mass of material collected from the surfaces of mineral substrata ($n=8$) in each mesocosm (see Ledger et al., 2008).

s0050 **2.4. Food web construction: Binary webs**

p0485 Binary food webs were constructed based on the presence/absence of resources in the diet of consumers sampled at the end of the experiment. Feeding linkages were determined directly by gut contents analysis of macroinvertebrates. In total, 3643 dissected guts were examined, with consumed items identified to the lowest practicable taxonomic unit. The guts of invertebrates were dissected at $\times 20$ magnification, and the gut contents were mounted on glass slides with an aqueous agent (Aquamount[®]). To determine the percentage contribution of food particle types in the diet, five fields of view were examined on each slide at $\times 200$ magnification using an ocular grid (1 cm^2 divided into 100 cells of 1 mm^2). Gut contents were identified as algae, fungi, invertebrates, large plant detritus and amorphous detritus (Ledger et al., 2002). Invertebrate, diatom and other algal components of diet were identified to genus or species, whenever possible. Diet could not be determined for suctorial predators using our methods, and they were excluded from our webs. Several qualitative (binary) food web metrics were derived from matrices of drought and control stream food webs. Metrics included linkage density (L/S), where L is number of consumer–resource links and S is the number of species in the web, directed connectance (L/S^2), generality ($L/S_{\text{consumers}}$) and vulnerability ($L/S_{\text{resources}}$) (Bersier et al., 2002). Mean and maximum prey-averaged trophic height was determined for each web, following Hudson et al. (2013). Characteristic path

lengths (d), the shortest number of links between all pairs of species, were computed using the social network analysis package *Pajek* v1.2 (Brown et al., 2011). Cumulative degree distributions were calculated as the proportion of taxa $P(k)$ having k or more undirected trophic links (both predator and prey links) (Dunne et al., 2002b). Yield–effort curves (number of food types vs. number of guts examined) were drawn for each taxon to determine when a sufficient number of individuals had been examined to describe its diet accurately.

s0055 2.5. Food web construction: Quantitative webs

p0490 The food web of each mesocosm community was quantified, with links expressed as flows of biomass from resources to consumers (see Ledger et al., 2013). The trophic basis of production method (Benke, 2012; Benke & Wallace, 1997) was used to quantify directly observed feeding links, with biomass flux (F_{ij} , $\text{mg m}^{-2} \text{year}^{-1}$) from resource i to consumer j estimated as follows.

p0495 Determine the proportion of production derived from food type i (B_i):

$$B_i = (G_i \times \text{AE}_i) / \sum_{G_i=1, \dots, n} \bullet \quad \boxed{\text{Au8}}$$

p0500 Calculate the flow of biomass via food type i to consumer j (F_{ij}):

$$F_{ij} = (B_i \times P_j) / (\text{AE}_i \times \text{NPE})$$

where G_i is the percentage cover of food type i , AE_i is the assimilation efficiency of food type i , P_j is the secondary production of consumer j and NPE is assumed net production efficiency. Values for AE and NPE were derived from Hall et al. (2000). To calculate G_i , the relative amount of each food type in gut contents mounted on slides was derived by counting the squares on the ocular grid dominated by that food type in each microscope field of view. The percentage of each food type for an individual was then calculated from five fields of view and expressed as a percentage of the total food particle area (Ledger et al., 2002).

p0505 Quantitative food webs were compared using metrics derived from information theory (Bersier et al., 2002; Ledger et al., 2013; Tylianakis et al., 2007). For each web, we determined the quantified, weighted measures of linkage density (LD_q), interaction diversity (ID_q), interaction evenness (IE_q), generality (G_q , mean number of resources per consumer) and vulnerability (V_q , mean number of consumers per resource) (see Bersier et al., 2002). The metrics incorporate the inflow and outflow of biomass

to each species in the food web, and the diversity of biomass flows derived from the resource (H_N , the diversity of inflows) and going to the consumers (H_P) of each taxon k was calculated as:

$$H_{N,k} = - \sum_{i=1}^s \frac{b_{ik}}{b_{\bullet k}} \log_2 \frac{b_{ik}}{b_{\bullet k}}$$

$$H_{P,k} = - \sum_{j=1}^s \frac{b_{kj}}{b_{k\bullet}} \log_2 \frac{b_{kj}}{b_{k\bullet}}$$

p0510 In each food web matrix, b_{ik} and b_{kj} represent the amount of inflowing biomass from taxon i to taxon k , and outflowing biomass from taxon k to taxon j per unit surface area and time, respectively. Column sum $b_{\bullet k}$ and row sum $b_{k\bullet}$ are the sum total biomass flux from resources, and to consumers, of taxon k , respectively. The reciprocals of $H_{N,k}$ and $H_{P,k}$ are:

$$n_{N,k} = \begin{cases} 2^{H_{N,k}} & \text{if } b_{\bullet k} = 0 \\ 0 & \text{if } b_{\bullet k} = 0 \end{cases}$$

$$n_{P,k} = \begin{cases} 2^{H_{P,k}} & \text{if } b_{k\bullet} = 0 \\ 0 & \text{if } b_{k\bullet} = 0 \end{cases}$$

p0515 Weighted quantitative linkage density (LD_q) was calculated as the average of the equivalent numbers of resources ($n_{N,k}$) and consumers ($n_{P,k}$), weighted by their inflows and outflows:

$$LD_q = \frac{1}{2} \left(\sum_{k=1}^s \frac{b_{k\bullet}}{b_{\bullet\bullet}} n_{P,k} + \sum_{k=1}^s \frac{b_{\bullet k}}{b_{\bullet\bullet}} n_{N,k} \right)$$

where $b_{\bullet\bullet}$ is the total biomass flux in the web matrix. Quantified connectance was calculated as LD_q/S . Weighted generality (G_q) and vulnerability (V_q) were calculated as:

$$G_q = \sum_{k=1}^s \frac{b_{\bullet k}}{b_{\bullet\bullet}} n_{N,k}$$

$$V_q = \sum_{k=1}^s \frac{b_{k\bullet}}{b_{\bullet\bullet}} n_{P,k}$$

p0520 The diversity and evenness of quantified links in each food web was calculated using the Shannon index of entropy:

$$ID_q = \sum p_i \log_2(p_i)$$
$$IE_q = \frac{\sum p_i \log_2(p_i)}{\log_2 N}$$

where p_i is the proportional contribution of interaction i to the total number of interactions in the web (N).

s0060

3. RESULTS

s0065

3.1. Connectance webs

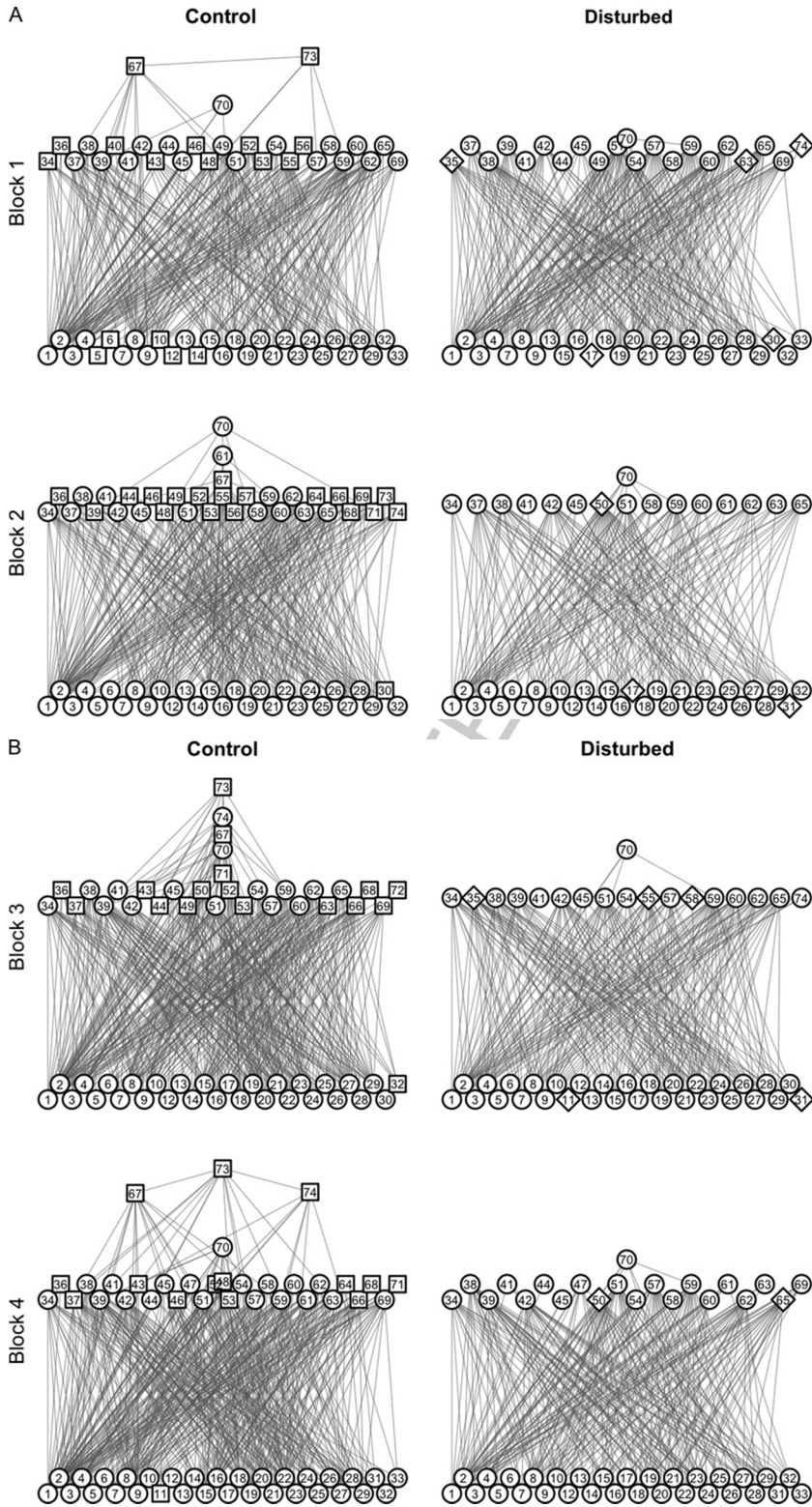
p0525

The mesocosm binary webs collectively encompassed 783 pairwise trophic interactions among 74 trophic elements (Fig. 3). Basal resources (trophic height = 1) consisted of detritus (leaf litter, amorphous detritus), fungi and benthic algae (green algae, diatoms) (Table 3). Twenty-eight taxa of benthic algae occurred in the webs and they formed two macroscopically distinct patch types with contrasting taxonomic composition (algal crusts and mats; Fig. 4). Basal resources (Table 3) supported a diverse array of macroinvertebrate primary consumers (trophic height = 2) and predators (trophic height > 2; Table 4). All of the predators were macroinvertebrates, namely leeches (mainly *Erpobdella octoculata*), larval caddis (*Polycentropus flavomaculatus*), alderflies (*Sialis lutaria*) and tanypod midges (Table 4). Macroinvertebrate consumers were trophic generalists that tended to be larger than their resources, generating upper triangularity in the web matrices (Figs. 5 and 6).

p0530

Drought significantly reduced web size (by 21%, from mean $61.0 \pm SE$ 1.6 to 48.0 ± 1.5 , ANOVA, $F_{1,3} = 28.5$, $P < 0.05$) and the number of feeding links (by 34%, from 376.3 ± 36.2 to 248.0 ± 23.1 , ANOVA, $F_{1,3} = 21.77$, $P = 0.019$; Fig. 7). The taxon richness of basal resources in the web was maintained (ANOVA, $F_{1,3} = 3.50$, $P = 0.165$), whereas 37% of invertebrate primary consumer taxa were eliminated by drought (ANOVA, $F_{1,3} = 29.44$, $P = 0.012$), although local extinction was most severe among the predators (78% loss of taxa, ANOVA, $F_{1,3} = 46.09$, $P = 0.007$; Fig. 7). For macroinvertebrate consumers, local extinctions were associated strongly with rarity (logistic regression, $\chi^2 = 9.398$, $P = 0.002$). Drought eroded food webs from the top-down, reducing proportions of predators and primary consumers relative to basal species. The loss of predators reduced mean (from 1.54 ± 0.004 to 1.39 ± 0.02 , ANOVA, $F_{1,3} = 31.58$, $P = 0.011$) and maximum (from 2.53 ± 0.05 to 2.16 ± 0.04 ,

B978-0-12-417199-2.00006-9, 00006



(Continued)

AECR, 978-0-12-417199-2

f0015 **Figure 3** —cont'd (A) Food webs from the manipulative field experiment (blocks 1 and 2, see (B) for blocks 3 and 4), in controls (permanent flow) and drought-disturbed (intermittent drying) channels. The webs are ordered vertically by trophic level, from basal resources to apex predators. Open circles denote species that were present in both webs, open diamonds denote species in the drought treatment but not in the control and open triangles denote species that were in the control but were lost from the webs exposed to drought. Numbers correspond to species identifiers (see Tables 3 and 4 for codes and taxonomic identities). (B) Food webs from the manipulative field experiment (blocks 3 and 4, see (A) for blocks 1 and 2), in controls (permanent flow) and drought-disturbed (intermittent drying) channels. The webs are ordered vertically by trophic level, from basal resources to apex predators. Open circles denote species that were present in both webs, open diamonds denote species in the drought treatment but not in the control and open triangles denote species that were in the control but were lost from the webs exposed to drought. Numbers correspond to species identifiers (see Tables 3 and 4 for codes and taxonomic identities).

