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Extreme climatic events alter aquatic food webs: a synthesis of evidence from a mesocosm drought experiment.

Mark E. Ledger[1], Lee E. Brown[2], François K. Edwards[3], Lawrence N. Hudson[4], Alexander M. Milner[1,5], Guy Woodward[4]

[1]School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK.

[2]School of Geography/water@leeds, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK.

[3]Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, OX10 8BB, UK.

[4]Division of Ecology and Evolution, Imperial College London, Silwood Park, Buckhurst Road, Ascot, Berkshire, SL5 7PY, UK.

[5]Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775, USA.

Correspondence: Dr Mark Ledger, School of Geography, Earth and Environmental Sciences,
University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK. email:
m.e.ledger@bham.ac.uk, phone 0121 414 5540, fax 0121 414 5528.

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I. 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 two-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.

II. INTRODUCTION

A. Extreme events and climate change

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).

Extreme events can be characterized 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 21st century, annual average runoff is projected to increase by 10-40 % at higher latitudes, and decrease by 10-30 % over mid-latitudes (Milly et al., 2005; Kundzewicz, 2011). There is already clear evidence that the frequency and intensity of droughts is 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. Vincente-Serrano et al., 2011), with unknown consequences for aquatic ecosystems.

B. Drought in river networks

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).

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 (Boulton, 2003; Lake, 2003; Fritz and Dodds, 2004; Bonada et al., 2007). 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 (Wood et al., 2010; Stubbington, 2012), 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.

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).

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; Wade et al., 2002; Suren et al., 2003; Ledger et al., 2008). Direct impacts on the secondary production of invertebrates and fish depend on drought intensity, with greatest effects occurring where flow cessation occurs (Matthews and Marsh-Matthews, 2003; Lake, 2011; Ledger et al., 2011).

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).

C. Food webs in climate change research: from qualitative to quantitative approaches

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 (Woodward et al., 2010; Stewart et al., 2013), 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).

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).

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.

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 (c.f. 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.

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.

D. Mesocosm experiments and climate change research

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 (Yodzis, 1988; Ledger et al., 2013).

Mesocosm experiments are especially important for studying extreme 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).

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).

In this paper 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 two 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.

III. METHODS

A. Stream mesocosms

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 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). While 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).

Physicochemical conditions were highly congruent among the mesocosms (Table 1; Harris et al., 2007). During the main study period, water temperature (mean 12.2 ºC) varied seasonally, with summer maxima (18.7 ºC in June 2000) and winter minima (6.0 ºC in December 2001) (Fig. 2). Inflowing water was nutrient rich (mean PO_4: 56.4 µg L^{-1}; NO_3: 5.62 mg L^{-1} from March 2000–February 2002) with alkaline pH (mean 8.1) and high conductivity (mean 460 µS cm^{-1}) (Harris et al., 2007), consistent with water quality in local chalk rivers (Casey, 1975; Bowes et al., 2005; 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).

B. Experimental design and application

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 colonization 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 supraseasonal 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 x 2 treatments = 8 channels in total).

C. Estimation of abundance, biomass and production of trophic elements.

Estimates of invertebrate abundance and biomass were made from samples (Surber sampler 0.025m^2, 300 µm mesh, n=3 per channel) collected monthly from each mesocosm between March 2000 and February 2002, immediately (1 hr) 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 while 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} yr^{-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 (Ledger and Winterbourn, 2000; Burrell and Ledger, 2003). Individual biomass (mg dry weight) was calculated for all invertebrate specimens using published length-mass regressions (see Edwards et al., 2009).

Secondary production (mg m^{-2} yr^{-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 in to 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).

D. Food web construction: binary webs

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 3,643 dissected guts were examined, with consumed items identified to the lowest practicable taxonomic unit. The guts of invertebrates were dissected at x20 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 x 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 versus 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.

E. Food web construction: quantitative webs

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

& Wallace, 1997; Benke, 2012) was used to quantify directly observed feeding links, with biomass flux (F_{ij}, mg m^{-2} yr^{-1}) from resource i to consumer j estimated as follows:

Determine the proportion of production derived from food type i (B_{i}):

$B_i = (G_i \times \mathrm{AE}_i) / \Sigma_{\mathrm{G}i=1,\ldots,n}$.

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

$F_{ij} = (\mathrm{B}_i \times \mathrm{P}_j) / (\mathrm{AE}_i \times \mathrm{NPE})$

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).

Quantitative food webs were compared using metrics derived from information theory (Bersier et al. 2002; Tylianakis et al., 2007; Ledger et al., 2013). For each web, we determined the quantified, weighted measures of linkage density (*LDq*), interaction diversity (*IDq*), interaction evenness (*IEq*), generality (*Gq*, mean number of resources per consumer) and vulnerability (*Vq*, 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:

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

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

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 $H_{N\bullet k}$ and $H_{P\bullet k}$ are:

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

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

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:

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

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

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).

III. RESULTS

A. Connectance webs

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 (Fig. 5, 6).

Drought significantly reduced web size (by 21%, from mean 61.0 ± 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, 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 (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).

B. Drought impact on trophic elements

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 olivaceum* and *Rhoicosphenia abbeviata*) (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 (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 9,282 ± 350 animals m^{-2}, disturbed 8,310 ± 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 (by 60 % to

3,596 ± 455 mg m^{-2} yr^{-1}, ANOVA, $F_{1,3}$ = 12.59, P = 0.038) and standing biomass (by 66% to 938 ± 112 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 filter-feeders, collector-gatherers, grazer-scrapers and shredders) (see Table 7), it became evident that the impact of the treatment on production varied *among* functional feeding groups (Figure 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. *Erpobdella octoculata*, *Polycentropus flavomaculatus*, *Sialis lutaria*), whereas the much smaller Tanypodinae larvae were more resilient, maintaining production in disturbed habitats.

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 A). Grazer-scraper production was dominated by the snail *Radix balthica* (2,903 ± 969 mg AFDM m^{-2} yr^{-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 A). Production of the dominant shredders *Gammarus pulex* (1291 ± 464 mg AFDM m^{-2} yr^{-1}) and *Sericostoma personatum* (108 ± 35 mg AFDM m^{-2} yr^{-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

A). 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).

C. *Quantified food webs*

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 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).

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 *Radix balthica* (32 % total ingestion) and *Valvata piscinalis* (3%), collector-gathering snails *Potamopyrgus antipodarum* (25 %) and mayflies *Ephemera danica* (5%), shredding amphipods *Gammarus 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 ± 25,451 to 39,792 ± 6,804 mg m^{-2} yr^{-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 processers 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 taxa: *i.e.*, 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, χ^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 (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).

V. DISCUSSION

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. Dewson et al., 2007b; Walters and Post, 1998; Chadwick and Huryn, 2007). 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).

In the present study, we simulated hydrologic drought in a series of stream mesocosms over two years to capture intra- and inter-generational 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 (Fig. 7, 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 socioeconomically and culturally valuable fish populations at the top of the food webs.

A. Primary Producers

Disturbance reduced the size of the food webs (see Fig. 3, 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 *Gongrosira 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).

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.

B. Qualitative webs, size structure and species traits

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*) versus 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 then 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 (Sabo et al., 2010; Ledger et al., 2013), or no change where flow reduction is less severe (Walters and Post, 2008).

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 (Warren, 1994; Beckerman et al., 2006). Consistent with the specialisation-disturbance (S-D) hypothesis (Vazquez 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 (Vazquez 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.

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).

Cumulative degree distributions for mesocosm webs were characterized by exponential decay functions both in 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).

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.

C. Secondary production and quantified food webs

The secondary production of consumers was combined with dietary data to quantify the flow of organic matter from resource to consumer (Benke and Wallace, 1997; Benke, 2012). 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.

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 methods), 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.

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 13; 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).

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.

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?

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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. Climate Change 81, 71-95.

Benke, A.C. 2012. Secondary production, quantitative food webs, and trophic position. Nature Education Knowledge 3, 26.

Benke, A.C., Wallace, J.B. 1997. Trophic basis of production among riverine caddisflies: 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: Aquatic Insects. Challenges to Populations (eds J. Lancaster and R.A. Briers). CAB, Wallingford, UK, 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. Tot. 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. Physical Review Letters 85, 5468-5471.

Camacho, J., Guimera, R., Nunes Amaral, L.A. 2002. Robust patterns in food web structure. Physical Review Letters 88, 228102.

Casey, H. 1975. Variation in chemical composition of the River Frome, England, from 196 to 1972. Freshwat. 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. Freshwat. Bio. 48, 1199-1206.

Crucitti, P., Latora, V., Marchiori, M. 2004. Model for cascading failures in complex networks. Physical Review 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., 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. Ecology Letters, 5, 558-567.

Dunne, J.A., Williams, R.J. 2009. Cascading extinctions and community collapse in model food webs. Phil. Trans. R. Soc. B 364, 1711-1723.

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.

Extence, C.A., Balbi, D.M., Chadd, R.P. 1999. River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. Regul. Rivers: Res. Mgmt. 15, 545–574.

Everard, M., 1996. The importance of periodic droughts for maintaining diversity in the freshwater environment. Freshwater Forum, 7, 33-50.

Fenoglio, S., Bo, T., Bost, G. 2006. Deep interstitial habitat as a refuge for *Agabus paludosus*, Fabricius) (Coleoptera : Dytiscidae) during summer droughts. Coleopterists Bulletin 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. Advances in Ecological Research, 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. Freshwat. 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.

Hannesdottir et al (this volume)

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. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson, Eds. 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? Freshwat. 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. Freshwat. Biol. 48, 1161-1172.

