AN INVESTIGATION INTO THE EFFECTS OF DROUGHT AND DROUGHT RECOVERY ON MACROINVERTEBRATE COMMUNITIES

by

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ABSTRACT

The effect of drought on freshwater ecosystems is a growing environmental concern. This study aimed to determine the effect of the supra-seasonal 2010-2012 drought on the macroinvertebrate communities and functional feeding groups (FFG) of chalk streams. Three rivers were sampled during and after the drought, three sites were analysed on each river, a perennial control site, a dewatering site (shallow during drought) and a rewetted site (dry during drought). All wetted sites were sampled for macroinvertebrates, algae, velocity and depth monthly. In addition an in-situ experiment investigated grazing rates in dewatering, rewetted and perennial sites and a mesocosm experiment investigated the effect of reduced water velocity and temporary drying on grazing function and macroinvertebrate mortality.

Macroinvertebrate data were analysed for structural and functional changes in communities and algal data were analysed for changes of biomass both during drought and recovery. Both found rapid recovery post-drought with high incidence of resilience in the macroinvertebrate communities. Functional recovery was determined by investigating grazing rates in dewatering, rewetted and perennial sites. Algal and macroinvertebrate biomass, and grazing function recovered within a month of rewetting. Despite a rapid recovery of overall biomass and grazing function, FFG results showed delayed effects, and four months following drought differences were still present. Mesocosm experiments showed that macroinvertebrate mortality increased due to dewatering for some species, however slower velocity had little effect. Thus, this study showed that ecological function can return despite changes to macroinvertebrate community structure, indicating that functional redundancy promotes the resilience of chalk stream communities to drought.

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Contents

List of Tables

List of Figures.

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

Freshwater ecosystems provide habitat for 9.5% of the known species on Earth even though they account for less than 1% of the Earth's surface (Dudgeon et al., 2006). Despite this, extinction rates in freshwaters are almost double those seen in terrestrial or marine habitats (Dudgeon, 2010) and this may be made worse by the effects of climate change (Dahm et al.,2003). For example, one of the outcomes of climate change is that it will alter the hydrological cycle (Dahm et al., 2003), which will lead to droughts becoming more likely in certain areas, including the south of England (Environment Agency, 2011; Watts et al., 2015). Human use of water is putting a further strain on river systems, and may exacerbate drought conditions (Wood and Petts, 1999; Acreman et al., 2008; Soley et al., 2012). These pressures make it essential to understand how low flows and drying are affecting river ecosystems and how the ecosystems recover after drought.

The functioning of river ecosystems is under constant pressure from natural events such as floods and droughts but most systems recover quickly from these pressures (Aldous et al., 2011; Lake, 2011). The south of England is home to most of the UK's chalk streams which are known for their biodiversity (Wright and Symes, 1999; Wright et al., 2004). Often chalk streams are winterbourne which means partly intermittent, with reaches of these rivers drying up within the summer season, however during supra-seasonal droughts these areas may dry for considerable periods of time (Wright et al., 2004). The species of macroinvertebrates in the intermittent reaches of winterbourne streams are adapted to drying and re-wetting, many species finding refuges to survive until the next re-wetting, whilst others have eggs or larval stages which are resistant to drying (James et al., 2008; Chester and Robson, 2011; Robson et al., 2011; Stubbington, 2012; Robson et al., 2013; Storey and Quinn, 2013; Verdonschot et al., 2015). However, the perennial stretches of the river generally contain fauna which are less resistant to drying (Berrie and Wright, 1984; Wood and Petts, 1999). Hence during supra-seasonal droughts, where normally perennial reaches dry, it is important to study how the macroinvertebrates respond to drought and follow the recovery of these normally perennial reaches.

A supra-seasonal drought occurred in 2010-2012, this arose when precipitation was lower than average from November 2009 until April 2012 (Environment Agency, 2011; Kendon et al., 2013; Parry et al., 2013). This led to UK groundwater levels being lower than they had been on record (Kendon et al., 2013) and chalk streams suffered extreme drying with normally perennial reaches becoming dry and intermittent reaches not wetting for almost two years. This drought was extreme for the UK, and if droughts are predicted to become more common it is important to know how the ecology of streams is affected by drought and how rapidly they recover following drought.

This study aimed to investigate the effects of drought on river ecology, specifically macroinvertebrate communities and algal biomass. Dewatering sites and perennial sites were compared to determine the effects dewatering had, and as the drought broke, the opportunity arose to study recovery with the rewetting of normally perennial sites. In-situ experiments were carried out both during and after drought to show the effect drought had on grazing function. In addition, mesocosm experiments were carried out to investigate macroinvertebrate grazing and mortality and determine changes in functioning under drought conditions.

The thesis is structured into seven chapters, chapter 1 consists of an introduction and literature review and chapter two is the site descriptions and information on the drought which was studied. Chapter's three to six are data chapters, within the data chapters, chapters three and four are the result of field samples taken during and after the drought respectively looked at the effect of drought and recovery on algal biomass and macroinvertebrate communities, chapter three specifically looked at sites which are in the process of drying to determine if macroinvertebrate communities demonstrate the effects of this as a stressor. Chapter four investigates sites on the streams which had completely dried during the drought and how the algal biomass and macroinvertebrate communities recover monthly for five months following rewetting. Chapter five is an in-situ experiment ran both during and after the drought in perennial, dewatering and rewetted areas to determine whether grazing by macroinvertebrates was effected by drought or recovery, grazing is used a measure of ecosystem functioning and therefore the streams functional redundancy is tested. Chapter six is an experimental investigation using mesocosm to replicate changes in flow and dewatering as stages of drought and determine how this effected grazing rates and mortality in macroinvertebrate grazers. In chapter seven conclusions from all four data chapters are incorporated into an overall discussion of drought in chalk streams linking macroinvertebrate communities, ecosystem functioning and speed of recovery to the appropriate literature and what this means for chalk streams if droughts become more frequent.

1.2 Background and Literature Review

1.2.1 Chalk Streams

Chalk bedrock is relatively uncommon globally, there are patches in parts of the southern United States and some in mainland Europe such as northern France, however a large amount of chalk resides in the UK, with the majority found in the south east but some residing in Yorkshire (Figure 1). In the South East of England many of the rivers are groundwater fed through chalk aquifers (Berrie, 1992; O'Neill and Hughes, 2014). Aquifers normally contain a large store of water, therefore changes in precipitation levels have a delayed effect on the rivers and flow rate is relatively stable (Berrie, 1992). Therefore, chalk streams react more slowly to extremes in precipitation level, and drought and floods have a lower frequency and magnitude than in run-off fed rivers. The water in chalk streams is calcareous with a pH of 7.4-8.0 and the temperature of the water leaving the source is usually 11°C which cools the water in the main channel in summer and warms it in the winter so that the warmest the water typically gets is 17°C and the coolest is 5°C (Mackey and Berrie, 1991). The upstream section of chalk streams are intermittent winterbournes. The upstream areas usually dry in the summer and typically rewet every winter. In drought conditions, the perennial part of the river may contract and intermittent areas may not rewet for long periods. This was the case in 1976 when there was an extreme drought in the UK. Wright (1992) studied the River

Lambourn during this time and found that the wetted areas retreated extensively and intermittent areas were dry for sixteen months.