Au1

f0015 **Table 3** List of basal resources in stream channel food webs

Basal resources: detritus and fungi

Amorphous detritus (FPOM) [1]
Fungal mycelia [4]
Fungal spores [3]
Plant fragments (CPOM) [2]

Basal resources: primary producers

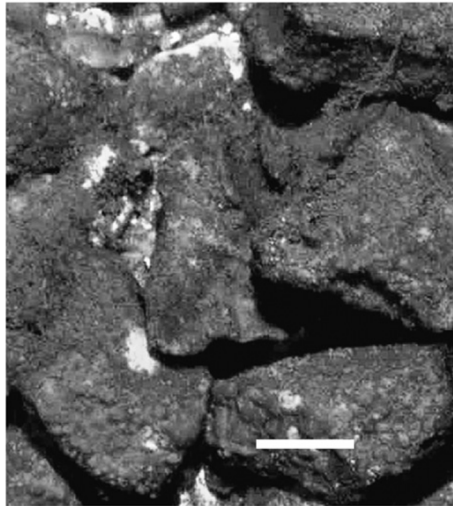
Algal cysts [7]
Amphora ovalis (Kützing) Kützing [8]
Amphora pediculus (Kützing) Grunow in Schmidt [9]
Chroococcus minor (Kützing) Nägeli [10]
Cocconeis placentula Ehrenberg [13]
Cymatopleura solea (Brébisson & Godey) W. Smith [14]
Cymbella lanceolata (Ehrenberg) Kirchner [11]
Diatoma vulgare Bory [15]
Encyonema minutum (Hilse in Rabenhorst) Mann [12]
Fragilaria vaucheriae (Kützing) Petersen [18]
Gomphonema olivaceum (Hornemann) Brébisson [20]
Gongrosira incrustans Reinsch [19]
Gyrosigma sp. [21]
Melosira varians Agardh [22]
Navicula gregaria Donkin [24]
Navicula lanceolata (Agardh) Ehrenberg [25]
Navicula menisculus Schumann [26]
Navicula tripunctata (O.F. Müller) Bory [28]
Nitzschia dissipata (Kützing) Grunow [23]
Nitzschia perminuta (Grunow) M. Peragallo [27]
Planothidium lanceolatum (Bréb. ex Kützing) Round & Bukhtiyarova [6]
Psammothidium lauenburgianum (Hustedt) Bukhtiyarova & Round [5]
Rhoicosphenia abbreviate (Agardh) Lange-Bertalot [29]
Spirulina sp. [31]

Table 3 List of basal resources in stream channel food webs—cont'd

<i>Staurosira elliptica</i> (Schumann) Williams & Round [16]
<i>Staurosirella leptostauron</i> (Ehrenberg) Williams & Round [17]
<i>Surirella brebissonii</i> Krammer & Lange-Bertalot [32]
<i>Surirella minuta</i> Brébisson in Kützing [30]
<i>Synedra ulna</i> (Nitzsch) Ehrenberg [33]

Numerical node identifiers (Fig. 3) are given in brackets.

A Algal crust



B Algal mat

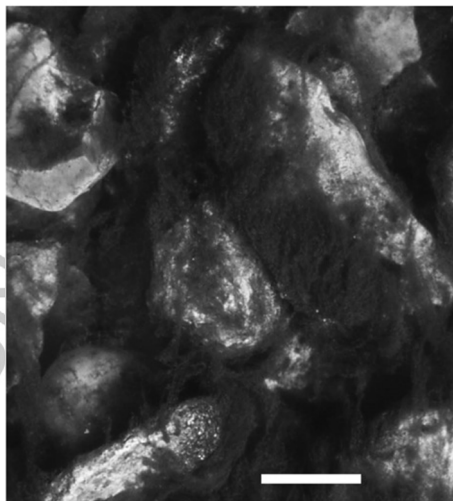


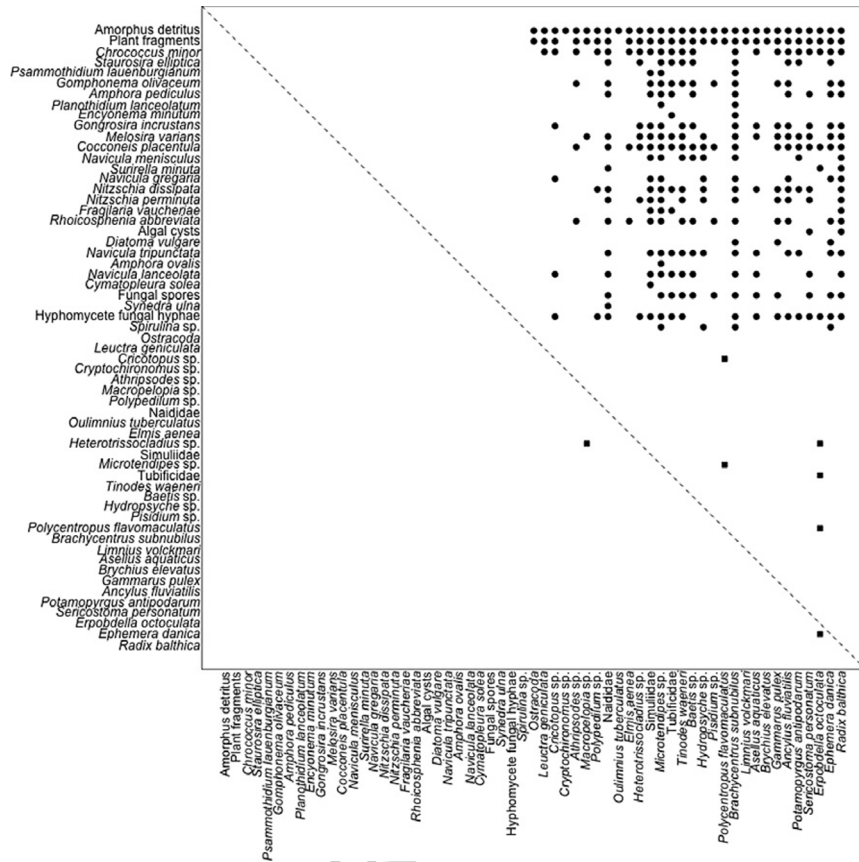
Figure 4 Physiognomy of algal patch types in stream mesocosms. Diatom crusts (A) were mainly *Gongrosira incrustans* and mats (B) were dominated by *Melosira varians* and bar = 10 mm. (For colour version of this figure, the reader is referred to the online version of this chapter.)

10020 **Table 4** List of consumers in stream channel food webs

Consumers: macroinvertebrates

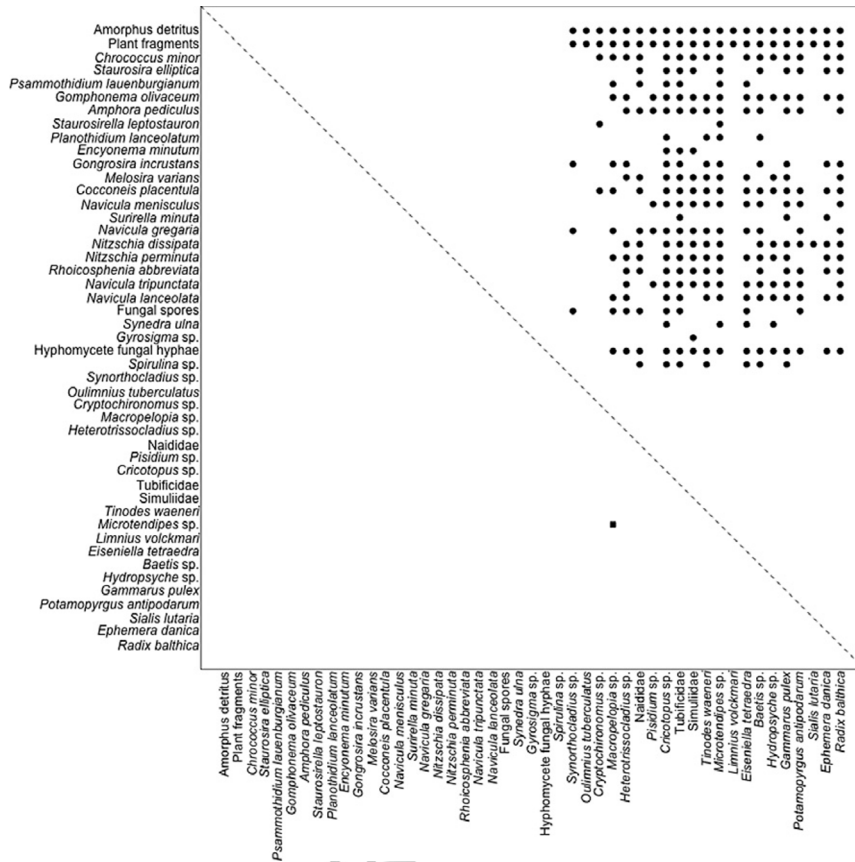
- Ancylus fluviatilis* (Müller) [52]
Asellus aquaticus (L.) [34]
Athripsodes spp. [53]
Baetidae [54]
Brachycentrus subnubilus Curtis [55]
Brychius elevatus (Panzer) [56]
Cricotopus sp. [57]
Cryptochironomus sp. [58]
Eiseniella tetraedra [35]
Elmis aenea (Müller) [36]
Ephemera danica Müller [37]
Erpobdella octoculata (L.) [67]
Gammarus pulex (L.) [38]
Halipilus lineatocollis (Marshall) [68]
Heterotrissocladius sp. [39]
Hydropsyche spp. [69]
Leuctra geniculata [40]
Limnius volckmari (Panzer) [41]
Macropelopia sp. [70]
Microtendipes sp. [60]
Naididae [42]
Ostracoda [43]
Oulimnius tuberculatus (Müller) [44]
Pentaneura sp. [71]
Pisidium sp. [45]
Platambus maculatus (L.) [72]
Polycentropus flavomaculatus (Pictet) [73]
Polypedilum sp. [46]
Potamopyrgus antipodarum (J.E. Gray) [61]
Procladius sp. [62]
Prodiamesa olivacea [47]
Radix balthica (L.) [59]
Sericostoma personatum (Spence) [48]
Sialis lutaria (L.) [74]
Simuliidae [49]
Synorthocladius sp. [63]
Theodoxus fluviatilis (L.) [64]
Tinodes waeneri (L.) [65]
Tipula montium Egger [50]
Tubificidae [51]
Valvata piscinalis (Müller) [66]

Numerical node identifiers (Fig. 3) are given in brackets.



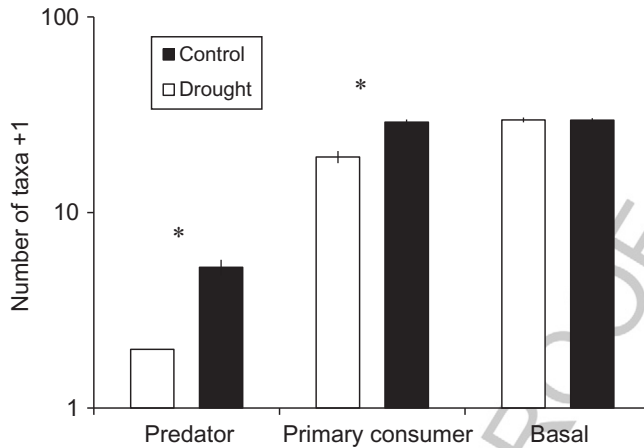
0025 **Figure 5** Food webs in undisturbed controls (replicate C1) incorporating abundance and body size data. The central matrix indicates an observed feeding interaction between a consumer (column) and a resource (row) with a black dot, and thus, each column reflects the diet of a consumer taxon. Consumer columns and resource rows are ordered by body size, with the smallest in the top left and the largest in the bottom right. Thus, feeding interactions in which a consumer is larger than its prey occur in the triangle above the diagonal dashed line. Detrital resources (i.e. amorphous detritus and plant fragments), which lack body size, were positioned arbitrarily in the two uppermost rows of the diet matrix.

ANOVA, $F_{1,3} = 58.33$, $P = 0.005$) prey-averaged trophic level. However, other properties of the binary webs were unaffected by drought, specifically linkage density, directed connectance, trophic generality (the number of resources per consumer) and vulnerability (the number of consumers per resource) (Table 5). Path length distances across the food webs indicated that the majority of taxa pairs were separated by fewer than two feeding links



0030 **Figure 6** Food webs in drought-disturbed mesocosms (replicate D1) incorporating abundance and body size data. The central matrix indicates an observed feeding interaction between a consumer (column) and a resource (row) with a black dot, and thus, each column reflects the diet of a consumer taxon. Consumer columns and resource rows are ordered by body size, with the smallest in the top left and the largest in the bottom right. Thus, feeding interactions in which a consumer is larger than its prey occur in the triangle above the diagonal dashed line. Detrital resources (i.e. amorphous detritus and plant fragments), which lack body size, were positioned arbitrarily in the two uppermost rows of the diet matrix.