Lake, P.S. 2008. Drought, the 'creeping disaster': Effects on ecosystems. Land & Water Australia, Canberra. 40 pp.

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., 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.

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.

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., Hildrew, A.G. 2001. Recolonization by the benthos of an acid stream following a drought. Arch. Hydrobiol. 152, 1-17.

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. Nature Clim. Change 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. Climate 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. Freshwat. 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., Sole, R.V. 2002. Small world patterns in food webs. J. Theor. Biol. 214, 405–412.

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.

Petersen, J.E., Englund, G. 1995. Dimensional approaches to designing better experimental ecosystems: a practitioner’s guide with examples. Oecologia 145, 216-224.

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.

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., Bledscoe, 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. Freshwat. Biol. 55, 147–170.

Raffaelli, D. 2004. How extinction patterns affect ecosystems. Science 306, 1141-1142.

Raffaelli, White (2013).

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. Internat. Rev. Hydrobiol. 96, 633-655.

Smith, H., Wood, P.J., Gunn, J. 2003. The influence of habitat structure and flow permanence on invertebrate communities in karst spring systems. Hydrobiologia 510, 53-66.

Sole, R.V., Montoya, J.M. 2001. Complexity and fragility in ecological networks. Proc. Roy. Soc. London 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 et al. 2013.

Stubbington, R. 2012. The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour. Mar. Freshwat. 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. Freshwat. 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. Amer. Wat. Res. Assoc. 45, 907-927.

Tilman, D. 1990. Constraints and trade-offs: toward a predictive theory of competition and succession. Oikos 58, 3-15.

Thompson, R.M., Dunne, J.A., Woodward, G. 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. Freshwat. Biol. 57, 1329–1341.

Townsend, C.R., Hildrew, A.G. 1994. Species traits in relation to a habitat templet for river systems. Freshwat. 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.

Vicente-Serrano, S.M., Cuadrat, J.M. 2007. North Atlantic Oscillation control of drought in N.E. Spain; evaluation since 1600 AD. Climate Change 85, 357-379.

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. Tot. 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 refugium for aquatic macroinvertebrates during severe low flow conditions? Fund. App. 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.

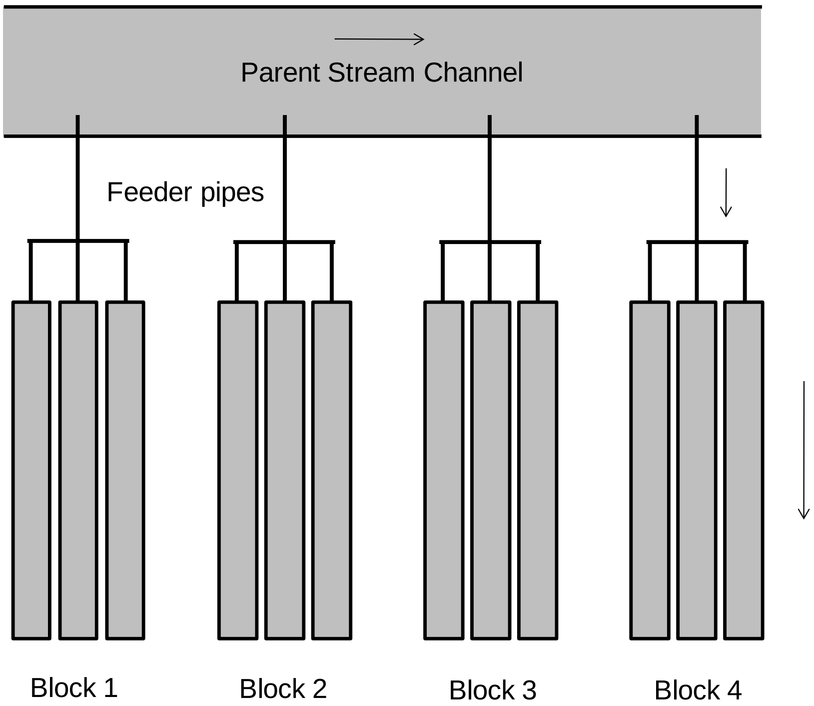
Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69, 508–515.

Young, B.A., Norris, R.H. Sheldon, F. 2011. Is the hyporheic zone a refuge for macroinvertebrates in drying perennial streams? Mar. Freshwat. Res. 62, 1373-1382.

Zar, J.H. 1999. Biostatistical Analysis, 4th Edition. Prentice Hall, London.

Figure 1. Schematic representation (a) and photographic image (b) of the stream mesocosm facility at the Freshwater Biological Association River Laboratory, Dorset, U.K. Four blocks of three stream mesocosms (each channel 12 m length x 0.3 m width) were fed water through pipes (6 m length) from the parent stream. Water flow (direction indicated by arrows) in to 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.

(a)



(b)

Figure 2. Temperature profiles of mesocosm replicates subject to continuous (a-d) and intermittent (e-h) flow.

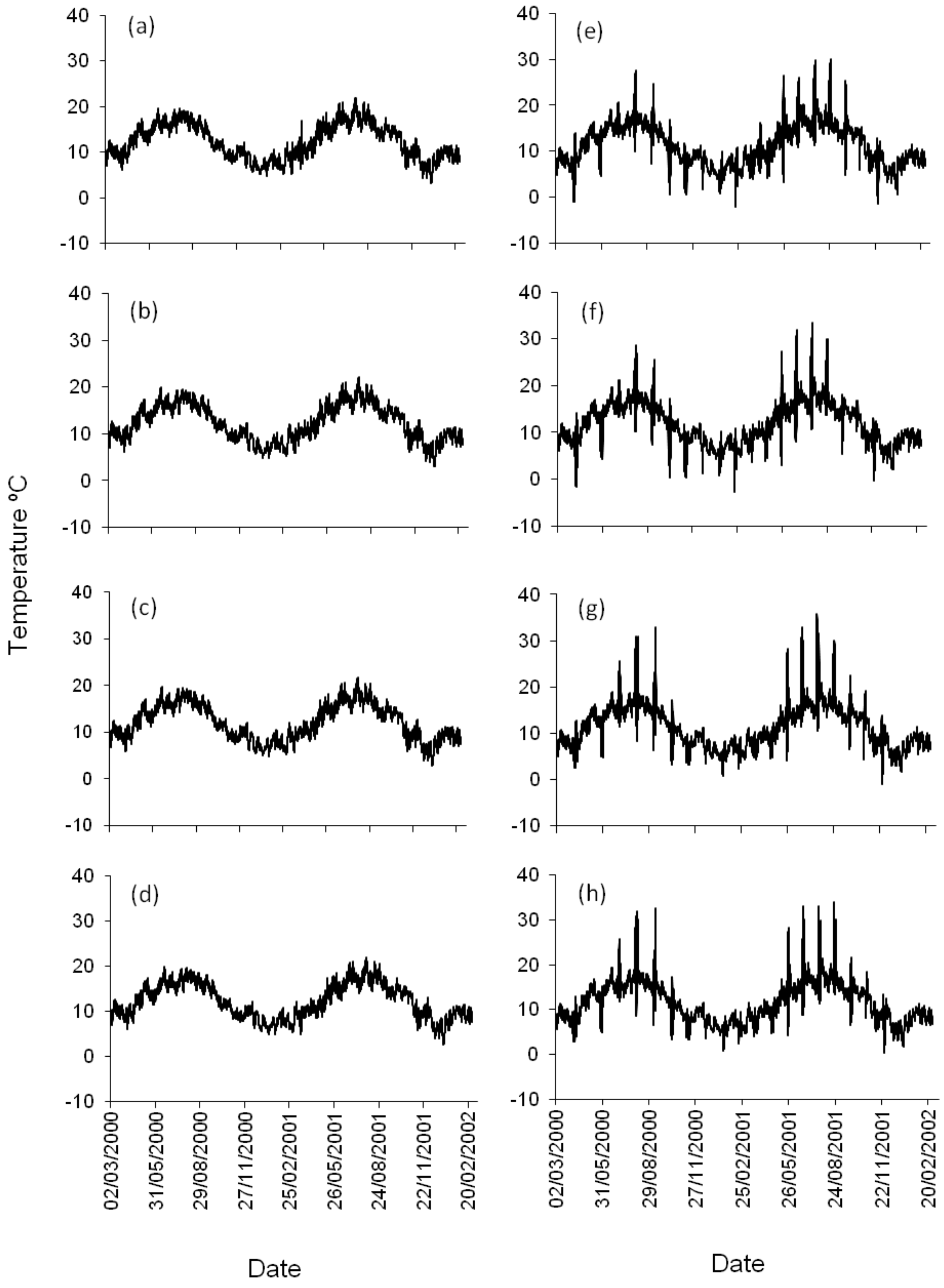


Figure 3a. Food webs from the manipulative field experiment (block 1 and 2, see Fig. 3b for block 3 and 4), in controls (permanent flow) and drought-disturbed (intermittent drying) channels. The webs are ordered vertically by trophic level, from basal resources to apex predators. Open circles denote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