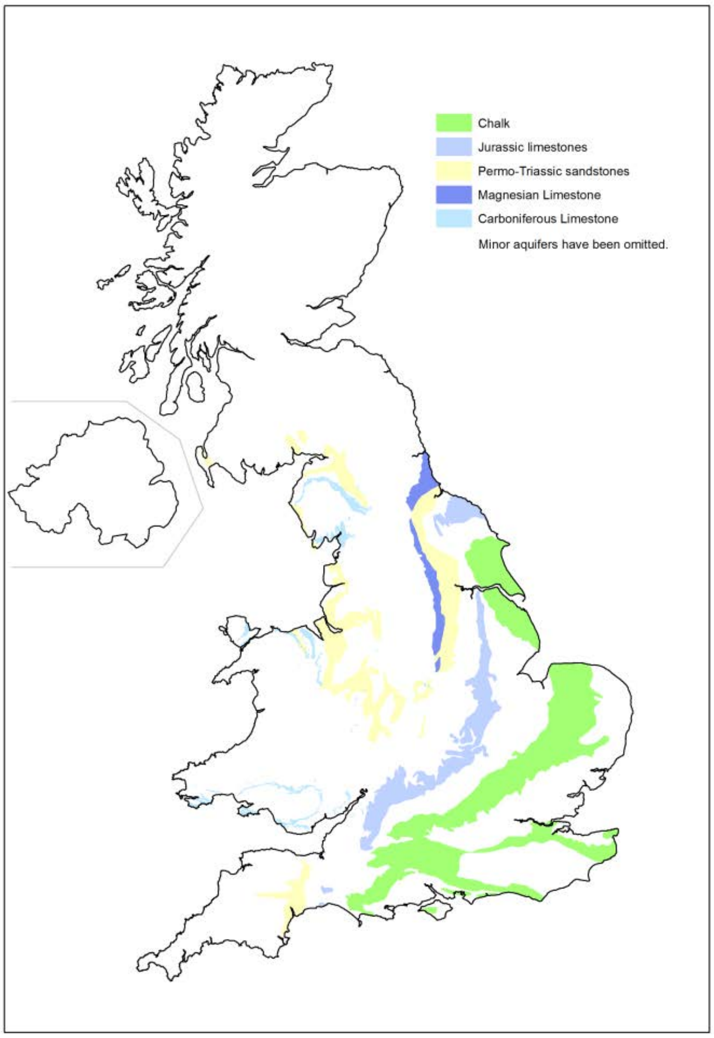

Figure 1.1. Map of UK rock types, light green areas indicate chalk.

The ecology of chalk streams is unique, due to the consistent flow in perennial areas, temperature and nutrient rich alkaline water (Berrie, 1992). Chalk streams were a Biodiversity Action Plan (BAP) priority habitat from 1999 before being encompassed into a larger priority habitat which includes all rivers where chalk streams still have special status (JNCC, 2007). The River Lambourn is also a Special Area of Conservation (SAC) and both the Lambourn and the River Kennet are Sites of Special Scientific Interest (SSSI) (English Nature, 2002). These designations show that chalk streams are known to be very important habitats and are important for biodiversity. The flora of chalk streams is unique, usually dominated by either *Ranunculus* spp*., Callitriche* spp. or *Berula erecta*. *Ranunculus spp.* is the dominant species in the spring and early summer, *Callitriche* spp. in late summer and autumn and *B. erecta* has constant growth but this peaks in the summer (Ham et al., 1982). However growth of macrophytes is also connected to flow, with *Ranunculus* spp. having slower growth patterns at low flows (Ham et al., 1982), thus drought may influence plant species dominance.

The macroinvertebrate community is species rich, with the highest species density in the perennial reaches (Berrie and Wright, 1984; Wright, 1992). Berrie and Wright (1984) surveyed a small chalk stream, the Winterbourne Stream, sampling at seventeen sites over several years. They found that some taxa were confined to intermittent areas but species richness increased incrementally downstream. There are some macroinvertebrate species which are especially associated with chalk streams such as the pea mussel *Pisidium tenuilineatum*, mayflies *Heptagenia longicauda* and *Ephemerella notate*, stonefly *Paraleptophlebia werneri* and caddisfly *Erotesis baltica* (Buglife - The Invertebrate Conservation Trust,2016), these species contribute to the macroinvertebrate fauna which is the majority of chalk stream food webs (Ledger et al.,2013). The tertiary consumers in Chalk streams are mostly fish, and chalk streams host many native species of fish. Prenda et al. (1997) found twelve species of fish within two chalk streams including lamprey, bull heads, brown trout and eels. Populations of brown trout (*Salmo trutta*) show faster growth in chalk streams than other streams (Mann et al., 1989) and the rivers are stocked with brown trout for recreational fishing purposes (Mann et al., 1989).

1.2.2 Climate Change and drought frequency and intensity

Climate change is predicted to reduce water availability in many populated areas, as droughts and floods are predicted to increase (Arnell, 1998; Arnell, 1999; Kundzewicz et al., 2008; IPCC, 2013). In the UK temperatures are set to rise leading to a switch in winter precipitation from snow to rain and this will change the annual pattern of run-off from rivers, which in turn will lead to heavier precipitation in many areas (Kundzewicz et al., 2008). With increasing occurrences of heavy rain, the water is more likely to run off, rather than saturating the soil and adding to ground water supplies which may lead to low supplies in chalk aquifers (Foster, 1998). Therefore although precipitation is likely to be heavier causing floods, this in fact increases the chances of drought later (Parry et al., 2013; Van Loon, 2015).

It is expected many areas globally will endure more frequent droughts especially in the frost-free seasons (Feyen and Dankers, 2009; IPCC, 2013). In the UK the South East of England is predicted to have increased frequency and length of droughts (Todd et al., 2013). Rahiz and New (2013) modelled drought frequencies up until 2099 and found that the 2050s and 2080s are predicted to have the most severe droughts. They also predicted that although droughts would be much more frequent, they did not necessarily last longer than current droughts. This is confirmed by models in other studies however, the robustness of the models for so far in the future is questioned as it is unlikely to be accurate, especially in fine details (Blenkinsop and Fowler, 2007; Burke and Brown, 2010).