(Fig. 8A). On average, 19% of taxa pairs interacted directly (i.e. $d=1$), 71% of taxa pairs were within two feeding links and 99% of taxa pairs were within three links of one another, irrespective of disturbance treatment. Cumulative degree distributions were well described by exponential decay functions ($R^2 > 0.98$) in control and disturbed webs (Fig. 8B).



fo035 **Figure 7** Mean (± 1 SE) taxon richness of basal resources, primary consumers and predators in drought and control food webs. Trophic group, drought treatment and their interaction significantly affect taxon richness (ANOVA, $n = 24$, $P < 0.0001$ in all cases). Asterisks above individual trophic groups denote significant differences between treatments (ANOVA, $n = 8$, $P < 0.05$).

t0025 **Table 5** Qualitative (binary) food web metrics for drought and control stream food webs

Metric	Control		Drought		ANOVA	
	Mean	SE	Mean	SE	$F_{1,3}$	P
Linkage density	5.96	0.53	4.94	0.38	2.20	0.212
Directed connectance	0.09	0.01	0.10	0.01	0.17	0.706
Generality	11.68	1.11	12.84	0.55	1.42	0.390
Vulnerability	6.63	0.63	5.26	0.40	3.37	0.164

Metrics were linkage density (L/S) where L is the number of consumer-resource links and S is the number of species in the web, directed connectance (L/S^2), generality ($L/S_{consumers}$) and vulnerability ($L/S_{resources}$). ANOVA tested for the effect of drought and block ($P > 0.05$, not shown).

s0070 3.2. Drought impact on trophic elements

p0535 Among the basal resources, particulate detritus was especially abundant, forming dense patches on the surface of stones, but leaf litter was less abundant (Harris, 2006). Benthic algae coated the upper surface of stones and in controls, these consisted of encrusting algae, mainly *Gongrosira incrustans* (Chlorophyceae) and epiphytic diatoms (*Amphora pediculus*, *Gomphonema*

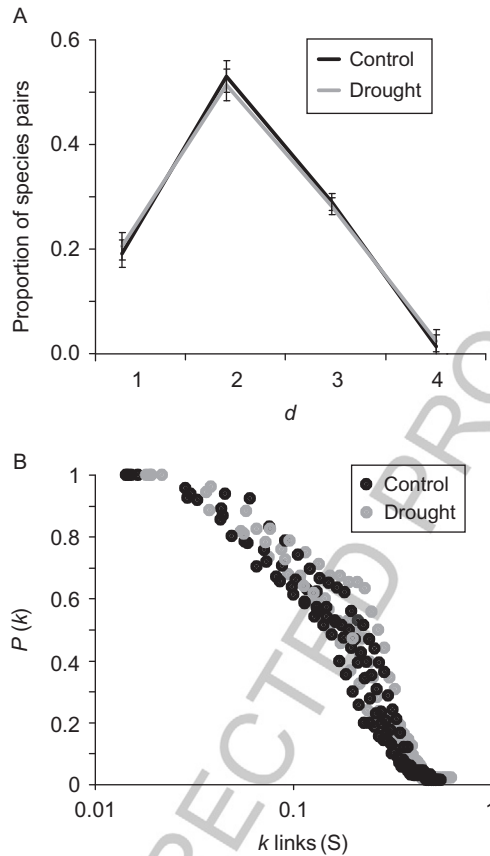


Figure 8 (A) Characteristic path lengths (d) and (B) degree distributions of control and drought-impacted food webs.

olivaceum and *Rhicosphenia abbreviata*) (Fig. 4, Table 6). However, dewatering episodes in the drought treatment markedly reduced algal densities (by 72%; ANOVA, $F_{1,3}=26.97$, $P=0.014$) and skewed the taxonomic composition of the assemblage (Table 6). Substratum drying damaged algal crusts (80% reduction; ANOVA, $F_{1,3}=22.96$, $P=0.017$), whereas mat-forming diatoms were more resilient to the disturbances (2% reduction; ANOVA, $F_{1,3}=0.01$, $P=0.870$; Table 6). Algal mats were a speciose group of unicellular and chain-forming diatoms, mainly *Melosira varians*, *Planothidium lanceolatum*, *Navicula menisculus*, *Navicula lanceolata* and *Nitzschia perminuta*, which formed loose, filamentous patches on stones (Fig. 4, Table 6). Nevertheless, the total biomass (mg AFDM cm^{-2}) of basal resources on stones remained relatively unchanged in the face of disturbance

t0030 **Table 6** Mean densities (10^3 cells cm^{-2}) of benthic algae in mesocosm food webs

	Control		Drought	
	Mean	SE	Mean	SE
Crust flora				
<i>Gongrosira incrustans</i>	7610.8	1258.1	1364.4	112.4
<i>Amphora pediculus</i>	469	45	213	33
<i>Gomphonema olivaceum</i>	58.2	4.3	43.3	13.6
<i>Navicula tripunctata</i>	13.9	2.4	12.0	33.6
<i>Rhoicosphenia abbreviata</i>	32.0	1.5	12.4	4.1
Total	8183.7	1310.9	1645.2	196.8
Mat flora				
<i>Amphora ovalis</i>	5.9	1.4	2.7	0.7
<i>Cocconeis placentula</i>	65.3	9.1	44.3	16.3
<i>Cymatopleura solea</i>	0.9	0.4	1.1	0.2
<i>Cymbella lanceolata</i>	0.2	0.0	0.5	0.0
<i>Diatoma vulgare</i>	7.7	2.5	5.7	1.5
<i>Encyonema minutum</i>	2.2	0.7	2.1	0.4
<i>Fragilaria vaucheriae</i>	27.1	15.6	16.8	10.7
<i>Gyrosigma</i> sp.	1.9	0.8	3.0	4.4
<i>Melosira varians</i>	193.8	72.2	175.5	74.5
<i>Navicula gregaria</i>	4.9	0.8	7.7	0.9
<i>Navicula lanceolata</i>	82.6	17.8	102.5	33.6
<i>Navicula menisculus</i>	157.4	12.8	206.2	29.4
<i>Nitzschia dissipata</i>	65.3	11.4	50.0	2.8
<i>Nitzschia perminuta</i>	10.8	2.6	22.0	5.9
<i>Planothidium lanceolatum</i>	221.0	23.3	181.6	16.9
<i>Psammothidium lanenburgianum</i>	21.5	5.4	16.5	2.4
<i>Staurosira elliptica</i>	4.0	0.9	10.3	2.4
<i>Staurosirella leptostauron</i>	2.8	0.7	3.4	1.4
<i>Surirella brebissonii</i>	1.1	0.4	0.6	0.2

Continued

Table 6 Mean densities (10^3 cells cm^{-2}) of benthic algae in mesocosm food webs—cont'd

	Control		Drought	
	Mean	SE	Mean	SE
<i>Surirella minuta</i>	7.7	2.3	13.7	5.9
<i>Synedra ulna</i>	8.6	2.1	6.6	4.5
<i>Spirulina</i> sp.	1.1	0.1	1.1	0.0
Total	892.6	183.1	872.6	215.0
Grand total	9076.3	1494.0	2517.8	411.8

Algae formed hard calcite-impregnated crusts or loosely attached filamentous mats on the surfaces of stones.

(ANOVA, $F_{1,3} = 7.59$, $P = 0.07$; Fig. 9), in contrast to that of primary consumers and predator, reflecting the abundance of detrital particles associated with populations of mat-forming diatoms (Ledger et al., 2008).

Consumer abundance in the food webs was not significantly affected by the drought treatment (control 9282 ± 350 animals m^{-2} , disturbed 8310 ± 567 animals m^{-2} , ANOVA, $F_{1,3} = 0.89$, $p = 0.414$; Fig. 10), but there was a sharp decline in both the mean annual secondary production

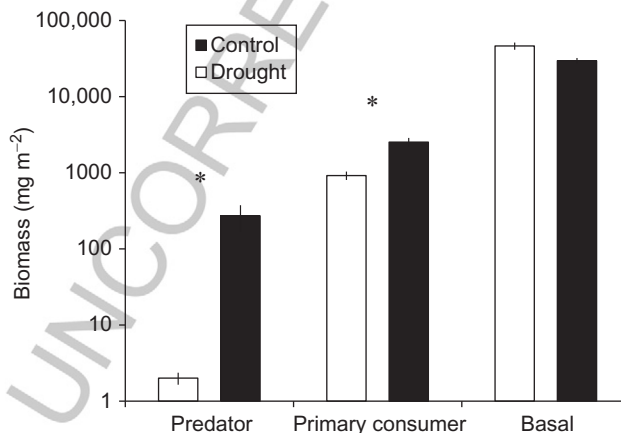
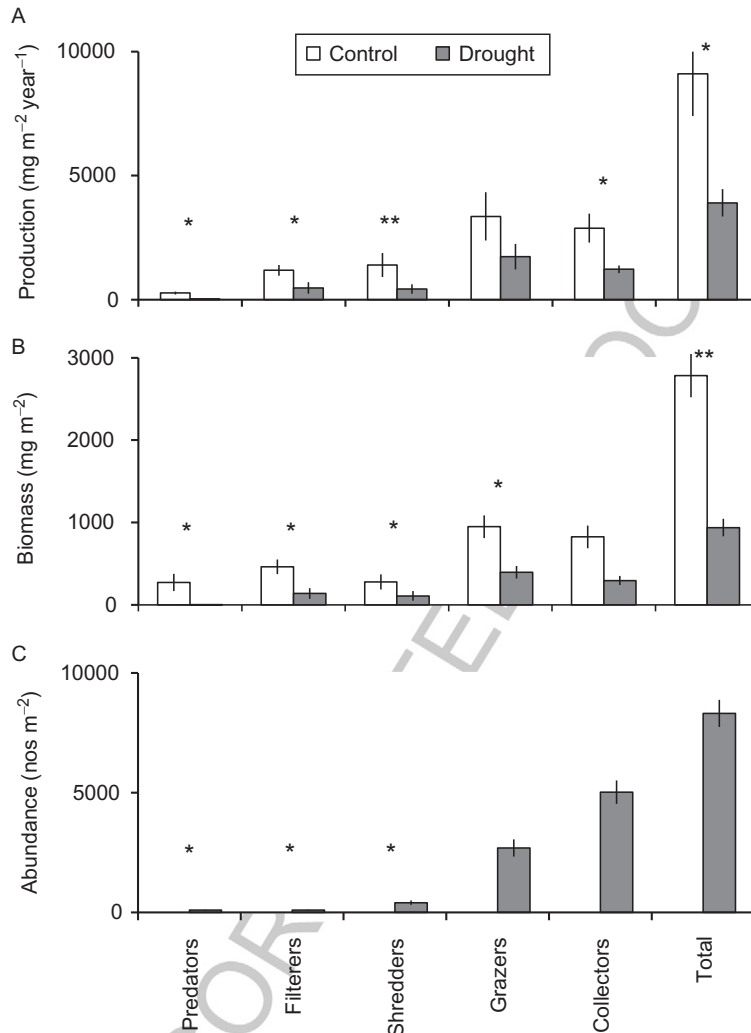


Figure 9 Mean (\pm SE) biomass of basal resources, primary consumers and predators in drought and control food webs. Trophic group, drought treatment and their interaction significantly affect taxon richness (ANOVA, $n = 24$, $P < 0.0001$ in all cases). Asterisks above individual trophic groups denote significant differences between treatments (ANOVA, $n = 8$, $P < 0.05$).



0050 **Figure 10** Mean (± 1 SE) annual secondary production (A), biomass (B) and numerical abundance (C) for all macroinvertebrates, and key functional feeding groups, in drought treatments and controls.