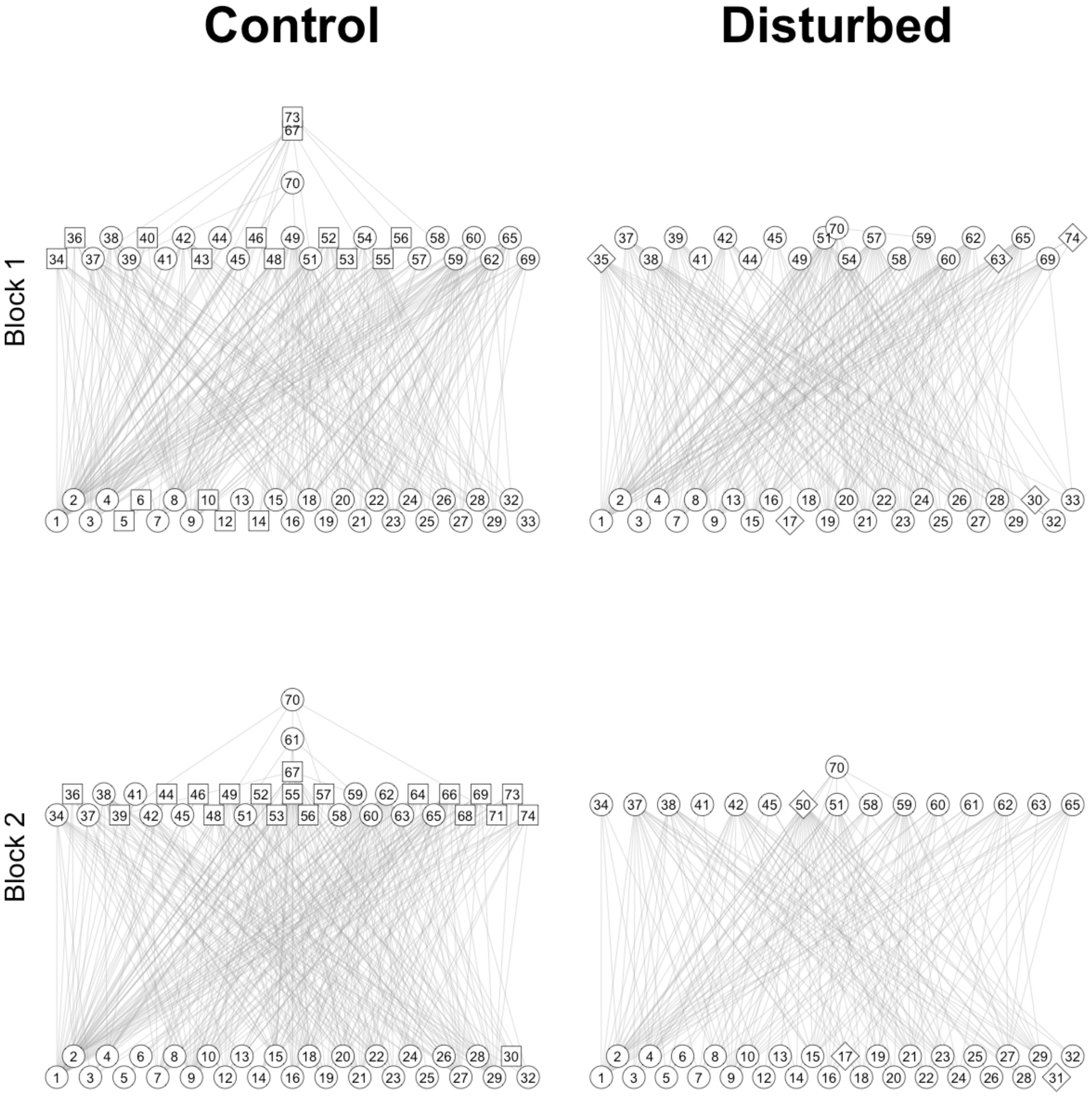


Figure 3b. Food webs from the manipulative field experiment (block 3 and 4, see Fig. 3a for block 1 and 2), in controls (permanent flow) and drought-disturbed (intermittent drying) channels. The webs are ordered vertically by trophic level, from basal resources to apex predators. Open circles denote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

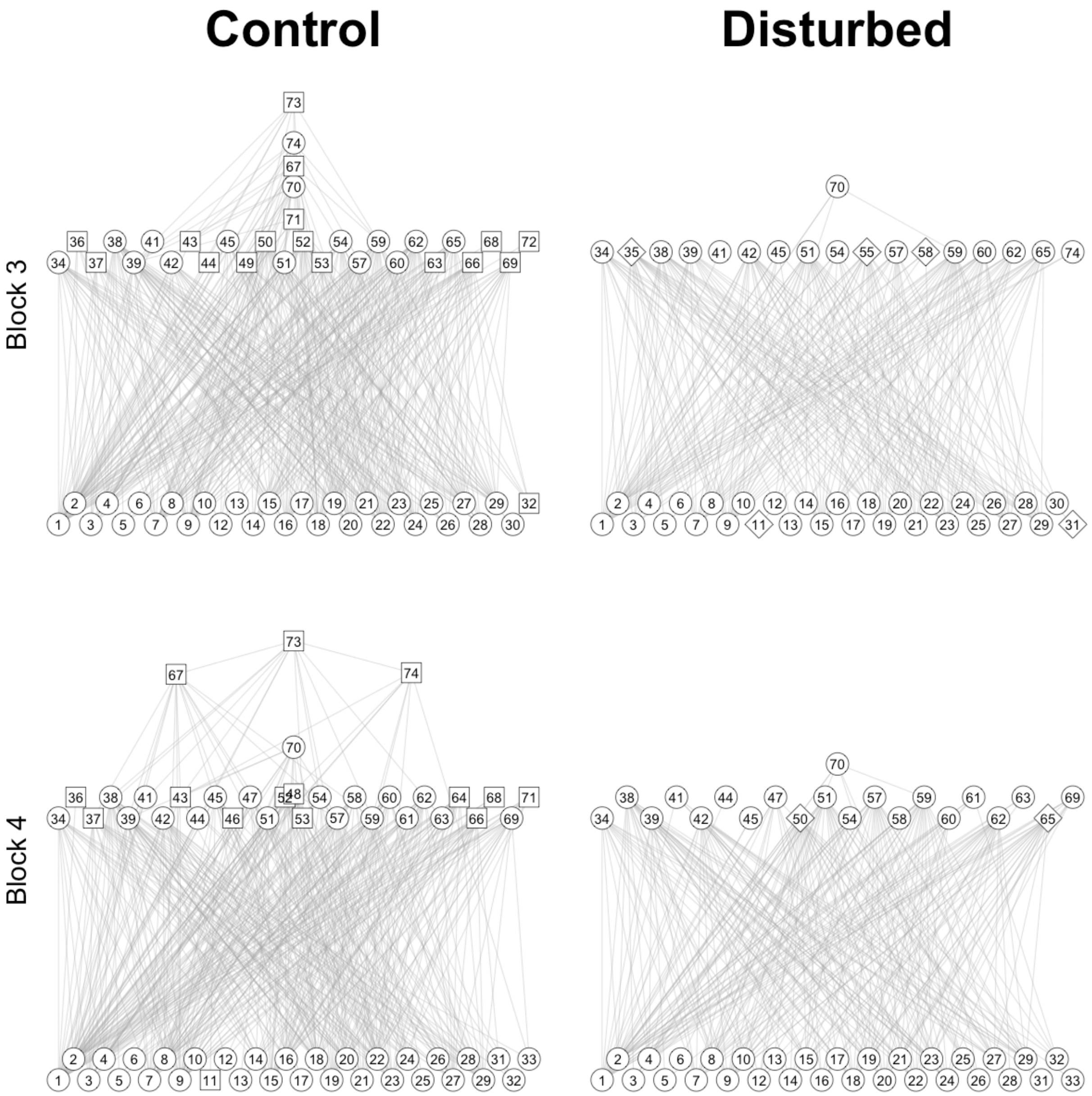


Figure 4. Physiognomy of algal patch types in stream mesocosms. Diatom crusts (a) were mainly *Gongrosira incrustans* and mats (b) were dominated by *Melosira varians* and. Bar = 10 mm.

(a) Algal crust

(b) Algal mat

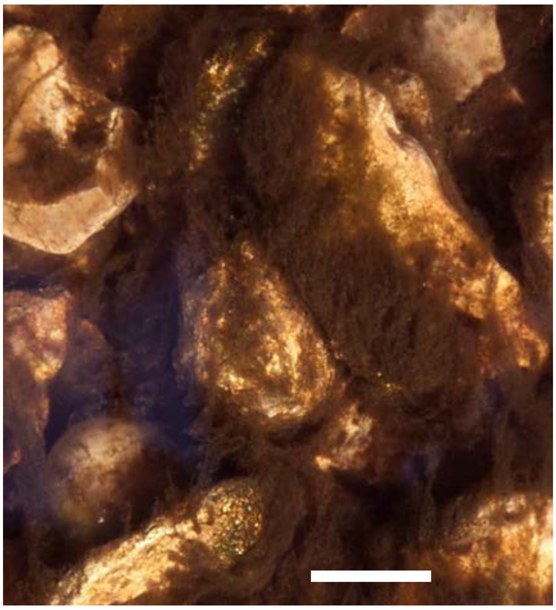


Figure 5. Food webs in undisturbed controls (replicate C1) incorporating abundance and body size data. The central matrix indicates an observed feeding interaction between a consumer (column) and a resource (row) with a black dot, and thus, each column reflects the diet of a consumer taxon. Consumer 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.