1.2.3 Drought and low flows: general processes and effects

The term drought is ambiguous as there are many types of drought which can occur (Humphries and Baldwin, 2003; Wood et al., 2008; Lake, 2011). Wood et al. (2008) suggest the term ‘low flow event’ and asked for a detailed description of each individual drought in publications due to the range of conditions which occur within a drought. Many definitions of drought focus on the impact it has on human activity, whilst other definitions focus on the physical attributes of drought (Lake, 2011). This study will focus on the natural phenomenon of drought, described as a reduction in precipitation over a period of seasons to years (Lake, 2011). There are two categories of physical drought definitions, meteorological and hydrological drought. Meteorological drought is defined as a deficit in the amount of precipitation which had fallen compared to the amount or precipitation expected over an extended duration, it is only associated with the lack of precipitation and does not necessarily relate to drying on the ground known as hydrological drought. Meteorological drought can lead to hydrological drought, which is when the reduced precipitation leads to lower than expected discharge, or even complete drying in rivers and streams (Lake, 2011). In the case of rivers fed by groundwater there can be a delay between lower precipitation and lower discharge in the rivers (Lake, 2011). Droughts can also be classified as seasonal or supra-seasonal. Seasonal droughts occur when annual change in precipitation causes lower flow which can initiate the drying of parts or of all of a stream. Supra-seasonal drought is an extreme event caused by precipitation changes which are aseasonal and therefore are not a predictable occurrence (Lake, 2011).

When hydrological drought occurs, many modifications occur including a change in the chemistry of the water. Build-up of organic matter takes place as leaf fall is not washed away (Acuna et al., 2005; Griswold et al., 2008), the chemistry of the remaining water and sediments changes and can become more eutrophic and deoxygenated, (Lake, 2011). Two studies examined the impact of a drought on aspects of water quality, one in the Rhine River in Western Europe (Zwolsman and van Bokhoven, 2007) and one in the highly modified river Meuse (van Vliet and Zwolsman, 2008), both using data from the 1976 and 2003 droughts. Both of these studies found that overall water quality dropped during drought, increased water temperature and incidence of eutrophication. Both studies found an increase in temperature, the Rhine study found that water temperature was higher by an average of 1.4-1.8°C. Both studies also found that chlorophyll *a* concentrations were higher during drought and ions such as chloride, sulphate, sodium, fluoride and bromide are all present at increased levels. In the Rhine, nutrient level increases were not found, and this could have been due to the increase in primary production during drought. Heavy metals in the Rhine showed an increase, but this was more noticeable in the 1976 drought than the 2003 drought, in the Meuse some metals increased (selenium, barium and nickel) while others decreased (lead, chrome, mercury and cadmium). The authors explained this being caused by increased levels of suspended solids masking the metals due to absorption capacities of the equipment. The authors emphasize that the river Rhine had improved in overall quality since the 1970s with nutrient levels, metals and ion inputs all reduced significantly in this time. They observed a much larger impact of drought in the 1970s when water quality was poorer overall, suggesting that cleaner streams will be less affected by drought with respect to water quality (Zwolsman and van Bokhoven, 2007). The results from the Meuse River are very similar, with the addition of a higher pH during drought in 2003 which was correlated to the higher chlorophyll-a levels, indicating an algal bloom at this time. The sampling sites with higher flows had reduced levels of chlorophyll *a* and lower pH when compared to slow or stagnant flowing areas (van Vliet and Zwolsman, 2008). One of the major differences between these studies was that in the Meuse, a reduction in dissolved oxygen occurred, which was expected from lower discharge and increased water temperatures, however in the Rhine no reduction was found and the reasons for this are unknown. Overall, comparing these two studies showed that drought decreases water quality, but the changes vary from river to river, those with lower initial water quality being affected the most. Changes in water quality are not automatically resolved once the water returns, and can take weeks or months to return to pre-drought conditions (Dahm et al., 2003).

Droughts can be exacerbated activities such as water extraction, pollution, river regulation and morphological changes such as channelling (Lake, 2011), creating a multiple stressor context that can lead to more extreme conditions during drought and a longer recovery period. This is particularly relevant to the south east of England as this is where drought is most likely to occur and also where the population densities and human influence are highest (Arnell and Delaney, 2006). For example, water extraction exacerbates the hydrological problems that climate change brings (Hannaford, 2015) and low water flows mean that pollution is not diluted and so has a stronger effect on ecosystems (Boulton, 2003). All of these problems need to be accounted for when predicting what changes will happen to river ecosystems under drought

1.2.4 Drought as a disturbance in streams

The effect of drought on the general ecology of streams depends on the duration and intensity of the drought in question, ecologists have attempted to organise the effects into a chronological order, however several theories exist to explain the order of changes which occur in streams. Wood et al. (2008) expand on Lake (2003) and describe drought as a ramp disturbance, this is a type of disturbance that begins as a small one but becomes more severe the longer its duration, with the gradual nature of drought affecting the response of the river biota. Humphries and Baldwin (2003) propose that drought is a more stepped disturbance, for example, when the watercourse goes completely dry, extreme changes in the biota; chemistry and the habitat as a whole take place (Lake, 2000; Boulton, 2003; Wood et al., 2008). Each step of the drought is caused by an increase in drought intensity as water levels fall causing decreasing connectivity in the ecosystem, such as the river retreating from the banks and pooling of the water after flow stops. Between each of the steps of drought disturbance, we see a ramp effect which is a gradual worsening of drought conditions (Lake, 2011). The steps which rivers typically go through in severe drought are as follows: 1: firstly water flow will be reduced; 2: as the water levels drop, the marginal habitats will dry, disconnecting the river from its riparian zone; 3: if water levels drop further riffles will be lost and smaller streams may cease flowing breaking the water into a series of pools which interrupts connectivity along the channel; 4: after further drought , these pools will start to become deoxygenated or dry-up completely. The more severe the drought becomes the more changes have occurred and species have been lost, hence recovery can be expected to take longer for each stage of the drought.