(by 60% to $3596 \pm 455 \text{ mg m}^{-2} \text{ year}^{-1}$, ANOVA, $F_{1,3} = 12.59$, $P = 0.038$) and standing biomass (by 66% to $938 \pm 112 \text{ mg AFDM m}^{-2}$, ANOVA, $F_{1,3} = 86.05$, $P = 0.003$) of the macroinvertebrate assemblage (Fig. 10, Table 7), reflecting turnover in assemblage taxonomic composition and a shift from large to small species (see Ledger et al., 2011, 2012, 2013). When primary consumers were classified according to their functional roles (i.e. as

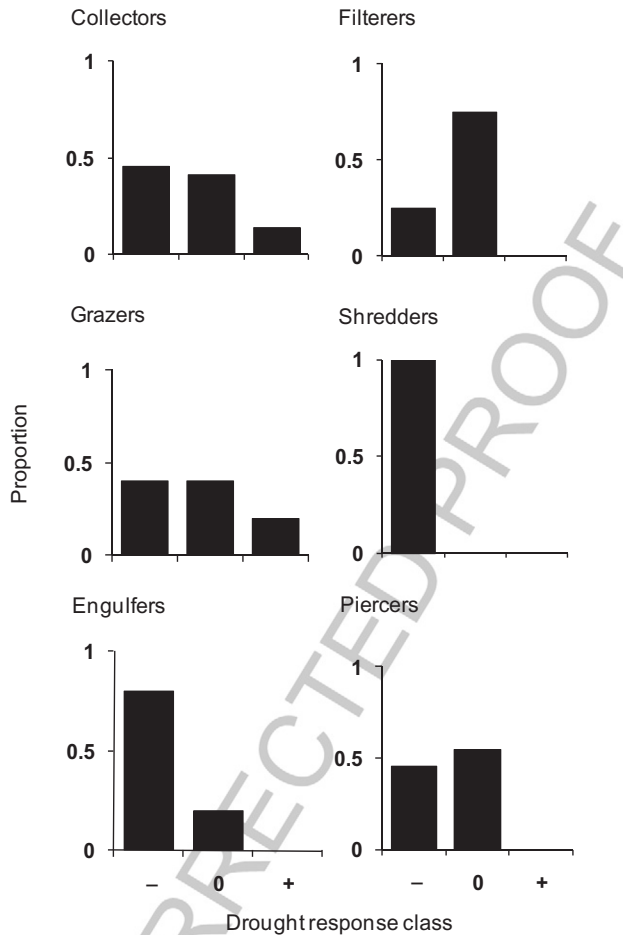
10035 **Table 7** Biomass, secondary production and numerical abundance of macroinvertebrates in control and drought disturbed food webs

Taxa	Control			Drought		
	B	P	N	B	P	N
Predators	271	271	431	2	34	100
<i>Erpobdella octoculata</i> (H)	215	143	45	–	–	–
<i>Macropelopia</i> sp. (D)	3	18	124	2	34	100
<i>Pentaneura</i> sp. (D)	<1	4	28	–	–	–
<i>Platambus maculatus</i> (C)	10	6	17	–	–	–
<i>Polycentropus flavomaculatus</i> (T)	19	74	196	–	–	–
<i>Procladius</i> sp. (D)	<1	4	25	–	–	–
<i>Sialis lutaria</i> (M)	23	23	10	–	–	–
Filter-feeders	461	1183	456	138	474	95
<i>Bithynia</i> sp. (G)	2	9	2	–	–	–
<i>Brachycentrus subnubilus</i> (T)	1	2	4	2	3	10
<i>Hydropsyche siltalai</i> (T)	448	1120	67	135	461	37
<i>Pisidium</i> sp. (B)	9	46	360	2	7	64
<i>Simulium</i> sp. (D)	<1	6	35	<1	4	22
Collector-gatherers	825	2886	4633	295	1226	4893
<i>Asellus aquaticus</i> (Cr)	30	89	116	9	25	43
<i>Athripsodes</i> sp. (T)	1	3	11	–	–	–
<i>Brychius elevatus</i> (C)	10	17	21	2	2	4
<i>Cryptochironomus</i> sp. (D)	5	58	140	10	115	340
<i>Eiseniella tetraedra</i> (O)	–	–	–	2	3	6
<i>Elmis aenea</i> (C)	1	3	33	–	–	–
<i>Ephemera danica</i> (E)	239	380	93	13	7	5
<i>Haliplus lineatocollis</i> (C)	54	225	67	14	59	20
<i>Leuctra geniculata</i> (P)	3	10	36	–	–	–
<i>Limnius volckmari</i> (C)	2	4	77	1	2	6
<i>Microtendipes</i> sp. (D)	17	195	459	22	268	796

Table 7 Biomass, secondary production and numerical abundance of macroinvertebrates in control and drought disturbed food webs—cont'd

Taxa	Control			Drought		
	<i>B</i>	<i>P</i>	<i>N</i>	<i>B</i>	<i>P</i>	<i>N</i>
Naididae (O)	6	21	976	10	39	2035
Ostracoda	<1	<1	371	<1	<1	49
<i>Oulimnius</i> sp. (C)	5	22	133	1	2	24
<i>Polypedilum</i> sp. (D)	3	32	79	2	27	74
<i>Potamopyrgus antipodarum</i> (G)	403	1631	562	128	414	127
Prodiamesinae (D)	<1	3	39	<1	3	42
<i>Tipula (Yamatotipula) montium</i> (D)	29	91	3	63	153	42
Tubificidae (O)	17	104	1844	17	105	1506
Grazer–scrapers	948	3359	2214	396	1736	2687
<i>Ancylus fluviatilis</i> (G)	25	60	43	–	–	–
<i>Baetis</i> sp. (E)	7	22	115	7	20	115
<i>Cricotopus</i> sp. (D)	6	73	658	8	106	995
<i>Heterotrissocladius</i> sp. (D)	6	74	659	8	110	1029
<i>Radix balthica</i> (G)	744	2903	363	368	1449	151
<i>Synorthocladius</i> sp. (D)	2	28	242	3	49	413
<i>Theodoxus fluviatilis</i> (G)	22	22	4	–	–	–
<i>Tinodes waeneri</i> (T)	4	25	149	1	1	14
<i>Valvata</i> sp. (G)	132	154	63	–	–	–
Shredders	277	1398	1178	107	433	408
<i>Gammarus pulex</i> (Cr)	248	1291	1165	107	432	406
<i>Sericostoma personatum</i> (T)	29	108	17	1	1	2
Total/mean	2783	9098	9282	938	3904	8360

B, mean annual biomass (mg AFDM m⁻²); *P*, mean annual secondary production (mg AFDM m⁻² year⁻¹); and *N*, mean abundance (numbers m⁻²). B, Bivalvia; C, Coleoptera; D, Diptera; E, Ephemeroptera; G, Gastropoda; H, Hirudinea; He, Hemiptera; M, Megaloptera; O, Oligochaeta; T, Trichoptera; Cr, Crustacea; Od, Odonata; P, Plecoptera. Taxa within functional feeding groups (totals in bold) are ranked alphabetically. “–” denotes a taxon absent in each replicate web in a treatment.



0055 **Figure 11** Distribution of high-frequency (approximately monthly) dewatering effects on secondary production of macroinvertebrate taxa in six functional feeding groups. Taxa were classified according to their statistically significant positive (+) negative (-) or lack of (0) response to HF drought, as revealed by one-sample *t*-tests. Figure redrawn after Ledger et al. (2011).

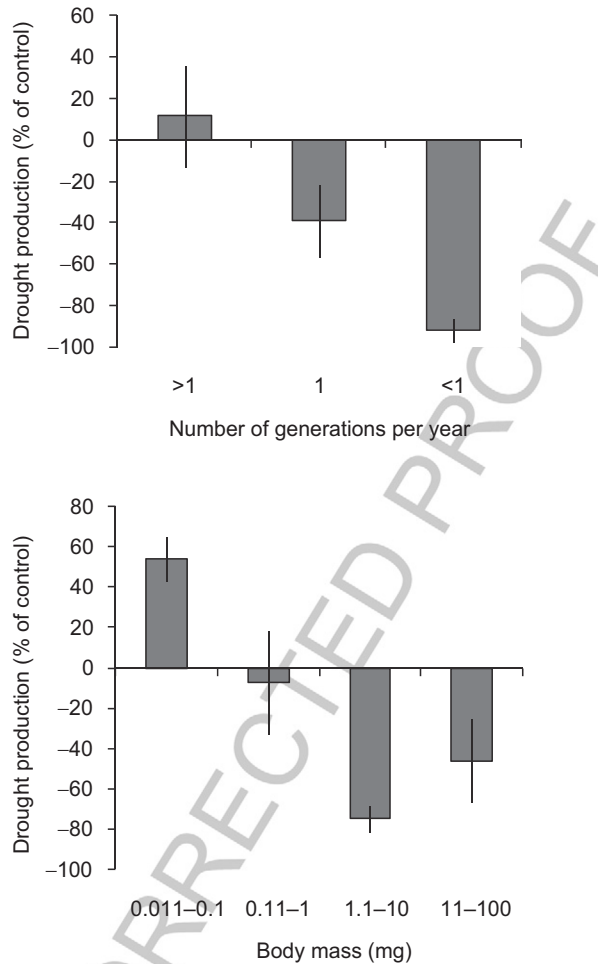
filter-feeders, collector-gatherers, grazer-scrappers and shredders) (see Table 7), it became evident that the impact of the treatment on production varied among functional feeding groups (Fig. 11, Table 7), with statistically significant reductions in production for engulfing predators (by 87%, ANOVA, $F_{1,3}=16.36$, $P=0.027$), shredders (by 69%, ANOVA, $F_{1,3}=38.07$, $P=0.009$), filterers (by 60%, ANOVA, $F_{1,3}=14.69$, $P=0.031$) and collector-gatherers (by 57%, ANOVA, $F_{1,3}=12.35$,

$P=0.013$) but not for grazers (Fig. 10A, ANOVA, $F_{1,3}=4.26$, $P=0.131$), and there were similar effects on the biomass of these groups (Fig. 10B). Responses to the drought also varied markedly among taxa *within* functional groups (Table 7). Drought excluded the larger predators from the webs (i.e. *E. octoculata*, *P. flavomaculatus*, *S. lutaria*), whereas the much smaller Tanypodinae larvae were more resilient, maintaining production in disturbed habitats.

p0545 Contrasting responses were also observed within the collector–gatherers, with production by the snails (*Potamopyrgus antipodarum*) and mayflies (*Ephemera danica*) being strongly reduced, whereas production by other collectors was weakly affected (Tubificidae, *Asellus aquaticus*, chironomids) or increased (Naididae, Tipulidae) (Table 7, Appendix). Grazer–scraper production was dominated by the snail *Radix balthica* (2903 ± 969 mg AFDM m^{-2} year $^{-1}$), which was strongly reduced by the drought (by 50%). Other snails (*Theodoxus fluviatilis*, *Valvata* sp.) and limpets (*Ancylus fluviatilis*) were eliminated by drought, whereas the small orthoclads were more resilient (Table 7, Appendix). Production of the dominant shredders *Gammarus pulex* (1291 ± 464 mg AFDM m^{-2} year $^{-1}$) and *Sericostoma personatum* (108 ± 35 mg AFDM m^{-2} year $^{-1}$) was strongly suppressed by drought (by 64% and 99%, respectively; Table 7). The dominant filterers were reduced (*Pisidium* sp.) or not significantly affected (*Hydropsyche siltalai*) by the drought treatment (Table 7, Appendix). On average, semivoltine (<1 year life cycle per year) and univoltine (1 cycle per year) taxa were more vulnerable to drought than multivoltine taxa (>1 cycle per year; Wilcoxon test, $P < 0.05$) (Fig. 12A), and taxa with large body mass were more susceptible to drought than smaller taxa (Kruskal–Wallis $H=11.49$, $P=0.009$) (Fig. 12B).

s0075 3.3. Quantified food webs

p0550 The majority of macroinvertebrate secondary production in both control and drought-disturbed webs was attributable to particulate detritus (cross-treatment mean 89%), with relatively small contributions from leaf litter (3.2%), algae (4.4%) and animal prey (3.2%, Table 8, Fig. 13). Only a small proportion of fluxes to primary consumers were transferred to predators (2.2%). Drought reduced the percentage of production attributable to animal predation (from 4.6% to 1.7%), as predators susceptible to periodic dewatering declined, but the contribution to production of other food types was not affected by the treatment ($P > 0.05$, see Table 8). Biomass fluxes



0060 **Figure 12** Mean (± 1 SE) effect of high-frequency drought on secondary production of macroinvertebrate taxa in relation to (A) the potential number of life cycles per year and (B) mean individual body mass. (B) Figure redrawn after Ledger et al. (2011).

through the food webs conformed to an approximately log-normal distribution, with a few strong and many weak fluxes (i.e. 90% of biomass flux was channelled through just 5% of links; Fig. 14). The largest flows in all webs were from amorphous detritus to primary consumers (85% and 89% of total fluxes in both control and disturbed channels, respectively), reflecting the low assimilation efficiency for this food type, with relatively small flows from the higher-quality algae and animal prey (Table 9).

t0040 **Table 8** Percentage of mean annual secondary production attributed to each resource type (B_i)

	Control		Drought		ANOVA	
	Mean	SE	Mean	SE	$F_{1,3}$	P
Amorphous detritus	87.3	0.8	90.4	0.5	9.41	0.055
Leaf detritus	3.3	0.4	3.0	0.5	1.94	0.258
Diatoms	3.3	0.7	3.4	0.4	0.01	0.948
Green algae	0.8	0.3	0.6	0.2	0.30	0.624
Cyanobacteria	0.3	0.1	0.4	0.1	1.17	0.358
Fungi	0.3	0.1	0.4	0.1	0.71	0.460
Animal	4.6	1.1	1.7	0.3	9.77	0.049

ANOVA tested for the effect of treatment and block ($P > 0.05$, results not shown).