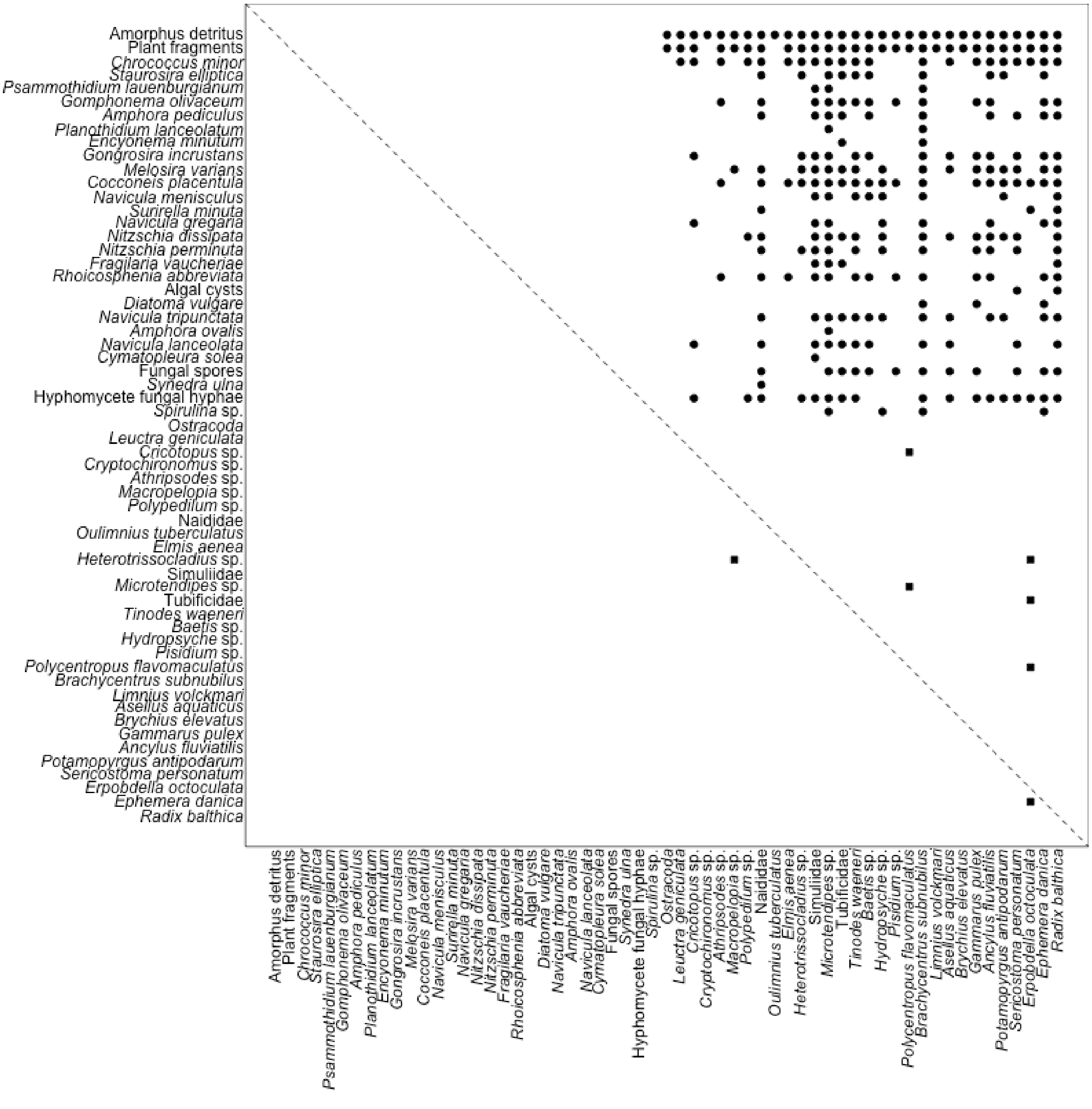


Figure 6. Food webs in drought-disturbed mesocosms (replicate D1) incorporating abundance and body size data. The central matrix indicates an observed feeding interaction between a consumer (column) and a resource (row) with a black dot, and thus, each column reflects the diet of a consumer taxon. Consumer 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.

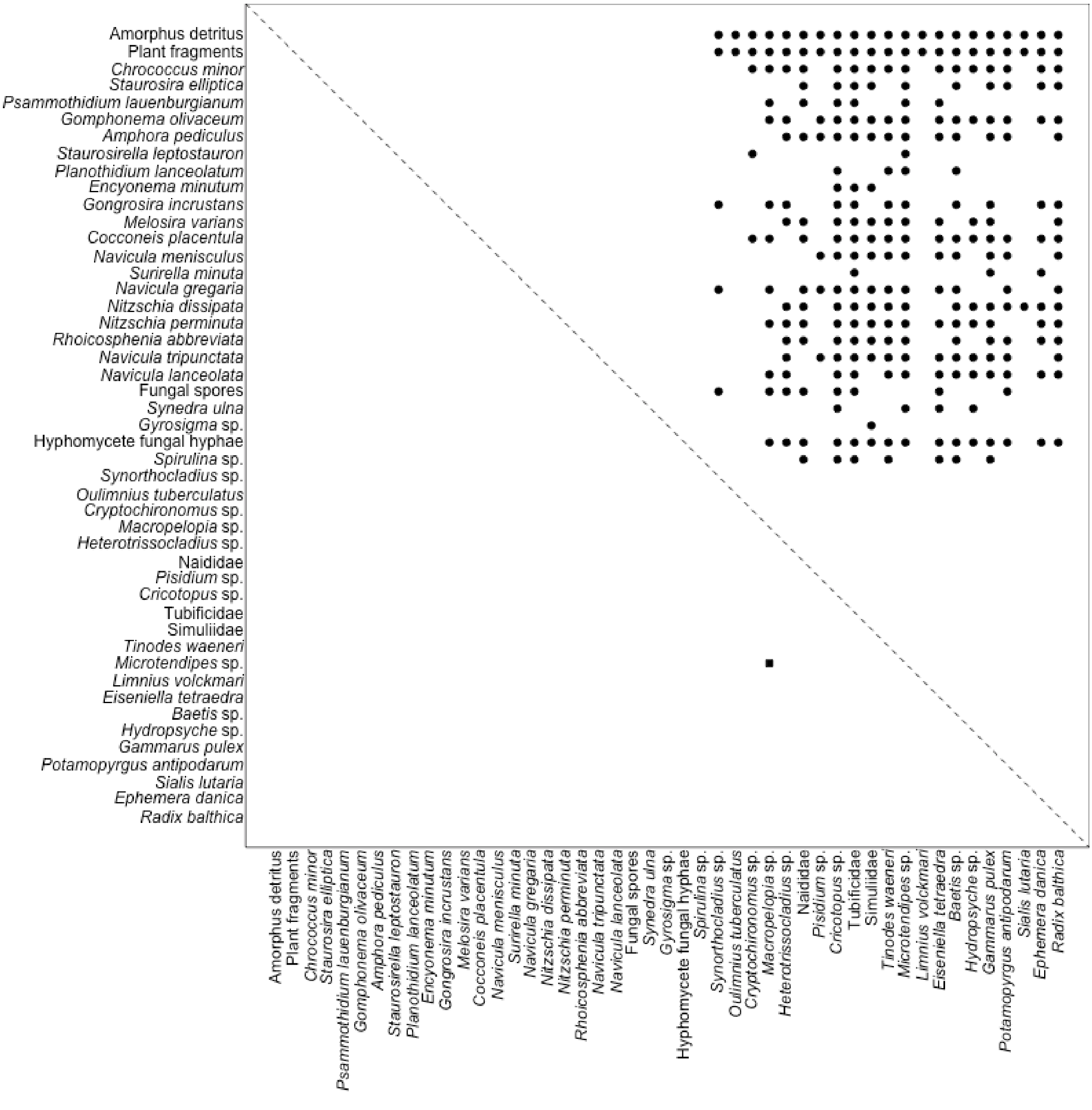


Figure 7. Mean (± 1 SE) taxon richness of basal resources, primary consumers and predators in drought and control food webs. Trophic group, drought treatment and their interaction significantly affect taxon richness (ANOVA, n=24, *P*< 0.0001 in all cases). Asterisks above individual trophic groups denote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

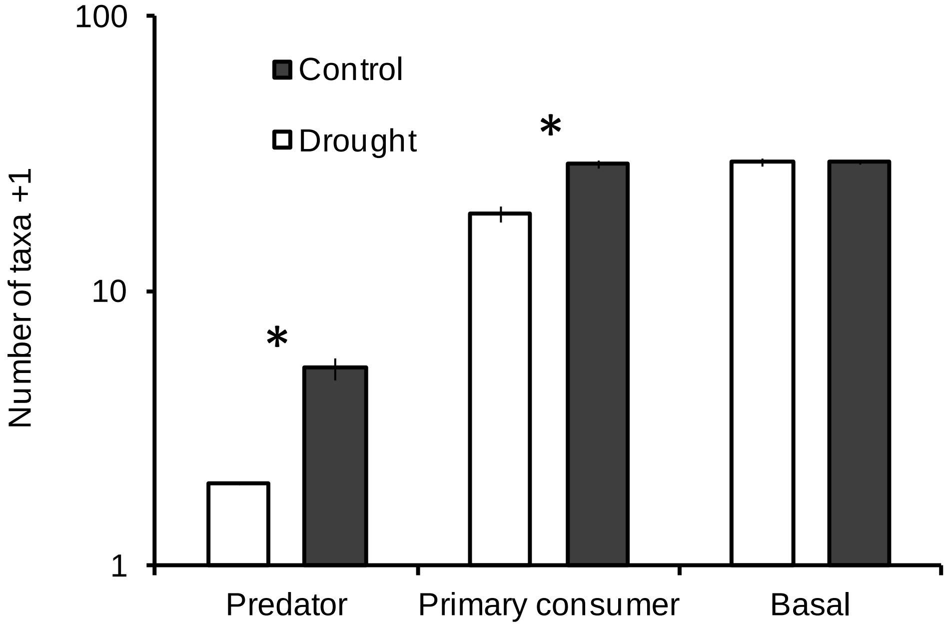


Figure 8. (a) Characteristic path lengths (*d*) and (b) degree distributions of control and drought-impacted food webs.