1.2.5 Recovery from drought

Recolonisation can happen from three sources, refuges within the river where either the organisms, viable eggs or propagules have survived the drought, from hyporheic where macroinvertebrates can live below the surface of the stream (Dole-Olivier 2011; Stubbington 2012), or from migration of organisms from perennial parts of the stream or other streams (Boulton, 2003; Brock et al., 2003; Chester and Robson, 2011). Refuges are thought to be important for the survival of macroinvertebrates in droughts. There are different types of refuge including remnant pools on the river bed, hyporheic water beneath the river bed (Wood et al., 2010; Stubbington et al., 2009) and wet areas of sediment or sand and areas under large rocks and stones (Chester and Robson, 2011). Chester and Robson (2011) found that in drying streams in Australia, the perennial pools were the most successful refuge with the largest number of taxa surviving within them, very few taxa were found beneath stones or in resistant stages in the sediment. However, Chester and Robson (2011) also found that in the year following drying the community of intermittent rivers was not correlated to the macroinvertebrates found in refuges the previous year, whereas in unaffected perennial streams the communities of macroinvertebrates were strongly correlated between the seasons. Robson et al. (2008) found that the species differences between these refuges were small. However, perennial pools correlated the strongest with post-drought communities. It was also found that once the sites rewetted, all algal species present had been found in the pools, meaning other potential refuges such as dried sediment were probably not important as they did not act as a refuge in this case. Stubbington and Datry (2013) reviewed studies where dry sediment from the river beds of temporary streams were rewetted to determine which species would appear from the macroinvertebrate seed-bank. This showed that up to half of the taxa usually present in a stream with running water were present in the seed-bank, although sediment moisture and environmental temperature were both negatively correlated with species abundance.

The recovery of ecology of a stream after drought depends on the duration of the drought. Datry et al. (2012) collected sediment from dry river beds which had been dry for 1.5 hours to 143 days. The longer the riverbeds had been dry, the fewer species were found after re-wetting, therefore recovery time was correlated with the length and frequency of the drought, and in longer droughts sediments will be less likely to act as a refuge. The studies which were reviewed by Datry et al (2012) were from annual temporary streams and not from streams in drought. During a drought the environmental harshness and dryness would increase, in turn decreasing the species survival in the seed-bank. In addition, if the streams were not normally temporary, the species present may not have the adaptations to survive in a seed-bank.

The evidence for the use of the hyporheic zone by macroinvertebrates as a refuge from drought is conflicting. There are some studies which show macroinvertebrates using the hyporheic zone during low flows or high temperatures (Clinton et al., 1996; Fowler and Death, 2001; Wood et al., 2010; Stubbington et al., 2011b; Young et al., 2011; Crossman et al., 2013) and some which do not (McElravy and Resh, 1991; Boulton et al., 1992; del Rosario and Resh, 2000). The variability between studies relates to the variability in the conditions encountered in the hyporheic zone (Dole-Olivier, 2011). The flowpath of the hyporheic zone between streams differs, this is linked to the length, depth and size of the hyporheic zone which is available for organisms to use as a refuge (Dole-Olivier, 2011). The type of sediment within the hyporheic zone is important, if it is very fine if can make the area hypoxic and lethal for many benthic fauna and the volume of sediment affects the amount of available habitat for macroinvertebrates. In addition, upwelling and downwelling areas are very important in the use of the hyporheic zone as these are the main entrance and exit points for macroinvertebrates, and downwelling areas have a greater capacity as a refuge (Dole-Olivier, 2011).

It is important to consider how different macroinvertebrates might use the hyporheic space, there are some taxa which can live in the hyporheic zone permanently. For example there are groundwater specialists such as *Niphargus spp.* and occasional users who move between the hyporheic zone and benthic environment such as Ostracoda, *Gammarus* species and the water mites *Hydracarina* (Stubbington, 2012). Insect species need to have access to the surface in order to emerge so would only be able to use the hyporheic zone in the short term and species which eat algae may be at a disadvantage as the lack of sunlight would reduce food availability. However, if the macroinvertebrates are able to freely move in and out of the hyporheic zone, many species may use it temporarily including as a refuge during a disturbance. The most frequent taxa found in active migration studies using the hyporheic zone during low flows is *Gammarus spp.* (DoleOlivier et al., 1997; Wood et al., 2010; Stubbington et al., 2011a). Other inhabitants include water lice *Asellidae* (Wood et al., 2010) and the snail *Potamopyrgus antipodarum* (Holomuzki and Biggs, 2000), and insects including stoneflies, mayflies, caddisflies and chironomids (Marchant, 1988; Doleolivier and Marmonier, 1992; DoleOlivier et al., 1997; Holomuzki and Biggs, 2000). Stubbington (2012) also suggests that macroinvertebrate behaviour also affects hyporheic zone use, for example macroinvertebrates which have a natural burrowing behaviour would be more likely to use vertical migration, and swimming or crawling rate and body shape and size may also be factors. Overall, the hyporheic zone may provide protection to some macroinvertebrates where it is accessible, but this response is not easily predicted or modelled and so it is unknown how well used this refuge is at the individual site level.

Refuges indicate a streams resistance to drought, however, resilience to drought is also very important in the recovery of streams to drought. In temporary streams, the flora and fauna will be adapted to periodic drying and low flows and resistance to drought will be a common trait. For example Boersma et al. (2014) studied the macroinvertebrates from an intermittent stream in Arizona, U.S.A. The study consisted of two mesocosm treatments, one with severe drying and one without, and the same community of macroinvertebrates was seeded into both at the beginning of the experiment. At the end of the experiment, no community or taxonomic diversity differences were found and it was concluded that the macroinvertebrate community of this system had a high resistance to drought. The same is true of algae, where the biomass of algae reduces during drought but recovers very quickly afterwards (Ledger & Hildrew 2001, Timoner et al., 2012). Species which can resist drying will be more common in in an intermittent stream and therefore resistance and resilience to drought should be higher than that of a stream which does not have cyclical drying (Lake, 2011; Boersma et al., 2014). However the adaptations of the biota is only to seasonal droughts, when a severe supra-seasonal drought occurs, the stream will be drier for a longer time period. This increases the area which dries completely and less refuges will persist throughout the drought. Fewer species may persist in the stream and hence the initial colonists which occur in a rewetted stream are more likely to come from another waterbody, and the initial macroinvertebrate community is likely to be different than that which would occur after a seasonal drought.

1.3 Stream Algal Ecology

The algae which inhabit rivers include phytoplankton which live in the water column and benthic algae which grow on the substrate. Benthic algae (principally diatoms and green algae) form part of a biofilm which includes other microorganisms such as bacteria, protozoa and fungus in a polysaccharide matrix which forms a layer on the substrate of rivers (Battin et al., 2003). There are many causes of change to algal species and biomass including: seasonal changes such as periods of growth and sloughing; floods; droughts; nutrient enrichment; light levels and substrate (Stevenson et al., 1996; Vilbaste and Truu, 2003; Janauer and Dokulil, 2006). The composition of biofilms changes seasonally and after disturbance events. Often, after disturbances, bacteria are the first to recolonise (Battin et al., 2003).