p0555 Ingestion varied among macroinvertebrate functional feeding groups, with greatest fluxes to grazers and collector–gatherers and smallest fluxes to predators in both treatments (Table 10). In both control- and drought-disturbed assemblages, ~80% of the flux flowed through just six taxa (Fig. 15, Table 11a,b). In controls, the strongest fluxes were to grazing snails *R. balthica* (32% total ingestion) and *Valvata piscinalis* (3%), collector–gathering snails *P. antipodarum* (25%) and mayflies *E. danica* (5%), shredding amphipods *G. pulex* (7%) and filter–feeding caddis *Hydropsyche* sp. (4%, Fig. 15, Table 11a). Drought markedly reduced the total ingestion of resources (by 60%, from mean $98,959 \pm 25,451$ to $39,792 \pm 6804 \text{ mg m}^{-2} \text{ year}^{-1}$), including amorphous detritus (by mean 58%), leaf detritus (75%), diatoms (60%), green algae (37%), fungi (44%) and animal prey (96%) (Table 9). Although the snails *Radix* and *Potamopyrgus* remained the dominant processors of organic matter in drought treatments, mortality caused by the disturbances strongly reduced the ingestion rates of their populations, by 61% and 80%, respectively, although these reduced fluxes were still the greatest fluxes in the disturbed channels. Drought also caused a turnover in other dominant fluxes of organic matter in the food webs, with increased ingestion by chironomids such as *Cryptochironomus* sp. (by 109%, ANOVA, $F_{1,3} = 12.79$, $P = 0.037$) *Microtendipes* sp. (by 41%, ANOVA, $F_{1,3} = 11.45$, $P = 0.043$) and *Cricotopus* sp. (by 106%, ANOVA, $F_{1,3} = 7.22$, $P = 0.043$) among others, but these compensatory dynamics only partially replaced declining ingestion by drought sensitive

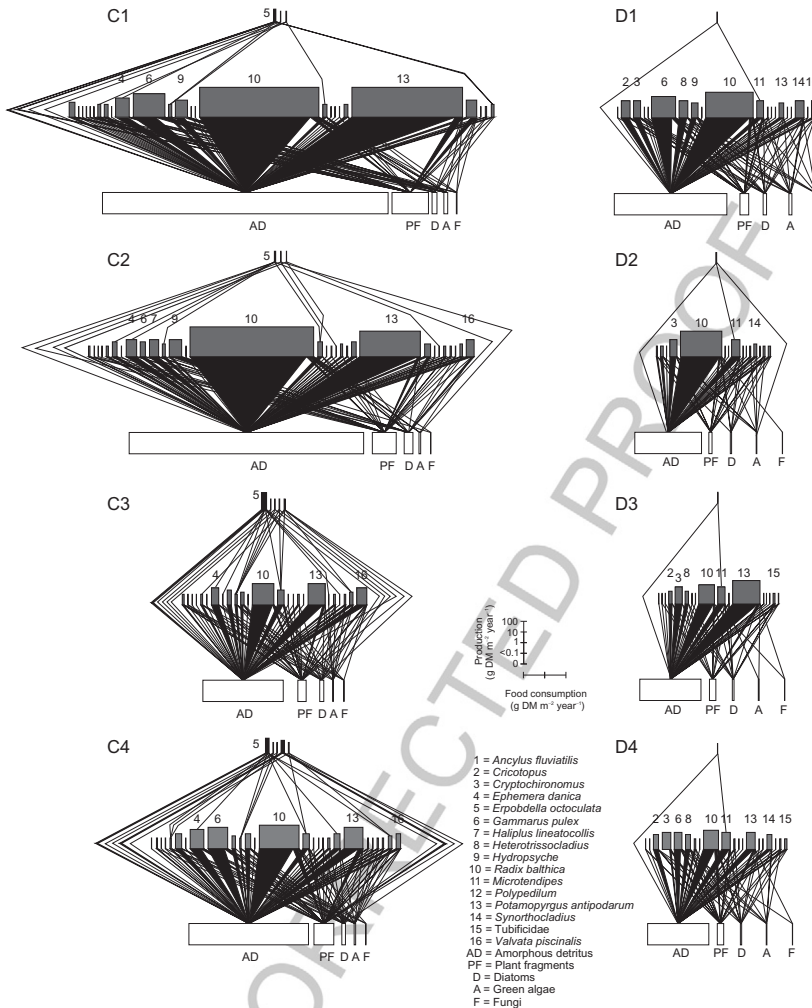
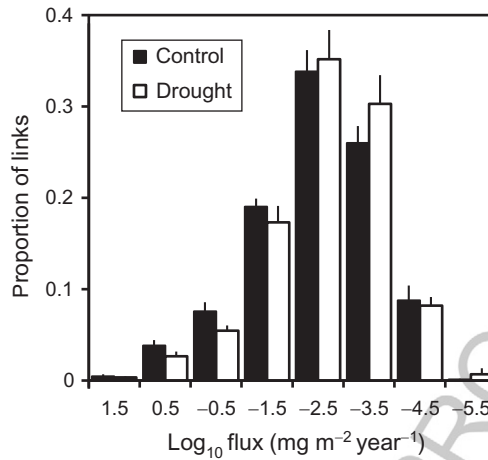


Figure 13 Quantitative food webs in replicate control (C1–C4) and drought (D1–D4) treatments. For each web, lower bars are basal resources, middle bars are primary consumers and top bars are predators. For each consumer, the height and width of the bars are proportional to mean annual secondary production and biomass flux from resources (total inflows), respectively. For basal species, the relative width of bars on the x-axis is proportional to total consumption by invertebrates (total outflows from each resource to consumers), and for this trophic level production (y-axis) was not quantified. The black triangles that link trophic levels illustrate the relative contribution of resource flows to the production of each consumer, summing to the total inflows. Numbers refer to consumer identity and letters distinguish categories of basal resource, omitting rare species (<1% total production). Flows from individual algal taxa are grouped for display only. See Tables 3 and 4 for full lists of resource and consumer taxa, respectively. Redrawn from Ledger et al. (2013).



t0070 **Figure 14** Biomass fluxes from resources to consumers in control- and drought-disturbed food webs as a mean (+1 SE) frequency distribution for all replicate webs.

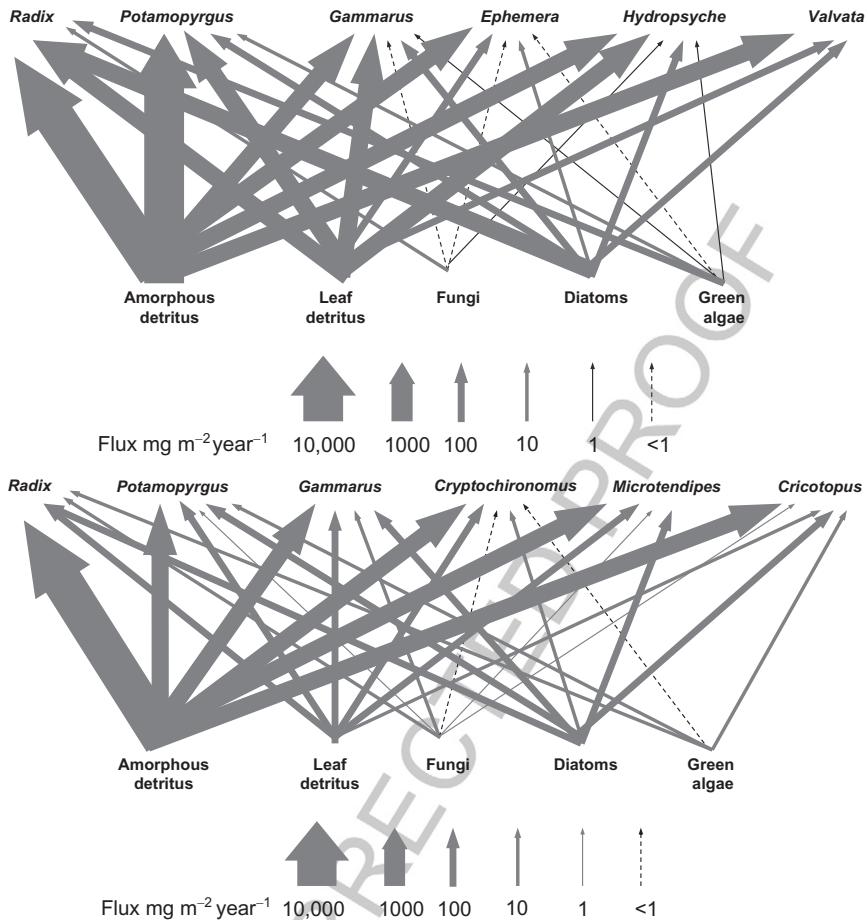
t0045 **Table 9** Total ingestion of each food type (mg AFDM m⁻² year⁻¹) and ANOVA results testing the effect of treatment

	Control		Drought		ANOVA	
	Mean	SE	Mean	SE	F _{1,3}	P
Amorphous detritus	84,386	22,480	35,515	5783	26.68	0.002
Leaf detritus	10,381	2718	2603	586	21.81	0.003
Diatoms	2487	553	1009	216	34.63	0.001
Green algae	862	324	541	308	9.83	0.020
Fungi	170	55	96	55	11.91	0.014
Animal	673	231	28	10	9.18	0.032
Total	98,959	25,451	39,792	6804	16.39	0.004

taxa: that is, network restructuring did not fully maintain ecosystem functioning (Table 11a,b). Overall, biomass flux increased through 43% of links under drought, with steep reductions in the remaining pathways. Shifts in biomass flux (i.e. faster vs. slower) to consumers were related to their body mass (logistic regression, $\chi^2 = 9.808$, $P = 0.002$), with increasing fluxes confined to small taxa such as midge larvae, and profound reductions for larger species, including snails, amphipod shrimps, caddis and mayfly larvae

t0050 **Table 10** Mean annual secondary production and ingestion of resources by consumers for key functional feeding groups

	Control						Drought					
	Predator	Filterer	Collectors	Grazers	Shredders	Total	Predator	Filterer	Collectors	Grazers	Shredders	Total
Production	271	1183	2886	3359	1398	9098	45	474	1028	1614	433	3596
Ingestion												
Amorphous detritus	1774	2701	35,434	38,347	6131	84,386	316	789	12,572	18,292	3546	35,515
Leaf detritus	103	1632	3896	2071	2679	10,381	10	193	796	851	753	2603
Diatoms	22	336	416	1513	198	2487	3	53	328	482	143	1009
Green algae	8	9	144	613	88	862	9	10	142	328	52	541
Fungi	1	2	38	91	38	170	<1	2	18	57	18	96
Animal	671	<1	<1	0	2	673	28	0	0	0	0	28
Total	2578	4680	39,929	42,635	9136	98,959	366	1048	13,855	20,011	4512	39,792

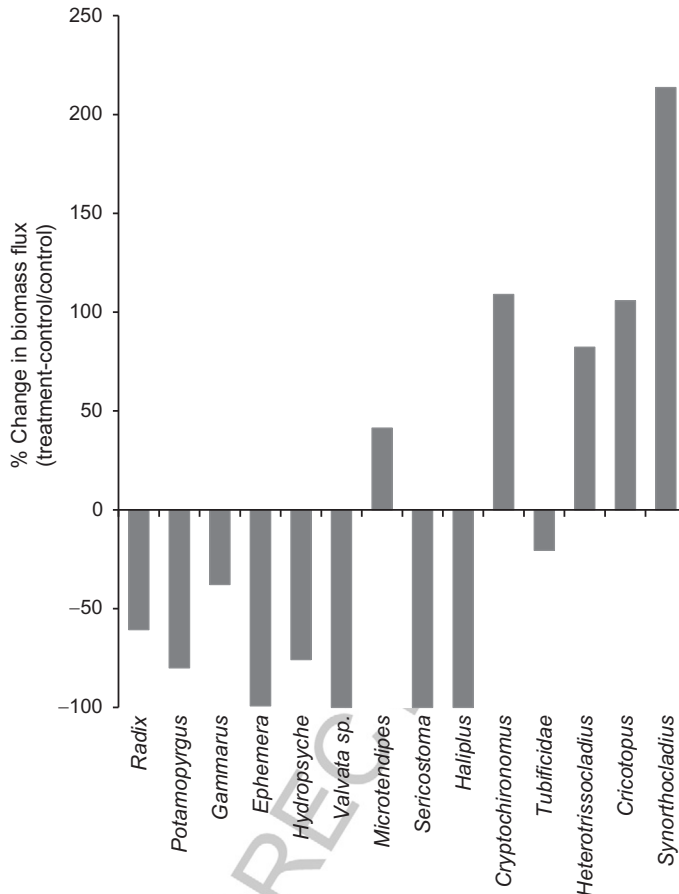


0075 **Figure 15** Biomass fluxes from resources to core consumers in controls (A) and drought-disturbed treatments (B). The thickness of the arrows is proportional to flux magnitude ($\text{mg m}^{-2} \text{year}^{-1}$).