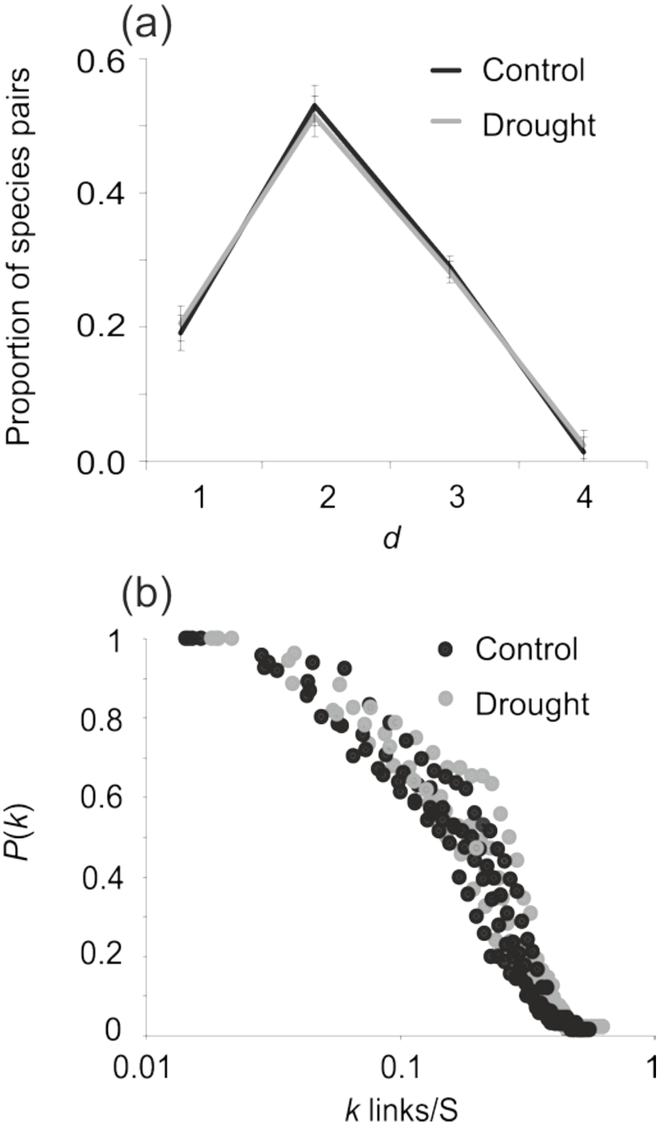


Figure 9. Mean (± 1 SE) biomass of basal resources, primary consumers and predators in drought and control food webs. Trophic group, drought treatment and their interaction significantly affect taxon richness (ANOVA, n=24, *P*< 0.0001 in all cases). Asterisks above individual trophic groups denote significant differences between treatments (ANOVA, n=8, *P*<0.05).

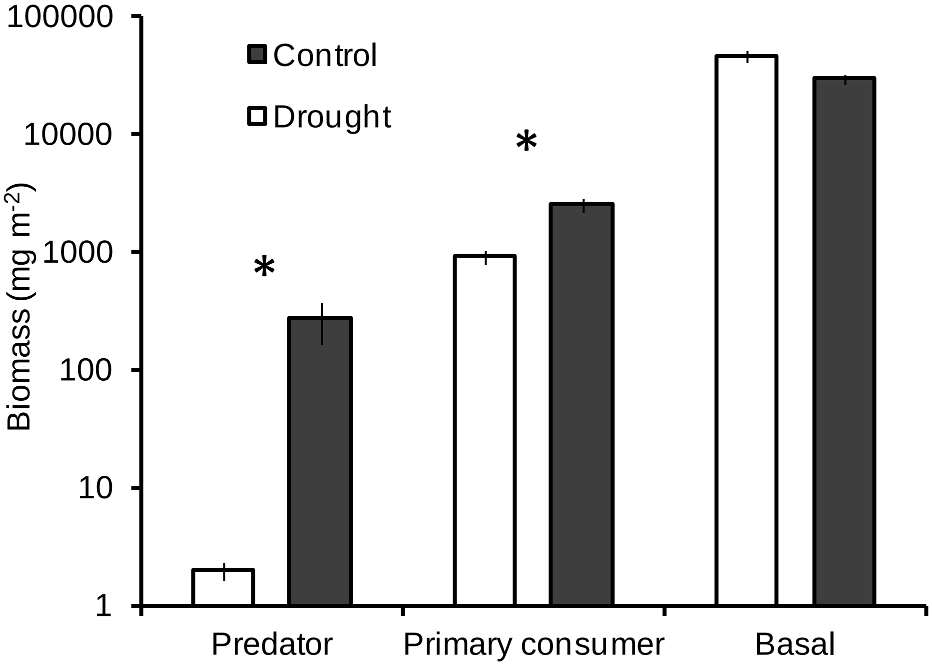


Figure 10. Mean (± 1 SE) annual secondary production (a), biomass (b) and numerical abundance (c) for all macroinvertebrates, and key functional feeding groups, in drought treatments and controls.

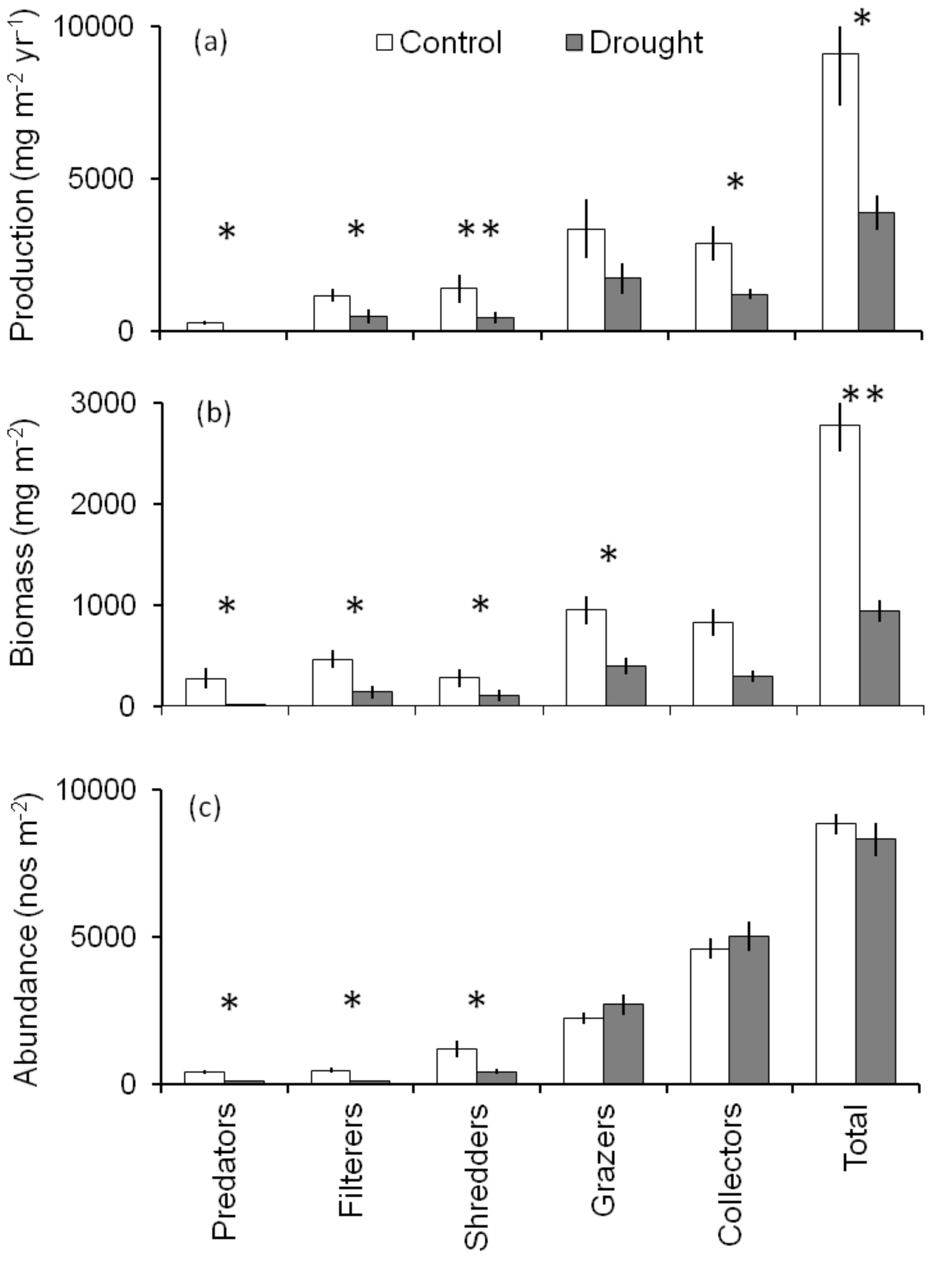


Figure 11. Distribution of high-frequency (approximately monthly) dewatering effects on secondary production of macroinvertebrate taxa in six functional feeding groups (figure redrawn after Ledger et al., 2011). Taxa were classified according to their statistically significant positive (+) negative (-)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