The biofilm of a river is an indicator of environmental conditions. Algae have a short life cycle, therefore they respond to environmental change quickly and are sessile so are good representatives of conditions at a discrete site (Law, 2011). Looking at the composition of the biofilm can be useful for biological monitoring, for example, a biofilm which has a high proportion of organic matter may be impacted by organic pollution (Lowe and Pan, 1996; Law, 2011). Looking at specific taxa can also be useful, diatoms are used as they are easy to sample, and their diversity is well described (Rimet, 2012). The Trophic Diatom Index is commonly used in the UK to determine levels of eutrophication (Kelly and Whitton, 1995).

Many studies have looked at how diatoms respond to human impacts such as acidity and contamination by metals and pesticides (Rimet, 2012), however responses to natural events are less well studied.

Factors which have been shown to cause differences in algal growth include: flow; nutrient availability; pH; competition; predation and temperature. The primary nutrients which are required for algal growth are nitrogen (N) and phosphorus (P), for diatoms silica is also required to grow the external frustule of the cell. In pristine streams algae are usually both N and P limited and in rivers which have extensive nutrient input such as the Thames, nutrient limitation is not present (Law, 2011; Bowes et al., 2012). Studies which compare nutrient and light, find light to be the dominant limitation (Law, 2011; Lange et al., 2011). Velocity of the water also has an effect, fast current scours algae from the substrata and may not have a chance to reattach further downstream (Law, 2011). In addition the nutrient uptake by algae is directly related to flow, with faster flows increasing uptake rates (Biggs et al., 1998).

There are grazing macroinvertebrates whom eat the algae almost exclusively (Lamberti, 1996; Steinman, 1996). It has a higher nutritional value than other food sources in plant sources such as detritus (Lamberti, 1996) which makes it a valuable food source. Diatoms are not the richest of the algae in nutrients, however they can be ingested and digested quickly by many animals which makes them a good food source. Other algae such as green filamentous algae are tougher to eat and digest hence despite the fact that they are nutritionally richer they are less likely to be eaten (Lamberti, 1996). Some predatory or detritivorous macroinvertebrates consume algae in addition to their normal diet, or in certain stages of the life cycle (Anderson and Cummins, 1979; Cummins and Klug, 1979). Also algae can be accidently ingested while eating other food whether it is detritus or animal (Lamberti, 1996). Hence the role of algae in rivers is not simply to feed herbivores but also to supplement many different macroinvertebrate diets.

1.3.2 Algae and Drought

There is evidence that algal biomass increases significantly during droughts in the wetted areas of the river (Freeman et al., 1994; Lake, 2003; Caramujo et al., 2008). The reasons for this are thought to include an increase in nutrients; temperature and light levels as well as a decrease in grazing activity. Robson et al. (2008) worked on seasonally flowing streams in Australia and have found that the algal species that are present after recovery are all found in refuges such as perennial pools which showed that the algae have resilience, but not resistance. The headwaters of chalk streams in the UK are usually winterbourne, this means the algae will be adapted to a seasonal environment. If a stream fully dries there is evidence that many algae can survive drying with viable algae found after rewetting (Ledger and Hildrew, 2001) and hence, after drought, algae are available as food for grazing macroinvertebrates. Ledger et al. (2008) found that frequent drought disturbance caused the community structure of algae to change from a dominance of crust-forming algae to mat-forming diatoms, but the response was spatially heterogeneous. If rivers in the UK are predicted to become more prone to droughts and floods they may become more ecologically similar to rivers found in a Mediterranean climate which typically have these extremes in hydrology. Studies on Australian rivers which have these characteristics show that, with slower flow, the algal flora changes from diatoms to filamentous algae (Chester and Norris, 2006; White et al., 2012). Filamentous algae may not be eaten as readily by herbivores as they can be difficult to remove from the substrate or digest (Chester and Norris, 2006), hence this may be a significant change in the ecosystem functioning of the river. The changes which occur within the algal communities during and after drought may be complex and as the primary producers in rivers this will have reverberations throughout the food chain.

1.3.3 Algal and Grazer Interactions

Grazing is one of the main controls of algal biomass, and in some cases it is the main food source for herbivorous macroinvertebrates in river systems, especially when there is little organic matter input such as leaf litter (Rosemond et al., 1993). The wide variety of macroinvertebrates which inhabit flowing waters, can be categorised by feeding modes, known as functional feeding groups (FFG) (Cummins, 1973). The non-predatory macroinvertebrates were separated into four main groups: the shredders; collectors; piercers and the scrapers (grazers) (Cummins, 1973; Jonsson and Malmqvist, 2003; Alba-Tercedor, 2006). Freshwater grazers include taxa such as Gastropoda, Ephemeroptera, Diptera, Tricoptera (particularly cased caddis) and some Plecoptera. In general the Gastropoda consume larger amounts of algae than insects (Hill and Knight, 1987; Jonsson and Malmqvist, 2003) due to their mouthpart morphology which consists of a radula which rasps at the algae as they move (Arens, 1994). They have also been shown to be the dominant grazer often causing food shortages for other macroinvertebrate grazers (Hill, 1992) and have been found to have a preference for cells which are larger in size (Dillon and Davis, 1991). The mayflies are more mobile and move from one area to another only eating a small amount from each using their mandibles to separate small amounts of algae at each location (Hill and Knight, 1987).

As well as the type of grazer other attributes are important, for example the size of the grazer is directly related to the size of diatom they can consume, Tall et al. (2006) found a significant link between head-width size and maximum size of diatoms found in the gut contents of grazers which showed resource partitioning within the grazing fauna caused by morphological differences. Dillon and Davis (1991) found that although three species of snails in California showed few differences in selection of diatoms, a few of the very large species were not consumed as readily due to ingestion difficulties with size. Lowe and Hunter (1988) found in a study of one snail, *Physa integra,* that certain species of algae were grazer resistant as their mass was not reduced by this snail in grazing experiments. It has been shown that grazer mass is the biggest factor in algal removal rate accounting for 65% (Cattaneo and Mousseau, 1995). Furthermore snails have been found to affect biofilms when they are moving on the substrate, encouraging sloughing which can waste up to ten times as much algae as is consumed (Cattaneo and Mousseau, 1995), a similar effect has been found with *Glossosomatidae* caddisflies who are slow moving and have flat cases which can slough off algae (Wellnitz and Poff, 2012).

Resource partitioning can also be a behavioural mechanism, and food choices or ingestion rates have been found to differ with competition, food availability (Aberle et al., 2009) and predator presence (Alvarez and Peckarsky, 2005). Mollusc grazers tend to have very little selectivity, however mayfly grazers have been found to be more selective, often changing their choice throughout seasons or as a result of competition (Hernandez and Peckarsky, 2014; Chuang et al., 2014). Even after ingestion, the ability to digest diatoms can vary between grazers. Peterson et al. (1998) found that mayfly grazers digested most diatoms completely, whereas a caddis grazer often had live diatoms in its faeces indicating that its digestion was not as efficient. If environmental change alters the size spectra of either the grazer or the diatom communities, then food web structure may change too.