(Fig. 16). This pronounced shift of production downwards through the size spectrum conserved the relative distribution of fluxes within the webs (Fig. 14; equivalent interaction evenness among treatments; Table 12). Other, quantified metrics of network structure (i.e. connectance, linkage density, trophic generality and vulnerability) were similarly unaffected by the drought treatment (Table 12).

t0055 **Table 11** Ingestion (mean mg m⁻² year⁻¹) by core taxa in (a) undisturbed control mesocosms and (b) drought-disturbed mesocosms

Taxon	Amorphous detritus	Leaf detritus	Diatoms	Green algae	Fungi	Total ingestion	% Total web ingestion
(a) Undisturbed control mesocosms							
<i>Radix balthica</i>	32,107	1754	1255	365	81	35,562	36
<i>Potamopyrgus antipodarum</i>	21,376	2720	252	60	0	24,409	25
<i>Gammarus pulex</i>	5123	1336	100	2	<1	6562	7
<i>Ephemera danica</i>	4463	715	42	1	<1	5221	5
<i>Hydropsyche</i> sp.	1949	1610	323	8	4	3894	4
<i>Valvata piscinalis</i>	2335	131	158	0	0	2624	3
Total	67,353	8267	2131	436	85	78,271	79
(b) Drought-disturbed mesocosms							
<i>Radix balthica</i>	12,813	714	301	95	41	13,965	35
<i>Potamopyrgus antipodarum</i>	4342	365	133	76	9	4924	12
<i>Gammarus pulex</i>	3357	604	107	0	16	4084	10
<i>Cryptochironomus</i> sp.	3387	151	10	<1	1	3549	9
<i>Microtendipes</i> sp.	3250	142	132	0	4	3527	9
<i>Cricotopus</i> sp.	1763	76	141	21	4	2006	5
Total	28,912	2051	825	192	75	32,056	81



fo080 **Figure 16** Mean percentage change in biomass flux to consumers for the strongest pathways ($>1 \text{ g m}^{-2} \text{ year}^{-1}$). Taxa are ranked from left to right in order of decreasing mean body mass (mg).

to060 **Table 12** Quantitative weighted network properties for drought-disturbed treatments and controls

Metric	Control		Drought		ANOVA	
	Mean	SE	Mean	SE	$F_{1,3}$	P
Connectance (LD_q/S)	0.09	0.02	0.08	0.01	0.39	0.575
Generality (G_q)	1.82	0.11	1.59	0.08	3.89	0.143
Interaction diversity (ID_q)	3.98	0.35	3.41	0.32	3.36	0.173
Interaction evenness (IE)	0.47	0.03	0.43	0.03	1.90	0.262
Linkage density (LD_q)	5.94	1.16	4.20	0.64	3.33	0.165
Vulnerability (V_q)	10.06	2.23	6.81	1.21	3.29	0.167



s0080

4. DISCUSSION

p0560

Climate change is expected to increase the frequency and intensity of extreme climatic events, including extreme droughts, with potentially severe implications for ecosystems across the globe (IPCC, 2007), and our data provide some of the first experimental evidence to support these predictions from field-based stream mesocosms. Whilst research on hydrologic drought has intensified in recent years, the majority of studies focus on responses of key assemblages, especially macroinvertebrates, whereas knowledge of impacts on ecosystem functioning and higher levels of biological organisation has been slower to emerge (but see, e.g. Chadwick and Huryn, 2007; Dewson et al., 2007b; Walters and Post, 1998). Experiments have been advocated as useful tools to explore the impact of unpredictable extreme events in natural systems (Jentsch et al., 2007), but research on drought and low flows in streams has tended to be phenomenological (but see, e.g. Dewson et al., 2007b; Walters and Post, 2011) and based on field surveys that are often confounded by environmental gradients or which lack the pre-impact data necessary to demonstrate causation (James et al., 2008).

p0565

In the present study, we simulated hydrologic drought in a series of stream mesocosms over 2 years to capture intra- and intergenerational responses to habitat loss caused by periodic dewatering of benthic habitat (see Ledger et al., 2008, 2011, 2012, 2013). Consistent with our first hypothesis, our results indicate that intensified drought could lead to heavy local extinctions, declining ecosystem productivity, and altered food web structure and functioning (Figs. 7 and 13). On a larger, landscape scale this has implications for the supply of ecosystem goods and services (reviewed by Raffaelli and White, 2013): if we consider the different treatments as “habitat patches” in a river basin exposed to drought, the impaired flow of energy to the higher trophic levels could have severe consequences for the socio-economically and culturally valuable fish populations at the top of the food webs.

s0085

4.1. Primary producers

p0570

Disturbance reduced the size of the food webs (see Figs. 3 and 13) and, whilst web extinctions were confined to the consumers, there was nevertheless both a marked decline in the abundance of algal primary producers, and a clear shift in dominance from encrusting green algae to filamentous diatoms

within the assemblage, as dewatering episodes caused disturbances that reversed algal succession (Fig. 4, Table 6). In a related research (Ledger et al., 2006, 2008), we observed that under perennial flow, mat-forming diatoms rapidly colonised and exploited empty space to form filamentous mats, but were subsequently displaced by relatively slow-growing but longer-lived colonies of *G. incrustans* and associated epiphytes, which formed hard, calcified crusts that covered stone surfaces. Under drought, dewatering bleached the crusts, which disintegrated, whereas mat diatoms were more resilient (Ledger et al., 2008). Diatoms have *r*-selected traits, including high reproductive output, short generation times and rapid recruitment, which enable efficient recovery from disturbances such as substratum drying. These patch dynamics may reveal trade-offs in species' ability to colonise and compete among the benthic algae, a condition of several key models of community structure (e.g. Petraitis et al., 1989; Tilman, 1990) in which disturbances promote the persistence of species by preventing the exclusion of opportunists by competitive dominants (Connell, 1978; Sousa, 1979).

p0575 Shifts in the presence and abundance of benthic algae may have both direct and indirect effects on consumer populations in drought treatments (Ledger et al., 2008). Although strong reductions in algal abundances in the webs (by 71%) potentially triggered food limitation in algivorous consumer populations, we speculate this was not the case since losses were steepest for grazer-resistant crustose algae uncommon in consumer diets, whereas dense mats of diatoms common in the diet (e.g. *Navicula* spp.) remained abundant in the drought treatments. Nevertheless, a shift from algal crusts to filaments may have shaped macroinvertebrate assemblages indirectly, by modifying benthic habitat architecture. We have shown in a related study that filamentous diatom mats provide habitat for large populations of midge larvae (Ledger et al., 2006) and it could be that their proliferation under drought is partly driven by the resilience of key producers to drought.

s0090 **4.2. Qualitative webs, size structure and species traits**

p0580 Drought triggered losses of consumer species and links from the food webs, with numerically rare and/or larger taxa, and those with long life cycles, being especially vulnerable. Large size and rarity are often correlated with one another and associated with increased extinction risk (Raffaelli, 2004). In a related study exploring drought impacts on size structure in the webs (Woodward et al., 2012), we also demonstrated a second order rarity-for-size effect in which species below the general *MN*-scaling line

(i.e. the $\log(N)$ vs. $\log(M)$ regression for all the trophically connected species in a food web) were also vulnerable to extinction, being already rarer in the absence of disturbance than expected for their size. Such species may already be in sub-optimal conditions, with drought stress sufficient to exclude them from disturbed habitats. Predatory taxa at the top of the food web were vulnerable to drought treatments, particularly those of large size with limited access to refugia such as caddis, alderflies and leeches, which reduced food chain length. However, these and other losses from the webs only slightly steepened the MN slope, and the extent to which this reflects a weakening of top-down effects in the webs is unclear (Woodward et al., 2012). Our results are consistent with predictions that disturbance results in the loss of upper trophic levels (e.g. Menge and Sutherland, 1976); however, empirical tests of disturbance impacts on food chain length in streams have yielded contrasting results, reflecting different approaches, methodologies and focal disturbance regimes. Flood disturbances have reportedly increased (Marks et al., 2000), decreased (Parker and Huryn, 2006) or not affected (Townsend et al., 1998) food chain length in streams. Drought disturbance studies have been slower to emerge, revealing reductions in food chain length where dewatering occurs (Ledger et al., 2013; Sabo et al., 2010), or no change where flow reduction is less severe (Walters and Post, 2008).

p0585 Drought stripped out species and links, particularly from the top of the webs, but contrary to our second hypothesis several network properties, including connectance, were unaltered by the treatment. Connectance reflects the extent of trophic generalism or specialism of consumers in the webs, which in turn reflects their foraging behaviour and the energetic value and abundance of resources (Beckerman et al., 2006; Warren, 1994). Consistent with the specialisation–disturbance (S–D) hypothesis (Vázquez and Simberloff, 2002), we expected that disturbance would favour trophic generalists over specialists, with specialists on average more susceptible to losses of specific resources, but we found no evidence to support this. The S–D hypothesis assumes disturbance acts indirectly, by changing resource availability, rather than directly, through increased consumer mortality (Vázquez and Simberloff, 2002), and thus, our results suggest the latter may be more important than the former in our experiment: drought caused physiological stress leading to high consumer mortality (Harris, 2006), with large species most strongly affected, probably reflecting their limited access to spatial refugia (Ledger et al., 2013) and relatively high metabolic demands (Brown et al., 2004), and food supply and diet remained stable in the face of the drought.

p0590 Despite extinctions, we found clear evidence for compensatory dynamics within the remaining consumers, with abundances of several taxa

increasing to offset losses of competitors and/or predators, thereby precluding changes in combined consumer densities in drought treatments. For example, among the primary consumers, recurrent dewatering produced irruptions in the abundance of *r*-selected chironomid midges and oligochaete worms and declines in more *K*-selected amphipod shrimps, caddis and mayflies, among others (Ledger et al., 2012). As with the diatoms among the primary producers, the primary consumer chironomids and oligochaetes also have *r*-selected traits that foster rapid exploitation of space and resources freed by disturbance, including high fecundity small size and short generation times (e.g. Brinkhurst and Jamieson, 1971; Townsend and Hildrew, 1994). Such marked shifts in assemblage structure and trait composition may yield greater average resistance and/or resilience to future disturbances (Ives and Cardinale, 2004). Nevertheless, assemblage turnover could not compensate for heavy losses of consumer biomass stocks or production, as populations of small species replaced larger species in the food webs, and on average production was more than halved (57% reduction) by the drought (Ledger et al., 2011).

p0595 Cumulative degree distributions for mesocosm webs were characterised by exponential decay functions in both control and drought treatments (i.e. most taxa were connected to only a small number of others). As these properties are commensurate with those of natural food webs (Brown et al., 2011), the mesocosm webs can be considered to provide realistic insights into responses to perturbations similar to those observed in “natural” systems (e.g. Montoya et al., 2009). Exponential degree distributions have been reported from other systems (Camacho et al., 2002), but the finding here that this property was robust in the face of perturbation is novel. It has been suggested previously that skewed link distributions confer structural robustness to food webs (Dunne and Williams, 2009). This robustness was evident in other structural measures (e.g. connectance, degree distribution, links per species) and likely reflects a lack of cascading secondary extinctions in these webs because the most highly connected “keystone” species were not lost (Sole and Montoya, 2001).

p0600 Characteristic path length (D) data remain scarce, particularly for freshwater ecosystems, but the “two degrees of separation” small-world property has been proposed observed consistently in most natural food webs (Williams et al., 2002). The eight new estimates for our mesocosm webs were not markedly different from data compiled for other terrestrial and aquatic ecosystems (see Brown et al., 2011). More notably, our experimental manipulation of food webs has further illustrated further the robustness of this structural property to perturbation. Most taxa were within either two

(71% taxa) or three (99% taxa) links of one other in both control and drought webs. The prevalence of short food chains has previously been considered important for the transmission of trophic cascades and other indirect effects through ecological networks (Berlow, 1999; Montoya et al., 2009), but these effects were not observed in our study.

s0095 **4.3. Secondary production and quantified food webs**

p0605 The secondary production of consumers was combined with dietary data to quantify the flow of organic matter from resource to consumer (Benke, 2012; Benke and Wallace, 1997). The quantified food webs revealed that macroinvertebrate production was based largely on amorphous detritus, with only small contributions from algal primary producers and other resources. These data do not necessarily indicate that allochthonous food sources are most important to consumers; however, because unknown proportions of amorphous material may be derived from autochthonous sources, such as the polysaccharide matrix of epilithic biofilms (Benke and Wallace, 1997). We identified and counted algal cells in the guts of consumers but since we could not differentiate biofilm polysaccharide matrix from other detrital particles (e.g. fine particles derived from leaves and soil) using our methods, our estimate of the algal contribution to secondary production are undoubtedly conservative.

p0610 The percentage of production derived from animal prey was low (<5%) in our food webs (Table 8), with macroinvertebrate predators accounting for <1% of total ingestion (see Table 9). Engulfing predators consumed only ~7% of secondary production in controls and <1% in disturbed channels. We must caution that production and ingestion by predators is underestimated in our webs, due to the exclusion of suctorial predators (see Section 2), which accounted for much (~70%) of predator production (see Ledger et al., 2011). Scaling ingestion to account for suctorial ingestion, we estimate that ~28% of production was consumed by the whole predator assemblage in controls, considerably less than was observed by Hall et al. (2000) in forested first-order streams in North Carolina, where 42–88% of all invertebrate secondary production was consumed by predators. The relatively weak impact of engulfing predators on prey may be related to size disparities between the two groups, particularly in our controls where some of the most productive primary consumers were apparently too large (max. body mass 42 mg) for the gape-limited predators (max. body mass 32 mg) to handle. These disparities may to some degree decouple production of primary and secondary consumers in our webs, thereby lessening the potential for cascading effects of predator losses in drought treatments.