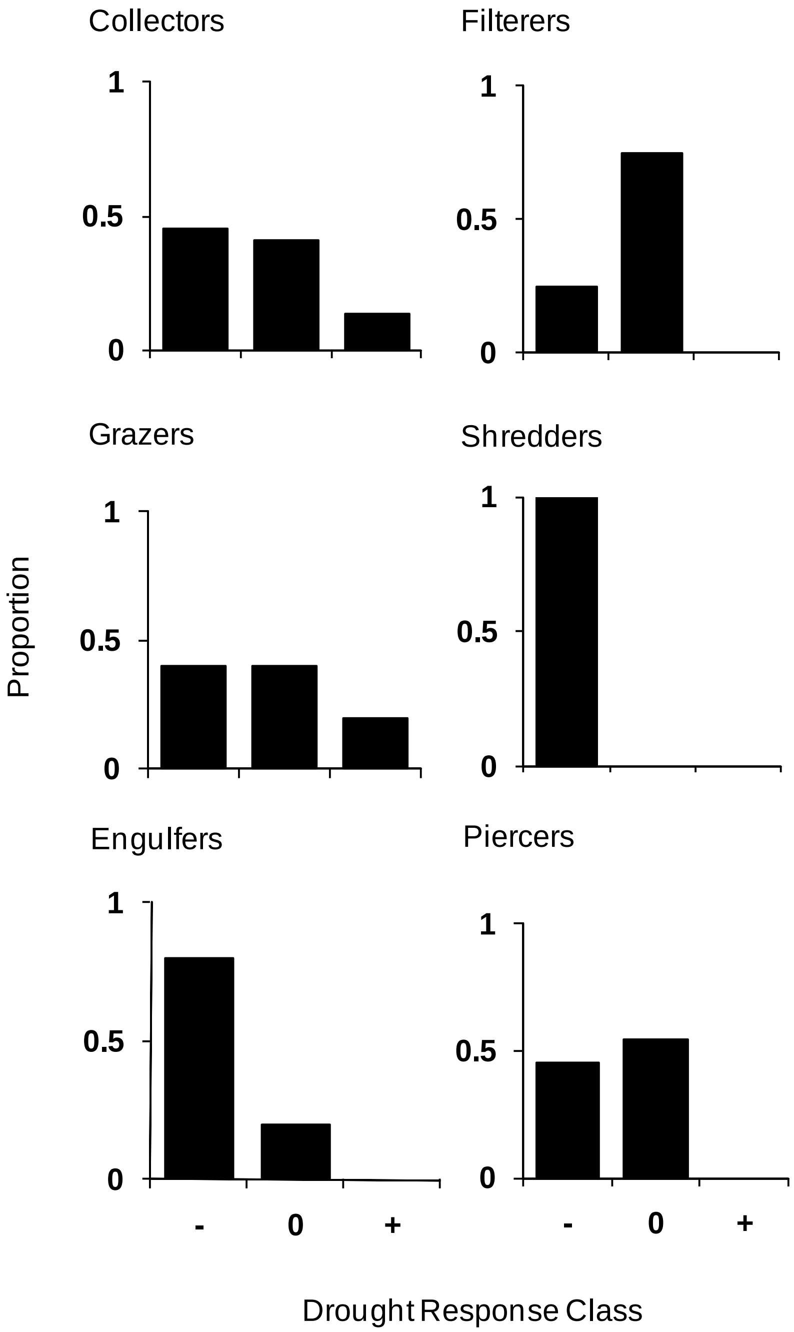


Figure 12. Mean (± 1 SE) effect of high-frequency drought on secondary production of macroinvertebrate taxa in relation to a) the potential number of life-cycles per year and b) mean individual body mass (figure redrawn after Ledger et al., 2011).

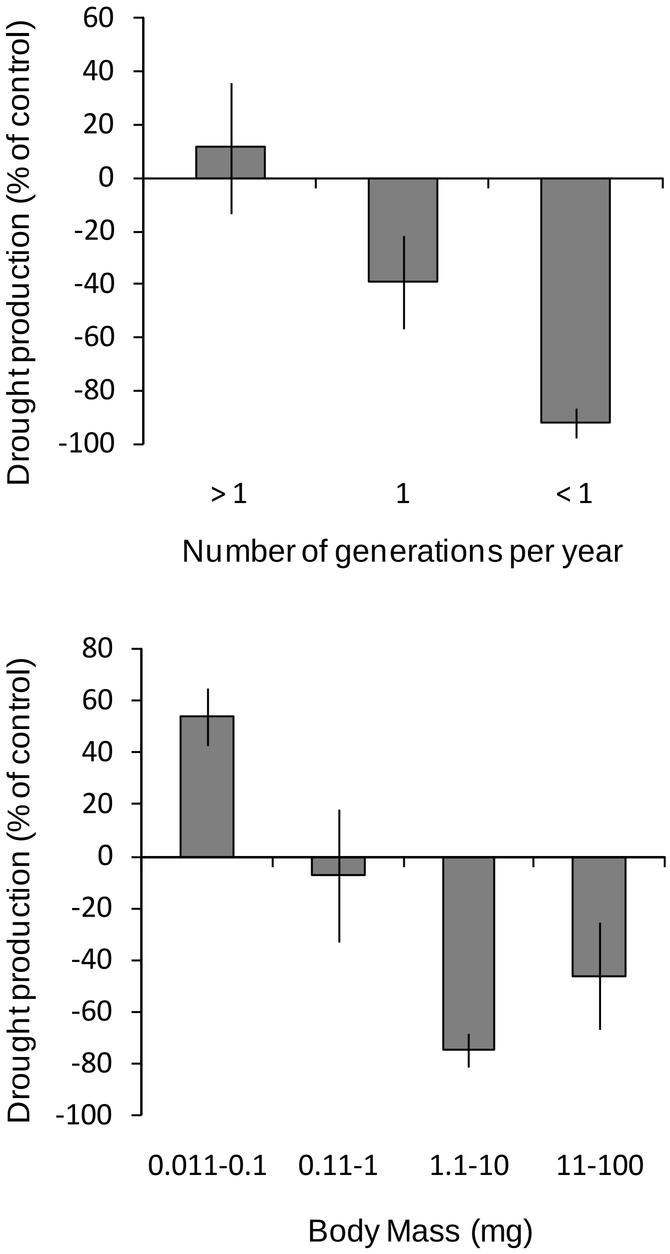


Figure 13. Quantitative food webs in replicate control (C1-C4) and drought (D1-D4) treatments, redrawn from Ledger et al. 2013. For each web, lower bars are basal resources, middle bars are primary consumers and top bars are predators. For each consumer, the height and width of the bars is proportional 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.

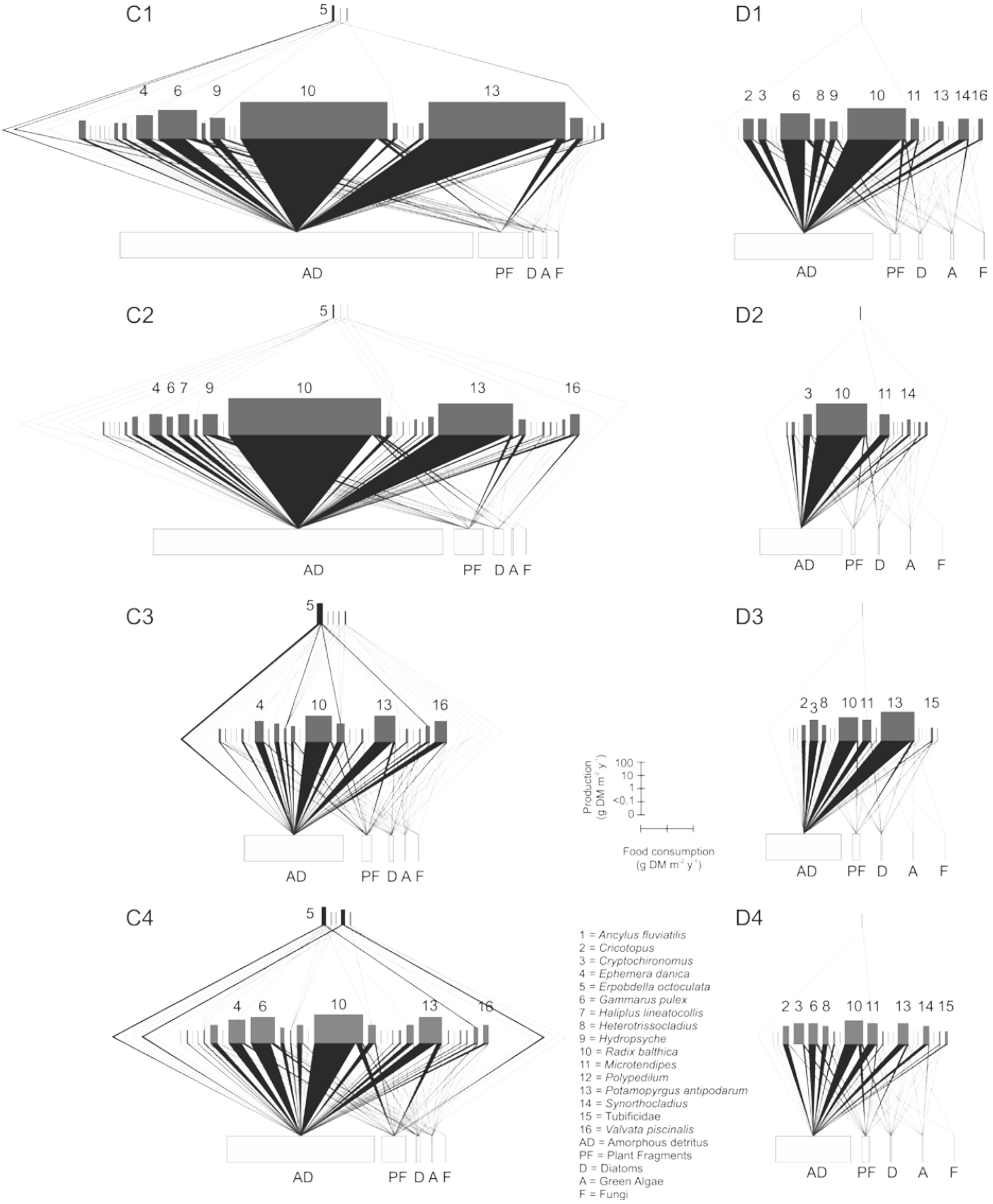


Fig. 14. Biomass fluxes from resources to consumers in control and drought-disturbed food webs as a mean (+ 1 SE) frequency distribution for all replicate webs.