In most cases, grazing reduces the biomass of algae. Feminella and Hawkins (1995) found in a review that 70% of studies observed a decrease in algal biomass in the presence of grazing macroinvertebrates. It is logical to assume that if grazing levels are high, edible algae biomass will decrease and resistant algal biomass will increase and this is often the case (Feminella and Hawkins, 1995), however the process of grazing can increase the growth rates of some algae (Saikia et al., 2011). Agrawal (1998) showed that categorising algae as edible and inedible is not an efficient system as edibility depends on grazer species, life stage and size. Agrawal (1998) also showed that when grazer numbers decline, inedible algae increase. In some ecosystems one grazing species may be the dominant grazer and out-compete other species (Jonsson and Malmqvist, 2003). In freshwater systems snails can often be the dominant grazers, and Jonsson and Malmqvist (2003) found that the snail *Radix balthica* consumed more algae than two mayfly species in a mesocosm experiment. They concluded that this would lead to the two mayfly species being suppressed in number. However mayfly grazers are highly mobile, and therefore could move to areas of the river bed that did not have such a high density of snails (Alba-Tercedor, 2006). Aberle et al. (2009) used isotope labelling as well as cell counts in a grazing experiment with two macroinvertebrate species, with the aim to determine the strategies and selective resource use which could lead to coexistence. The assimilation of the algae by the two species was similar in single species treatments, but when together, one species began assimilating the algae more efficiently. This showed that competition can not only affect grazing rates, but also how the animals digest the food.

1.4.1 Macroinvertebrates and Drought

Droughts are difficult to predict and hence difficult to study, often studies begin after the drought has started (Lake, 2011). Studies on the effects of drought on ecosystems have covered many habitats from deserts to tropical streams. Areas of the world which typically have annual seasonal droughts are more intensively studied than temperate regions, although the majority of freshwater biodiversity studies are carried out in these temperate regions (Dudgeon et al., 2006). Studies of macroinvertebrates affected by drought can be generally separated into studies of seasonal droughts and supra-seasonal droughts.

1.4.2 Macroinvertebrates and Seasonal Drought

Much of the research for seasonal droughts comes from Mediterranean climates where droughts are far more common than in the UK. However intermittent streams are present all over the world. Studies of completely intermittent streams in Canada in the 1970s (Williams and Hynes, 1976; Williams and Hynes, 1977) found that the species present in temporary waters consisted of three types, 1: species which are adapted to permanent streams but are tolerant enough to withstand living in temporary waters; 2: are species which can live in still water as well as flowing, and 3: are the species which are adapted especially for life in temporary waters. In partially intermittent streams there is evidence that there is a relationship between desiccation resistance and species occurrence, so that intermittent areas lack desiccation sensitive species and have more species adapted to drying (Arscott et al., 2010).

Acuna et al. (2005) studied intermittent streams in the Mediterranean over three years, two of which had average precipitation and one was a wet year. They found that the response to seasonal drought by macroinvertebrates was stepped, the density and diversity of macroinvertebrates increased as the water levels reduced and pools formed. Diversity and density then decreased due to changes in water chemistry including increased electrical conductivity and reduced dissolved oxygen related to the lack of flow. The macroinvertebrate community which was present directly after drying was significantly different to that which was present before drying, with the community on rewetting being characterized by r selected species such as Chironomidae and Ceratopogoniidae. The wet year had less community changes than the two average years as the flow did not stop through the summer. It was found that resilience was more important than resistance in this system. Similar results have been found in Brazil (Rocha et al., 2012) and Australia (Leigh, 2013) which confirms resilience is important across Mediterranean climates to drought.

In macroinvertebrates, some traits can improve or reduce the survival chances during drought by conferring resistance or resilience. Bonada et al. (2007) and Garcia-Roger et al. (2013) looked at the differences in traits in macroinvertebrates in Mediterranean streams which were permanent either flowing, intermittent (no flowing water but remaining pools present in the summer) and ephemeral (completely dried during summer). Bonada et al. (2007) did not find traits associated with permanent areas, however Garcia-Roger et al. (2013) found that permanent streams were associated with several traits (see table 1.1). Both studies agreed on both intermittent and ephemeral site traits (see table 1.1). In addition they found that permanent and intermittent sites did not differ in macroinvertebrate community in the winter after rewetting, however the ephemeral site differed from both others. This showed that as long as there is remaining water the macroinvertebrate community can recover quickly, however with complete drying community changes occur. Chessman (2015) conducted a study of a drought in Australia which lasted 10 years, the traits of the animals during and after the drought were analysed and found traits associated with perennial sites not found elsewhere (table 1.1). All three studies found traits associated with r selection in the disturbed (intermittent and ephemeral) sites, and K selection in the undisturbed perennial areas.

Table 1.1. Macroinvertebrate traits associated with area of rivers, intermittent sites are those which dry to pools and ephemeral are sites which dry completely (Bonada 2007). Source of data [1](Bonada 2007, [2](Garcia-Rover et al. 2013), and [3] (Chessman 2015).

Area of River and Traits		
Perennial	Intermittent (Dry to pools)	Ephemeral (dry completely)
Large Body Size[2]	Aerial dispersal[1, 2]	Air breathing[1,2]
Aquatic Eggs[2]	Tolerance to high temperatures[3]	Burrowing[1, 2]
Aquatic dispersal[2]		Asexual reproduction[1,2]
Long life span[3]		Aquatic passive dispersal[1,2]
High oxygen needs[3]		
Needs for fast water[3]		
Pupil stage[3]		

1.4.3 Macroinvertebrates and Supra-seasonal Drought

Supra-seasonal droughts occur due to lower than expected precipitation extending over the winter and are not as predictable as seasonal summer drought (Lake, 2011). UK chalk streams are non-perennial and have dry reaches in the summer (Berrie, 1992;), however with supra-seasonal drought the dry reaches can extend much further and stay dry for longer. Although, organisms which live in these winterbourne rivers may have traits which confer resistance and resilience to drought (Bonada et al., 2007; Lake, 2011; Garcia-Roger et al., 2013; Chessman, 2015), they may take longer to recover from supra-seasonal drought. The effects of drought on macroinvertebrates will differ across the seasons due to differences in life-cycle stage. Insect fauna pupate, emerge or lay eggs in the spring meaning the body size of the insects will be smaller in the summer which is a trait associated with resistance to drought (Bonada et al., 2007), so if the drought occurs when these insects are larger and have a larger body size/surface ratio such as autumn or winter, they will have less resistance to drought. Fully aquatic taxa such as molluscs and crustaceans also usually have life cycles that entail lower densities or smaller sizes during summer months. The macroinvertebrate life cycles vary from species to species so the effects of supra-seasonal drought on each may vary. However, if complete drying occurs, survival is unlikely regardless of body size. Recovery can also be constrained by the water chemistry. When an area re-wets, the pH and oxygen saturation of the water can be low (Chester and Robson, 2011), and nutrients, sediments and organic matter can be high at the first stages of rewetting (Acuna et al., 2005) and high build-up of organic matter and sediment can occur (Wood and Armitage, 1999; Ylla et al., 2010).