p0615 Drought strongly suppressed the processing of organic matter by consumers, but resistance and resilience among some core taxa, together with compensatory shifts in production, conserved the approximately log-normal distribution of fluxes within the disturbed food webs (Fig. 14, Table 12; Ledger et al., 2013). Ingestion of organic matter varied markedly among the consumers, with a few strong and many weak fluxes within each web, consistent with observations by Hall et al. (2000) in first-order forest streams. The greatest flows through the food webs were from resources with low assimilation efficiencies (i.e. detritus) to highly productive consumers, most notably from amorphous detritus to snails (*Radix* and *Potamopyrgus*). Snails are key processors of organic matter in many aquatic systems and their persistence through periods of intermittency sustained, albeit at a reduced rate, some of the strongest fluxes thorough the food webs. Many fluxes to small species, especially chironomids, increased, but ingestion by these groups neither compensated for, nor exceeded, declines in productive larger species (e.g. mayflies and caddis). Thus, we did not observe the potentially destabilising concentration of production and fluxes into fewer species that is predicted by theory (Bascompte et al., 2006; Sabatino et al., 2010) and has been observed elsewhere (Tylianakis et al., 2007).

p0620 Our repeated disturbances had especially strong impacts on those taxa that were rare, large and/or high in the web, because their populations are typically slow to rebound and prone to stochastic local extinctions. We now have some generic species traits we can use to predict likely changes in the composition and abundance of the food web nodes, as well as other more species-specific orthogonal traits (e.g. ability to air breathe). In addition to these fixed autecological traits, there is also compelling evidence that synecological traits or attributes that emerge at the system level (e.g. rarity-at-size and trophic height) that are associated with vulnerability to extreme events. When we consider in more detail what may be occurring in the food web, we would expect the structure and dynamic stability to fluctuate in response to drought. In particular, during the recovery phase one hypothesis is that there may be a time lag or hysteresis in its trajectory, as community closure or ecological inertia may retard the ability of *K*-selected species to reassert their dominance. Priority or legacy effects become important here, as demonstrated by Ledger et al. (2006). Analogous arguments have been put forward for the seemingly tardy and patchy biological recovery of previously acidified systems, which contrast with their much smoother, progressive and more monotonic chemical recovery (Layer et al., 2010, 2011). This highlights how it is critical to consider the food web level of organisation rather than simply its component parts, if we are to understand and predict multispecies systems' responses to, and recovery from, environmental stressors.

p0625 Within the food web, encounter rates will increase when consumers and resources are concentrated into shrinking refugia patches, and eventually, in extreme cases, handling time might conceivably become limiting, at least temporarily. This could alter network structure, as connectance is driven by the balance between handling time and encounter or attack rates (Petchey et al., 2010). Given that most predators in freshwaters appear to feed far below their potential capacity this seems unlikely: one prediction, though, is that both interaction frequency and connectance increase, unless and until the predators themselves are exposed to sufficient physiological stress that they suffer local extinction. This winnowing effect of species loss could help explain the homogenisation of several aspects of network structure and various mass–abundance scaling relationships for food web patterns, from pairwise links, to food chains, and ultimately to the constraint space of the entire trophic network. A key question that emerges from this study is: how general (and hence predictable) are such responses to drought in other aquatic and terrestrial systems?

ACKNOWLEDGEMENTS

The Freshwater Biological Association (FBA) and the Centre for Ecology and Hydrology Dorset generously supported this research. The project was funded by a FBA/Natural Environmental Research Council (NERC) postdoctoral fellowship to M. E. L., a tied studentship to Dr. Rebecca Harris, and NERC grants NER/B/S/2002/00215 and NE/J02256X/1. Dr. Iwan Jones kindly supplied the photograph for Fig. 1. We are grateful to the many people who assisted in the field, with special thanks to Mr. Brian Godfrey and Dr. Bethan Ledger.

s0100



APPENDIX. TWO-WAY ANOVA TESTING THE EFFECT OF DROUGHT TREATMENT (RESULTS BELOW) AND MESOCOSM BLOCK ($P > 0.05$, RESULTS NOT SHOWN) ON SECONDARY PRODUCTION OF KEY TAXA

Taxon	ANOVA	
	$F_{1,3}$	P
<i>Asellus aquaticus</i>	5.20	0.107
<i>Cricotopus</i> sp.	1.66	0.288
<i>Cryptochironomus</i> sp.	5.97	0.092
<i>Ephemera danica</i>	49.39	0.006
<i>Gammarus pulex</i>	7.36	0.024
<i>Heterotrissocladius</i> sp.	2.87	0.189

Extreme Climatic Events Alter Aquatic Food Webs		49
<i>Hydropsyche</i> sp.	3.10	0.177
<i>Macropelopia</i> sp.	1.49	0.310
<i>Microtendipes</i> sp.	3.848	0.145
Naididae	25.65	0.015
<i>Pisidium</i> sp.	11.06	0.045
<i>Polypedilum</i> sp.	0.311	0.616
<i>Potamopyrgus antipodarum</i>	6.73	0.041
<i>Radix balthica</i>	9.38	0.014
<i>Sericostoma personatum</i>	10.04	0.050
<i>Synorthocladius</i> sp.	0.824	0.431
Tipulidae	3.27	0.168
Tubificidae	0.01	0.915

REFERENCES

- Bascompte, J., Jordano, P., Melian, C.J., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.
- Beckerman, A.P., Petchey, O.L., Warren, P.H., 2006. Foraging biology predicts food web complexity. *Proc. Natl. Acad. Sci. U.S.A.* 103, 13745–13749.
- Beniston, M., Stephenson, D.B., Christensen, O.B., Ferro, C.A.T., Frei, C., Goyette, S., Halsnaes, K., Holt, T., Jylhä, K., Koffi, B., Palutikof, J., Schöll, R., Semmler, T., Woth, K., 2007. Future extreme events in European climate: an exploration of regional climate model projections. *Clim. Change* 81, 71–95.
- Benke, A.C., 2012. Secondary production, quantitative food webs, and trophic position. *Nat. Educ. Knowledge* 3, 26.
- Benke, A.C., Wallace, J.B., 1997. Trophic basis of production among riverine caddis flies: implications for food web analysis. *Ecology* 78, 1132–1145.
- Benton, T.G., Solan, M., Travis, J.M.J., Sait, S.M., 2007. Microcosm experiments can inform global ecological problems. *Trends Ecol. Evol.* 22, 516–521.
- Berlow, E.L., 1999. Strong effects of weak interactions in ecological communities. *Nature* 398, 330–334.
- Bersier, L.-F., Banašek-Richter, C., Cattin, M.-F., 2002. Quantitative descriptors of food web matrices. *Ecology* 83, 2394–2407.
- Bonada, N., Rieradevall, M., Prat, N., Resh, V.H., 2006. Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean—climate streams of northern California. *J. N. Am. Benthol. Soc.* 25, 32–43.
- Bonada, N., Rieradevall, M., Prat, N., 2007. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. *Hydrobiologia* 589, 91–106.
- Boulton, A.J., 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshw. Biol.* 48, 1173–1185.
- Boulton, A.J., Lake, P.S., 2008. Effects of drought on stream insects and its ecological consequences. In: Lancaster, J., Briers, R.A. (Eds.), *Aquatic Insects. Challenges to Populations*. CAB, Wallingford, UK, pp. 81–102.

- Bowes, M.J., Leach, D.V., House, W.A., 2005. Seasonal nutrient dynamics in a chalk stream: the river Frome, Dorset, U.K. *Sci. Total Environ.* 336, 225–241.
- Brinkhurst, R.O., Jamieson, B.G.M., 1971. *Aquatic Oligochaeta of the World*. Oliver and Boyd, Edinburgh.
- Brown, J.H., Gilooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecol. Lett.* 85, 1173–1185.
- Brown, L.E., Edwards, F.K., Milner, A.M., Woodward, G., Ledger, M.E., 2011. Food web complexity and allometric scaling relationships in stream mesocosms: implications for experimentation. *J. Anim. Ecol.* 80, 884–895.
- Burrell, G.P., Ledger, M.E., 2003. Growth of a stream-dwelling caddisfly (*Olinga feredayi*: Conosucidae) on surface and hyporheic food resources. *J. N. Am. Benthol. Soc.* 22, 92–104.
- Callaway, D.S., Newman, M.E.J., Strogatz, S.H., Watts, D.J., 2000. Network robustness and fragility: percolation on random graphs. *Phys. Rev. Lett.* 85, 5468–5471.
- Camacho, J., Guimera, R., Nunes Amaral, L.A., 2002. Robust patterns in food web structure. *Phys. Rev. Lett.* 88, 228102.
- Casey, H., 1975. Variation in chemical composition of the River Frome, England, from 196 to 1972. *Freshw. Biol.* 5, 507–514.
- Chadwick, M.A., Huryn, A.D., 2007. Role of habitat in determining macroinvertebrate production in an intermittent-stream system. *Freshw. Biol.* 52, 240–251.
- Connell, J.H., 1978. Diversity of tropical rainforests and coral reefs. *Science* 199, 1302–1310.
- Covich, A.P., Crowl, T.A., Scatena, F.N., 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshw. Biol.* 48, 1199–1206.
- Crucitti, P., Latora, V., Marchiori, M., 2004. Model for cascading failures in complex networks. *Phys. Rev. E* 69, 045104(R).
- Dewson, Z.S., James, A.B.W., Death, R.G., 2007a. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *J. N. Am. Benthol. Soc.* 26, 401–415.
- Dewson, Z.S., James, A.B.W., Death, R.G., 2007b. Stream ecosystem functioning under reduced flow conditions. *Ecol. Appl.* 17, 1797–1808.
- Dunne, J.A., Williams, R.J., 2009. Cascading extinctions and community collapse in model food webs. *Phil. Trans. R. Soc. B* 364, 1711–1723.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002a. Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci. U.S.A.* 99, 12917–12922.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5, 558–567.
- Edwards, F.K., Lauridsen, R.B., Armand, L., Vincent, H.M., Jones, J.I., 2009. The relationship between length, mass and preservation time for three species of freshwater leeches (Hirudinea). *Fundam. Appl. Limnol.* 173, 321–327.
- Espinoza, J.C., Ronchail, J., Guyot, J.L., Junquas, C., Drapeau, G., Martinez, J.M., Santini, W., Vauchel, P., Lavado, W., Ordoñez, J., Espinoza, R.L., 2011. From drought to flooding: understanding the abrupt 2010–11 hydrological annual cycle in the Amazonas River and tributaries. *Environ. Res. Lett.* 7, 024008.
- Everard, M., 1996. The importance of periodic droughts for maintaining diversity in the freshwater environment. *Freshw. Forum* 7, 33–50.
- Extence, C.A., Balbí, D.M., Chadd, R.P., 1999. River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. *Regul. Rivers Res. Manage.* 15, 545–574.
- Fenoglio, S., Bo, T., Bost, G., 2006. Deep interstitial habitat as a refuge for *Agabus paludosus* (Fabricius) (Coleoptera: Dytiscidae) during summer droughts. *Coleopterists Bull.* 60, 37–41.
- Friberg, N., Bonada, N., Bradley, D.C., Dunbar, M.J., Edwards, F.K., Grey, J., Hayes, R.B., Hildrew, A.G., Lamouroux, N., Trimmer, M., Woodward, G., 2011. Biomonitoring of