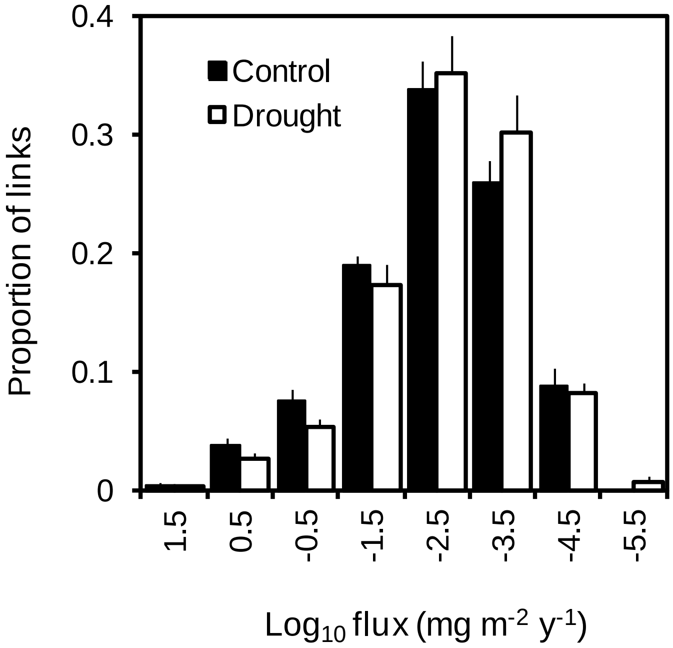


Fig. 15. Biomass fluxes from resources to core consumers in controls (a) and drought-disturbed treatments (b). The thickness of the arrows is proportional to flux magnitude (mg m^{-2} yr^{-1}).

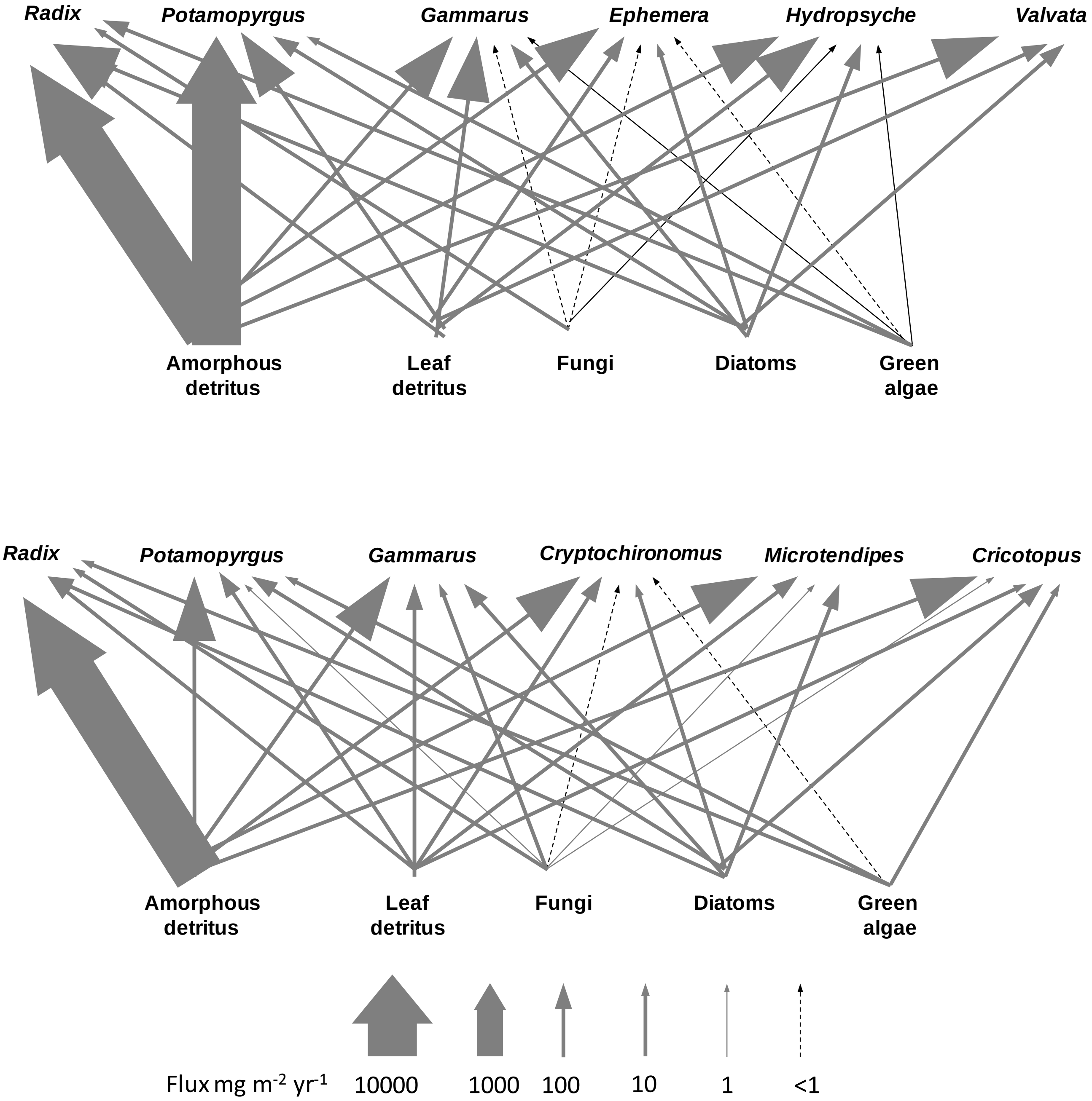


Fig. 16. Mean percentage change in biomass flux to consumers for the strongest pathways (> 1 g m^{-2} yr^{-1}). Taxa are ranked from left to right in order of decreasing mean body mass (mg).

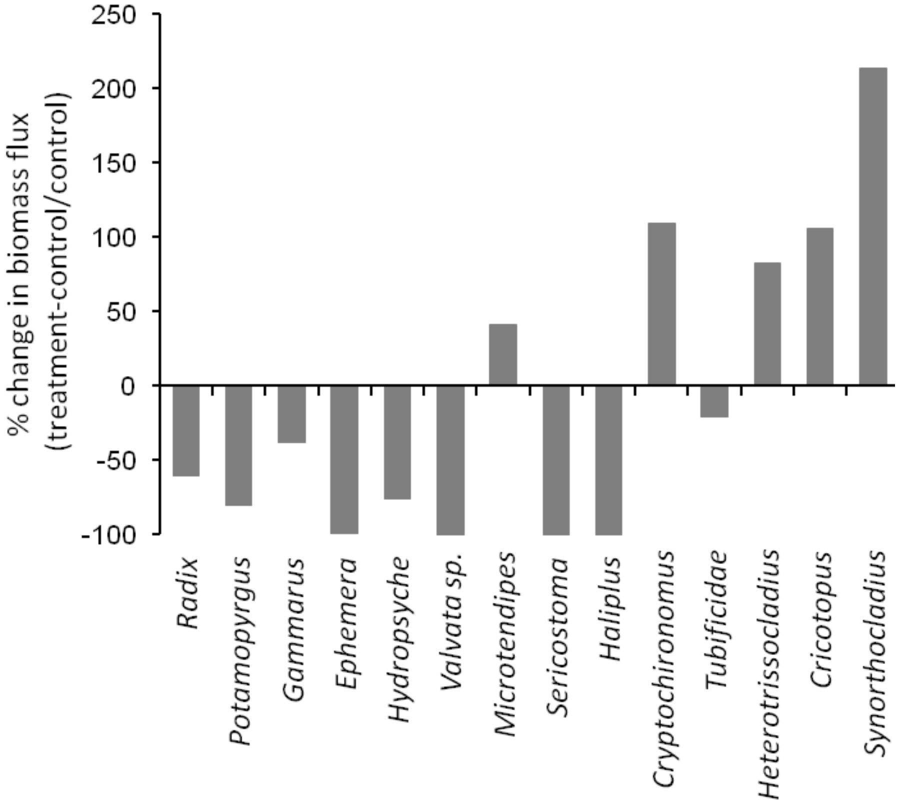


Table 1. Physicochemistry (outside dewatering periods) demonstrating mesocosm replicability among controls (C1-C4) and drought impacted (D1-D4) channels. Determinands were measured approximately monthly, excepting nitrate and soluble reactive phosphorus (SRP) which were both sampled once that the end of the experiment.

		Control				Drought			
		C1	C2	C3	C4	D1	D2	D3	D4
Conductivity (µS/cm)	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)	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 °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)	Endpoint	6.8	6.9	6.9	7.0	6.9	7.0	6.9	7.0
SRP (µg/L)	Endpoint	59.2	54.3	55.5	59.2	58.0	54.8	56.0	54.1

Table 2. Descriptors of flow and thermal regimes in undisturbed control (C1-C4) and drought-disturbed (D1-D4) stream mesocosms. Temperature profiles in drought-disturbed channels include heating/cooling at the substratum surface during dewatering episodes.