Severe droughts in the UK occurred in 1976 (a supra-seasonal drought), 1990-1992, and 1995-1997 (Cole and Marsh, 2006). Studies on the Rivers Lambourn and Kennet have included the run-up to the 1976 drought which is one of the most severe droughts on record, as well as a less severe drought in 1996 (Wright et al., 2002; Wright et al., 2004; Wright and Symes, 1999; Wright et al., 2003). Wright et al. (2002) analysed data from the 1970s and 1990s and found very little change in the macroinvertebrate fauna in this time after drought periods. Wright and Symes (1999) found that in certain microhabitats (type of substrate or macrophyte) some species numbers increased in 1976, showing these microhabitats were refuges for animals which had been displaced from further upstream during the drought. However, Wright et al. (2004) found little change in species richness from 1997-2001, although 1997 was a drought year, it was not as severe a drought as 1976 or 2011.

Berrie and Wright (1984) conducted a longitudinal study along the length of the Winterbourne Stream in 1972 and 1976-1977 including the drought of 1976. They found that sites which were still wet but close to becoming dry had a significantly lower species richness. Some species were found to be adapted to the intermittent reaches of the stream including twenty one species of Coleoptera and five species of Hemiptera. Throughout all years, species richness of Gastropoda, Ephemeroptera and Trichoptera increased downstream, which is a sign that these groups are sensitive to seasonal drought and had used behavioural avoidance by emigrating downstream.

Table 1.2 shows that the studies mentioned above and others were carried out during supra-seasonal droughts in the UK. However, different sampling techniques and whether macroinvertebrates were identified to species or family level makes generalisation difficult. Studies also differed in duration and number of replicates with most studies commencing after the drought started and finishing as the drought ended. This means very few data on the recovery of streams to drought exist. Some studies showed one season of post-drought data including Cowx et al. (1984) who found that in the year following the drought numbers of Plecoptera and Coleoptera reduced significantly and numbers of r-selected Chironomidae and Simuliidae increased. Wright et al. (2004) studied the Rivers Lambourn and Kennet from 1997, the year the drought that began in 1995 broke, and thus had no pre-drought control. However, one can infer recovery in some families which increased in number between 1997 and 1998 (Table 1.2), including Lymnaeidae, Baetidae, Rhyacophilidae and Leuctridae. Wright et al. (2002) covered the same sites on the Kennet but comparing the 1976 and 1997 droughts looking at macrophytes and invertebrates and found very similar results to Wright et al. (2004) for both the 1970s and 1990s drought. Studies which actually follow recovery have shown some degree of similarity, with increases of pioneer or r-selected species such as Simuliidae, Chironomidae and Oligochaeta. Studies which covered the drought itself have found reductions in abundance of hydrophilic and k-selected species such as Baetidae and cased Trichoptera. None of these studies specifically look at the recovery of sites which have completely dried. More studies are needed into how completely dried areas recover in these systems.

Table 1.2. Comparison of studies of UK droughts in 1972, 1988-1992 and 1996-1997.

Reference	**Location and years of study**	**Area of river sampled**	**Macroinvertebrates increases during drought**	**Macroinvertebrate decreases during drought**	**Macroinvertebrate increases after drought**	**Macroinvertebrate decreases after drought**	**Methods**	**Other factors**
(Extence, 1981)	River Roding, Essex, England 1975-1976	1 area which was pooled and 3 urban areas which remained wet	Orthocladiinae Chironomidae, *Asellus aquaticus*, *Helobdella stagnalis* and Tubificidae worms	Lost completely: Plecoptera, cased Trichoptera. Reduced in number: *Potamopyrgus jenkinsi* and *Ancylus fluviatilis*	N/A	N/A	3-4 week interval core sampling, species level ID.	Increased organic pollution was found in all sites but especially the pooled area.
(Cowx et al., 1984)	Severn Catchment, Wales 1976-1977	One site no mention of permeability	Not mentioned	Plecoptera, Coleoptera and Oligochaeta	More Chironomidae and Simuliidae	Not mentioned	Monthly Surber sampling family level ID.	
(Berrie and Wright, 1984)	The Winterbourne Stream. 1972 and 1976-77	17 sampling sites in 1972. During drought sites 8-17 were studied.	Not mentioned	Not mentioned	N/A	N/A	Bimonthly 5 minute kick sample. Species level ID.	Species which are only or never found in intermittent areas are listed.
(Wright and Symes, 1999)	Bagnor on the River Lambourn. 1971-1979	Bagnor – not directly impacted by drought	No individual taxa but general densities of macroinvertebrates increased	Not mentioned	*Serratella ignita*, *Gammarus pulex*	Not mentioned	5 biotopes sampled – *Berula*, *Callitriche*, *Ranunculus*, gravel and silt Family level macroinvertebrate ID	