- human impacts in natural ecosystems: the good, the bad, and the ugly. *Adv. Ecol. Res.* 44, 1–68.
- Fritz, K.M., Dodds, W.K., 2004. Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system. *Hydrobiologia* 527, 99–112.
- Gagnon, P.M., Golladay, S.W., Michener, W.K., Freeman, M.C., 2004. Drought responses of freshwater mussels (Unionidae) in coastal plain tributaries of the Flint River basin, Georgia. *J. Freshw. Ecol.* 19, 667–679.
- Golladay, S.W., Gagnon, P., Kearns, M., Battle, J.M., Hicks, D.W., 2004. Response of freshwater mussel assemblages (Bivalvia: Unionidae) to a record drought in the Gulf Coastal Plain of southwestern Georgia. *J. N. Am. Benthol. Soc.* 23, 494–506.
- Hall, R.O., Wallace, J.B., Eggert, S.L., 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* 81, 3445–3463.
- Hannesdóttir, E.R., Gíslason, G.M., Ólafsson, J.S., Ólafsson, Ó.P., O’Gorman, E.J., 2013. TS1 Increased stream productivity with warming supports higher trophic levels Hannes. *Adv. Ecol. Rev.* 48.
- Harris, R.M.L., 2006. The effect of experimental drought disturbance on macroinvertebrate assemblages in stream mesocosms. Ph.D. Thesis, University of Birmingham, UK.
- Harris, R.M.L., Milner, A.M., Armitage, P.D., Ledger, M.E., 2007. Replicability of physicochemistry and macroinvertebrate assemblages in stream mesocosms: implications for experimental research. *Freshw. Biol.* 52, 2434–2443.
- Hudson, L.N., Emerson, R., Jenkins, G.B., Layer, K., Ledger, M.E., Pichler, D.E., Thompson, M.S.A., O’Gorman, E.J., Woodward, G., Reuman, D.C., 2013. Cheddar: analysis and visualisation of ecological communities in R. *Methods Ecol. Evol.* 4, 99–104.
- Hynes, H.B.N., Coleman, M.J., 1968. A simple method of assessing the annual production of stream benthos. *Limnol. Oceanogr.* 13, 569–573.
- Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., Van Veen, F.F., Warren, P.H., Woodward, G., 2009. Ecological networks—beyond food webs. *J. Anim. Ecol.* 78, 253–269.
- IPCC, 2007. Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK, 976pp.
- Ives, A.R., Cardinale, B.J., 2004. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* 429, 174–177.
- James, A.B.W., Dewson, Z.S., Death, R.G., 2008. Do stream macroinvertebrates use instream refugia in response to severe short-term flow reduction in New Zealand streams? *Freshw. Biol.* 53, 1316–1334.
- Jentsch, A., Kreyling, J., Beierkuhnlein, C., 2007. A new generation of climate-change experiments: events, not trends. *Front. Ecol. Environ.* 5, 365–374.
- Johnson, K.A., Steinman, A.D., Keiper, William D., Ruetz, C.R., 2011. Biotic response of low concentration urban runoff. *J. N. Am. Benthol. Soc.* 30, 710–727.
- Kauffman, G.J., Vonck, K.J., 2011. Frequency and intensity of extreme drought in the Delaware Basin, 1600–2002. *Water Resour. Res.* 47, 1–13.
- Krause, A.E., Frank, K.A., Mason, D.M., Ulanowicz, R.E., Taylor, W.W., 2003. Compartments revealed in food-web structure. *Nature* 426, 282–285.
- Kundzewicz, Z.W., Yukiko, H., Shinjirodoi, K., 2011. River floods in the changing climate—observations and projections. *Water Resour. Manag.* 24, 2633–2646.
- Lake, P.S., 2003. Ecological effects of perturbation by drought in flowing waters. *Freshw. Biol.* 48, 1161–1172.
- Lake, P.S., 2008. Drought, the ‘Creeping Disaster’: Effects on Ecosystems. *Land & Water Australia*, Canberra, 40pp.

- Lake, P.S., 2011. *Drought and Aquatic Ecosystems: Effects and Responses*. John Wiley and Sons, Chichester, UK.
- Lancaster, J., 1996. Scaling the effects of predation and disturbance in a patchy environment. *Oecologia* 107, 321–331.
- Layer, K., Riede, J.O., Hildrew, A.G., Woodward, G., 2010. Food web structure and stability in 20 streams across a wide pH gradient. *Adv. Ecol. Res.* 42, 265–299.
- Layer, K., Hildrew, A.G., Jenkins, G.B., Riede, J.O., Rossiter, S.J., Townsend, C.R., Woodward, G., 2011. Long-term dynamics of a well-characterised food web: four decades of acidification and recovery in the Broadstone Stream model system. *Adv. Ecol. Res.* 44, 69–117.
- Ledger, M.E., Hildrew, A.G., 2001. Recolonization by the benthos of an acid stream following a drought. *Arch. Hydrobiol.* 152, 1–17.
- Ledger, M.E., Winterbourn, M.J., 2000. Growth of New Zealand stream insect larvae in relation to food type. *Arch. Hydrobiol.* 149, 353–364.
- Ledger, M.E., Crowe, A.L.M., Woodward, G., Winterbourn, M.J., 2002. Is the mobility of stream insects related to their diet? *Arch. Hydrobiol.* 154, 41–59.
- Ledger, M.E., Harris, R.M.L., Milner, A.M., Armitage, P.D., 2006. Disturbance, biological legacies and community development in stream mesocosms. *Oecologia* 148, 682–691.
- Ledger, M.E., Harris, R.M.L., Armitage, P.D., Milner, A.M., 2008. Disturbance frequency influences patch dynamics in stream benthic algal communities. *Oecologia* 155, 809–819.
- Ledger, M.E., Harris, R.M.L., Armitage, P.D., Milner, A.M., 2009. Realism of model ecosystems: an evaluation of physicochemistry and macroinvertebrate assemblages in artificial streams. *Hydrobiologia* 617, 91–99.
- Ledger, M.E., Edwards, F.K., Brown, L.E., Milner, A.M., Woodward, G., 2011. Impact of simulated drought on ecosystem biomass production: an experimental test in stream mesocosms. *Global Change Biol.* 17, 2288–2297.
- Ledger, M.E., Harris, R.M.L., Armitage, P.D., Milner, A.M., 2012. Climate change impacts on community resilience: experimental evidence from a drought disturbance experiment. *Adv. Ecol. Res.* 46, 211–258.
- Ledger, M.E., Brown, L.E., Edwards, F., Woodward, G., Milner, A.M., 2013. Drought impacts on the structure and functioning of complex food webs. *Nat. Clim. Chang.* 3, 223–227.
- Lehner, B., Doll, P., Alcamo, J., Henrichs, T., Kaspar, F., 2006. Estimating the impact of global change on flood drought risks in Europe: a continental integrated analysis. *Clim. Change* 75, 273–299.
- Marks, J.C., Power, M.E., Parker, M.S., 2000. Flood disturbance, algal productivity, and interannual variation in food chain length. *Oikos* 90, 20–27.
- Matthews, W.J., Marsh-Matthews, E., 2003. Effects of drought on fish across axes of space, time and ecological complexity. *Freshw. Biol.* 48, 1232–1253.
- Menge, B.A., Sutherland, J.P., 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.* 110, 730–757.
- Milly, P.C.D., Dunne, K.A., Vecchia, A.V., 2005. Global pattern of trends in stream flow and water availability in a changing climate. *Nature* 438, 347–350.
- Montoya, J.M., Woodward, G., Emmerson, M.C., Sole, R.V., 2009. Press perturbations and indirect effects in real food webs. *Ecology* 90, 2426–2433.
- Parker, S.M., Huryn, A.D., 2006. Food web structure and function in two arctic streams with contrasting disturbance regimes. *Freshw. Biol.* 51, 1249–1263.
- Petchey, O.L., Brose, U., Rall, B.C., 2010. Predicting the effects of temperature on food web connectance. *Phil. Trans. R. Soc. B* 365 (1549), 2081–2091.
- Petersen, J.E., Englund, G., 1995. Dimensional approaches to designing better experimental ecosystems: a practitioner's guide with examples. *Oecologia* 145, 216–224.

- Petraitis, P.S., Latham, R.E., Niesenbaum, R.A., 1989. The maintenance of species diversity by disturbance. *Q. Rev. Biol.* 64, 393–418.
- Poff, N.L., Richter, B.D., Arthington, A.H., Bunn, S.E., Naiman, R.J., Kendy, E., Acreman, M., Apse, C., Bledsoe, B.P., Freeman, M.C., Henriksen, J., Jacobsen, R.B., Kennen, J.G., Merritt, D.M., O’Keefe, J.H., Olden, J.D., Rodgers, K., Tharme, R.E., Warner, A., 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshw. Biol.* 55, 147–170.
- Raffaelli, D., 2004. How extinction patterns affect ecosystems. *Science* 306, 1141–1142.
- Raffaelli, D., White, P.C.L., 2013. Ecosystems and their services in a changing world: an ecological perspective. *Adv. Ecol. Rev.* 48. TS1
- Sabatino, M., Maceira, N., Aizen, M.A., 2010. Direct effects of habitat area on interaction diversity in pollination webs. *Ecol. Appl.* 20, 1491–1497.
- Sabo, J.L., Finlay, J.C., Kennedy, T., Post, D.M., 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science* 330, 965–967.
- Schindler, D.W., 1998. Replication versus realism: the need for ecosystem-scale experiments. *Ecosystems* 1, 323–334.
- Schlief, J., Mutz, M., 2011. Leaf decay processes during and after a supra-seasonal hydrological drought in a temperate lowland stream. *Int. Rev. Hydrobiol.* 96, 633–655.
- Sole, R.V., Montoya, J.M., 2001. Complexity and fragility in ecological networks. *Proc. R. Soc. Lond. B* 2, 2039–2045.
- Sousa, W.P., 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60, 1225–1239.
- Stewart, R.I.A., Bohan, D.A., Jeppesen, E., Korda, R.L., Ledger, M.E., Meerhoff, M., Moss, B., Mulder, C., Shurin, J.B., Suttle, B., Thompson, R., Trimmer, M., 2013. Mesocosm experiments as a tool for ecological climate change research. *Adv. Ecol. Rev.* 48. TS1
- Stubbington, R., 2012. The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour. *Mar. Freshw. Res.* 63, 293–311.
- Suren, A.M., Biggs, B.J.F., Duncan, M.J., Bergey, L.R., Lambert, P., 2003. Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 2. *Invertebrates. N. Z. J. Mar. Freshw. Res.* 37, 71–83.
- Taulbee, W.K., Nietch, Christopher T., Brown, D., Ramakrishnan, B., Tompkins, M.J., 2009. Ecosystem consequences of contrasting flow regimes in an urban effect stream mesocosm study. *J. Am. Wat. Res. Assoc.* 45, 907–927.
- Thompson, R.M., Dunne, J.A., Woodward, G., 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. *Freshw. Biol.* 57, 1329–1341.
- Tilman, D., 1990. Constraints and trade-offs: toward a predictive theory of competition and succession. *Oikos* 58, 3–15.
- Townsend, C.R., Hildrew, A.G., 1994. Species traits in relation to a habitat templet for river systems. *Freshw. Biol.* 31, 265–275.
- Townsend, C.R., Thompson, R.M., McIntosh, A.R., Kilroy, C., Edwards, E., Scarsbrook, M.R., 1998. Disturbance, resource supply, and food web architecture in streams. *Ecol. Lett.* 1, 200–209.
- Trimmer, M., Maanoja, S., Hildrew, A.G., Pretty, J.L., Grey, J., 2010. Potential carbon fixation by methane oxidation in well-oxygenated riverbed gravels. *Limnol. Oceanogr.* 55, 560–568.
- Tylianakis, J.M., Tscharntke, T., Lewis, O.T., 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445, 202–205.
- Vázquez, D.P., Simberloff, D., 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. *Am. Nat.* 159, 606–623.

- Villeneuve, A., Montuelle, B., Bouchez, A., 2011. Effects of flow regimes and pesticides on periphyton communities: evolution and role of biodiversity. *Aquat. Toxicol.* 102, 123–133.
- Wade, A.J., Whitehead, P.G., Hornberger, G.M., Snook, D.L., 2002. On modelling the flow controls on macrophyte and epiphyte dynamics in a lowland permeable catchment: the River Kennet, southern England. *Sci. Total Environ.* 282, 375–393.
- Walters, A.W., Post, D.M., 2008. An experimental disturbance alters fish size structure but not food chain length in streams. *Ecology* 89, 3261–3267.
- Walters, A.W., Post, D.M., 2011. How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. *Ecol. Appl.* 21, 163–174.
- Warren, P., 1994. Making connections in food webs. *Trends Ecol. Evol.* 9, 136–141.
- Wellnitz, T., Poff, N.L., 2012. Current-mediated periphyton structure modifies grazer interactions and algal removal. *Aquat. Ecol.* 46, 521–530.
- Williams, R.J., Berlow, E.L., Dunne, J.A., Barabasi, A., Martinez, N.D., 2002. Two degrees of separation in complex food webs. *Proc. Natl. Acad. Sci. U.S.A.* 99, 12913–12916.
- Wood, P.J., Boulton, A.J., Little, S., Stubbington, R., 2010. Is the hyporheic zone a refuge for aquatic macroinvertebrates during severe low flow conditions? *Fundam. Appl. Limnol.* 176, 377–390.
- Woodward, G., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L.E.L., Cross, W.F., Friberg, N., Ings, T.C., Jacob, U., Jennings, S., Ledger, M.E., Milner, A.M., Montoya, J.M., O’Gorman, E.O., Olesen, J.M., Petchey, O.L., Pichler, D.E., Reuman, D.C., Thompson, M.S., Van Veen, F.J.F., Yvon-Durocher, G., 2010. Ecological networks in a changing climate. *Adv. Ecol. Res.* 42, 71–138.
- Woodward, G., Brown, L., Edwards, F.K., Hudson, L.N., Milner, A.M., Reuman, D.C., Ledger, M.E., 2012. Climate change impacts in multispecies systems: drought alters food web size-structure in a field experiment. *Phil. Trans. R. Soc. B* 367 (1605), 2990–2997.
- Yodzis, P., 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69, 508–515.
- Young, B.A., Norris, R.H., Sheldon, F., 2011. Is the hyporheic zone a refuge for macroinvertebrates in drying perennial streams? *Mar. Freshw. Res.* 62, 1373–1382.
- Zar, J.H., 1999. *Biostatistical Analysis*, fourth ed. Prentice Hall, London.

B978-0-12-417199-2.00006-9, 00006

Non-Print Items

Keywords: Climate change, Extreme climatic events, Streams, Disturbance, Drought, Food webs, Experiment, Macroinvertebrates, Algae

UNCORRECTED PROOF

AECR, 978-0-12-417199-2