		Control				Drought			
		C1	C2	C3	C4	D1	D2	D3	D4
Flow (L/s)	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 (°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

Table 3. List of basal resources in stream channel food webs. Numerical node identifiers (Fig. 3) are given in brackets.

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

Table 4. List of consumers in stream channel food webs. Numerical node identifiers (Fig. 3) are given in brackets.

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]
Haliplus lineatocollis (Marsham) [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 ap. [63]
Theodoxus fluviatilis (L.) [64]
Tinodes waeneri (L.) [65]
Tipula montium Egger [50]
Tubificidae [51]
Valvata piscinalis (Müller) [66]

Table 5. Qualitative (binary) food web metrics for drought and control stream food webs. Metrics were 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 ($L/S_{\text{consumers}}$), vulnerability ($L/S_{\text{resources}}$). ANOVA tested for the effect of drought (below) and block (P >0.05, not shown).

	Control		Drought		ANOVA	
Metric	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

Table 6. Mean densities (10^3 cells cm^{-2}) of benthic algae in mesocosm food webs. Algae formed hard calcite-impregnated crusts or loosely-attached filamentous mats on the surfaces of stones.

	Control		**Drought**	
	Mean	SE	Mean	SE
Crust flora				
Gongrosira incrustans	7610.8	1258.1	1364.4	112.4
Amphora pediculus	469	45	213	33
Gomphonema olivaceum	58.2	4.3	43.3	13.6
Navicula tripunctata	13.9	2.4	12.0	33.6
Rhoicosphenia abbreviata	32.0	1.5	12.4	4.1
Total	**8183.7**	**1310.9**	**1645.2**	**196.8**
Mat flora				
Amphora ovalis	5.9	1.4	2.7	0.7
Cocconeis placentula	65.3	9.1	44.3	16.3
Cymatopleura solea	0.9	0.4	1.1	0.2
Cymbella lanceolata	0.2	0.0	0.5	0.0
Diatoma vulgaris	7.7	2.5	5.7	1.5
Encyonema minutum	2.2	0.7	2.1	0.4
Fragilaria vaucheriae	27.1	15.6	16.8	10.7
Gyrosigma sp.	1.9	0.8	3.0	4.4
Melosira varians	193.8	72.2	175.5	74.5
Navicula gregaria	4.9	0.8	7.7	0.9
Navicula lanceolata	82.6	17.8	102.5	33.6
Navicula menisculus	157.4	12.8	206.2	29.4
Nitzschia dissipata	65.3	11.4	50.0	2.8
Nitzschia perminuta	10.8	2.6	22.0	5.9
Planothidium lanceolatum	221.0	23.3	181.6	16.9
Psammothidium lauenburgianum	21.5	5.4	16.5	2.4
Staurosira elliptica	4.0	0.9	10.3	2.4
Staurosirella leptostauron	2.8	0.7	3.4	1.4
Surirella brebissonii	1.1	0.4	0.6	0.2
Surirella minuta	7.7	2.3	13.7	5.9
Synedra ulna	8.6	2.1	6.6	4.5
Spirulina 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**

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

Taxa	Control			Drought		
	B	*P*	*N*	*B*	*P*	*N*
Predators	**271**	**271**	**431**	**2**	**34**	**100**
Erpobdella octoculata (H)	215	143	45	-	-	-
Macropelopia sp. (D)	3	18	124	2	34	100
Pentaneura sp. (D)	<1	4	28	-	-	-
Platambus maculatus (C)	10	6	17	-	-	-
Polycentropus flavomaculatus (T)	19	74	196	-	-	-
Procladius sp. (D)	<1	4	25	-	-	-
Sialis lutaria (M)	23	23	10	-	-	-
Filter feeders	**461**	**1183**	**456**	**138**	**474**	**95**
Bithynia sp. (G)	2	9	2	-	-	-
Brachycentrus subnubilus (T)	1	2	4	2	3	10
Hydropsyche siltalai (T)	448	1120	67	135	461	37
Pisidium sp. (B)	9	46	360	2	7	64
Simulium sp. (D)	<1	6	35	<1	4	22
Collector-gatherers	**825**	**2886**	**4633**	**295**	**1226**	**4893**
Asellus aquaticus (Cr)	30	89	116	9	25	43
Athripsodes sp. (T)	1	3	11	-	-	-
Brychius elevatus (C)	10	17	21	2	2	4
Cryptochironomus sp. (D)	5	58	140	10	115	340
Eiseniella tetraedra (O)	-	-	-	2	3	6
Elmis aenea (C)	1	3	33	-	-	-
Ephemera danica (E)	239	380	93	13	7	5
Haliplus lineatocollis (C)	54	225	67	14	59	20
Leuctra geniculata (P)	3	10	36	-	-	-
Limnius volckmari (C)	2	4	77	1	2	6
Microtendipes sp. (D)	17	195	459	22	268	796
Naididae (O)	6	21	976	10	39	2035
Ostracoda	<1	<1	371	<1	<1	49
Oulimnius sp. (C)	5	22	133	1	2	24
Polypedilum sp. (D)	3	32	79	2	27	74
Potamopyrgus antipodarum (G)	403	1631	562	128	414	127
Prodiamesinae (D)	<1	3	39	<1	3	42
Tipula (Yamatotipula) montium (D)	29	91	3	63	153	42
Tubificidae (O)	17	104	1844	17	105	1506
Grazer-scrapers	**948**	**3359**	**2214**	**396**	**1736**	**2687**
Ancylus fluviatilis (G)	25	60	43	-	-	-
Baetis sp. (E)	7	22	115	7	20	115
Cricotopus sp. (D)	6	73	658	8	106	995
Heterotrissocladius sp. (D)	6	74	659	8	110	1029
Radix balthica (G)	744	2903	363	368	1449	151
Synorthocladius sp.(D)	2	28	242	3	49	413
Theodoxus fluviatilis (G)	22	22	4	-	-	-
Tinodes waeneri (T)	4	25	149	1	1	14

Valvata sp. (G)	132	154	63	-	-	-		
Shredders	**277**	**1398**	**1178**	**107**	**433**	**408**		
Gammarus pulex (Cr)	248	1291	1165	107	432	406		
Sericostoma personatum (T)	29	108	17	1	1	2		
Total /Mean			**2783**	**9098**	**9282**	**938**	**3904**	**8360**

Table 8. Percentage of mean annual secondary production attributed to each resource type (B_i). ANOVA tested for the effect of treatment (below) and block (*P* >0.05, results not shown).

	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

Table 9. Total ingestion of each food type (mg AFDM m^{-2} yr^{-1}) and ANOVA results testing the effect of treatment.

	Control		Drought		ANOVA	
	Mean	SE	Mean	SE	$F_{1,3}$	P
Amorphous detritus	84386	22480	35515	5783	26.68	0.002
Leaf detritus	10381	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	98959	25451	39792	6804	16.39	0.004

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	35434	38347	6131	84386	316	789	12572	18292	3546	35515
Leaf detritus	103	1632	3896	2071	2679	10381	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	39929	42635	9136	98959	366	1048	13855	20011	4512	39792

Table. 11a. Ingestion (mean mg m^{-2} yr^{-1}) by core taxa in undisturbed control mesocosms.

Taxon	Amorphous detritus	Leaf detritus	Diatoms	Green algae	Fungi	Total ingestion	% total web ingestion
Radix balthica	32107	1754	1255	365	81	35562	36
Potamopyrgus antipodarum	21376	2720	252	60	0	24409	25
Gammarus pulex	5123	1336	100	2	<1	6562	7
Ephemera danica	4463	715	42	1	<1	5221	5
Hydropsyche sp.	1949	1610	323	8	4	3894	4
Valvata piscinalis	2335	131	158	0	0	2624	3
Total	67353	8267	2131	436	85	78271	79

Table 11b. Ingestion (mean mg m^{-2} yr^{-1}) by core taxa in drought-disturbed mesocosms.

Taxon	Amorphous detritus	Leaf detritus	Diatoms	Green algae	Fungi	Total ingestion	% total web ingestion
Radix balthica	12813	714	301	95	41	13965	35
Potamopyrgus antipodarum	4342	365	133	76	9	4924	12
Gammarus pulex	3357	604	107	0	16	4084	10
Cryptochironomus sp.	3387	151	10	<1	1	3549	9
Microtendipes sp.	3250	142	132	0	4	3527	9
Cricotopus sp.	1763	76	141	21	4	2006	5
Total	28912	2051	825	192	75	32056	81

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

	Control		Drought		ANOVA	
Metric	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

Appendix A. 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
Asellus aquaticus	5.20	0.107
Cricotopus sp.	1.66	0.288
Cryptochironomus sp.	5.97	0.092
Ephemera danica	49.39	0.006
Gammarus pulex	7.36	0.024
Heterotrissocladius sp.	2.87	0.189
Hydropsyche sp.	3.10	0.177
Macropelopia sp.	1.49	0.310
Microtendipes sp.	3.848	0.145
Naididae	25.65	0.015
Pisidium sp.	11.06	0.045
Polypedilum sp.	0.311	0.616
Potamopyrgus antipodarum	6.73	0.041
Radix balthica	9.38	0.014
Sericostoma personatum	10.04	0.050
Synorthocladius sp.	0.824	0.431
Tipulidae	3.27	0.168
Tubificidae	0.01	0.915