Table 1.2 Cont'd

Reference	**Location and years of study**	**Area of river sampled**	**Macroinvertebrates increases during drought**	**Macroinvertebrate decreases during drought**	**Macroinvertebrate increases after drought**	**Macroinvertebrate decreases after drought**	**Methods**	**Other factors**
(Wood and Petts, 1999)	Little Stour River, Kent 1992-1995 Drought was 1988-1992		Upstream: *Potamopyrgus jenkinsi, Lymnaea palustris, Lymnaea peregra, Gammarus pulex, Baetidae, Agapetus fuscipes, Simuliidae* Downstream: *Bithynia tentaculata*, *P.jenkinsi*, *Lymnaea peregra*, *Physa fontinalis*, *Planorbis*, *Sphaeriidae*	Upstream *Sialis lutaria* Downstream *Sialis lutaria,* Notonectidae	Upstream: *Potamopyrgus jenkinsi, Lymnaea palustris, Gammarus pulex, Erpobdella octoculata, Agapetus fuscipes, Simuliidae, Elmis aenea, Limnius volckmari, Glossiphonia complanata*. Downstream: *P. jenkiinsi, Asellus aquaticus, G. pulex,* Corixidae, *Haliplus spp. Laccophilus hyalinus, Potamonectes depressus elegans*	Upstream *Lymnaea palustris* Downstream N/A	14 sites sampled across river. Two minute kick samples. Species level ID	Upstream areas contained high levels of silt during drought. No baseline survey comparison.
(Wright et al., 2002)	The River Kennet 1974-1976 and 1997-1999 Ended before 1976 drought and covered 1996-1997 drought	Two sites Littlecote U/S of Hungerford and Savernake d/s of Marlborough	No baseline data, in 1997 more than any other year: Piscicolidae, Lumbricidae, Chironomidae, Glossiphoniidae, Erpobdellidae, Asellidae	Baetidae	Baetidae ,Rhyacophilidae	Ephemerellidae, Piscicolidae, Glossiphoniidae, Erpobdellidae, Asellidae,	Lambourn Sampler which takes a 20_25-cm^2 by 6cm depth. Five replicates were taken. Family level ID	
(Wright et al., 2004)	River Kennet and River Lambourn 1997-2001	Lambourn: Little Stour and Bagnor Kennet: Littlecote U/S and D/S	Not mentioned	General mention of macroinvertebrates being less abundant	Increase of Baetidae at all sites. Between 1997 and 1998 increases at some sites of Leuctridae, Rhyacophilidae and Lymnaeidae	Ephemeridae, Caenidae and Hydroptilidae.	Gravel and macrophytes sampled. Family level ID	Macroinvertebrate data at family level and no specific families mentioned for drought responses.
(Wood and Armitage, 2004)	Little Stour River, Kent.	9 usually perennial sites sampled. 3 of	Not mentioned	*Gammarus pulex*	*Gammarus pulex*	Two-year recovery	Two minute kick samples. Species level ID.	

Reference	**Location and years of study**	**Area of river sampled**	**Macroinvertebrates increases during drought**	**Macroinvertebrate decreases during drought**	**Macroinvertebrate increases after drought**	**Macroinvertebrate decreases after drought**	**Methods**	**Other factors**
	1992-1998. Covering 1992 and 1997 droughts	which dried during study.		General low abundance of all species				

The effects of drought in areas where it occurs more frequently will differ from where it is a rare phenomenon. Boulton (2003) compared Australian and UK rivers during several drought periods and found that, for both countries, longer droughts had greater impacts on the macroinvertebrate fauna, yet there was no evidence that recovery was slower. However, taxa which did not survive drying took longer to recolonise the rivers and there are less desiccation resistant UK species, so full complete recovery would have taken longer in UK rivers. They found that some macroinvertebrates such as shrimps, stoneflies and uncased caddisflies survived the first year, but that they did not recruit successfully the following year creating a lag effect in the population response. Recovery of the macroinvertebrate community to pre-drought conditions was then observed in the following year. However, there are very few studies in the UK which have data for macroinvertebrates when the flow starts to cease and pools form and our understanding of refuges in these streams needs to be improved.

1.5.1 Flow Modulation of grazer/algal interactions

As studies of supra-seasonal droughts in nature are ad-hoc, an experimental approach is needed in order to study relationships between macroinvertebrates and flow. In table 1.3 studies of grazing macroinvertebrates under different flow treatments are summarised. Most studies have found that increased velocity meant higher grazing rates (Poff et al., 2003; Opsahl et al., 2003; Wellnitz and Poff, 2006; Wellnitz and Poff, 2012). This was not always the case and experiments using the mayfly *Drunella grandis* found a steady grazing rate across all velocities (Poff et al., 2003; Wellnitz and Poff, 2012). Species identity may be a strong determinant of the effect of changing flows. During the beginning stages of drought when flows are slowing, species which prefer fast flows will be outcompeted by those which can carry on consuming algae in slowing flows. Indirect effects may also play a part in species resilience to slow flows, for example, Wellnitz and Poff (2012) found that slower flows increased the growth of filamentous algae which the cased caddisfly *Glossosoma verdona* then became trapped in, preventing them from consuming algae, and leading to increased mortality and lower body weights.

Table 1.3. Studies of grazers in flow modulation experiments.

Citation	Study System	Species used	Species preferences	Grazing changes with velocity	Combined treatments results	Other comments
(Poff et al., 2003)	Streamside. Velocities: Slow 3-5 cm s-^{1} Medium 15-20 cm s-^{1} Fast 32-41 cm s-^{1}	*Baetis bicaudatus* (Baetidae) *Drunella grandis* (Ephemerellidae) *Glossosoma verdona* (Glossosomatidae)	*G. verdona* removed more periphyton at fast flow *B. bicaudatus* similar to above but not significant *D. grandis* always removed ~75% of periphyton mass	*G. verdona* and *B. bicaudatus* increase grazing with velocity.	Fast treatment: grazing equal among all species. Medium: *D. grandis* removed more than both other species. Slow: *D. grandis* removed more than *B. bicaudatus* who removed more than *G. verdona*	
(Wellnitz and Rader, 2003)	Field Experiment – 45 day growth of periphyton. Some tiles scoured	*Rhithrogena robusta* (Heptageniidae)	All algae were reduced by grazing except cryophyte *Hydrurus foetidus*	N/A		Scouring of tiles made the algal community more diverse.
(Poff et al., 2003)	30 day growth of periphyton Velocities: Slow 3-5 cm s-^{1} Medium 15-20 cm s-^{1} Fast 32-41 cm s-^{1}	*Baetis bicaudatus* (Baetidae) *Drunella grandis* (Ephemerellidae) *Glossosoma verdona* (Glossosomatidae)	*G. verdona* fast	*G. verdona* increased grazing in fast. *B. bicaudatus* similar but non-significant *D. grandis* similar grazing rate at all velocities	Overall grazing increased with increasing velocity (not significant)	

Table 1.3. Cont'd

Citation	**Study System**	**Species used**	**Species preferences**	**Grazing changes with velocity**	**Combined treatments results**	**Other comments**
(Wellnitz and Poff, 2006)	Velocities: Slow 2-5 cm s-^{1} Medium 15-20 cm s-^{1} Fast 30-40 cm s-^{1} 2 and 10 day treatments	*Baetis bicaudatus* (Baetidae) *Epeorus longimanus* (Heptageniidae)	Grazing effect did not differ between species or velocity	N/A	None	Algal biomass reduced with longer periods of grazing, however growth rate of the algae was also accelerated after removal of grazers. This was most pronounced at slower velocities.
(Wellnitz and Poff, 2012)	Velocities: Slow 1-5 cm s-^{1} Medium 15-20 cm s-^{1} Fast 30-40 cm s-^{1}	*Glossosoma verdona* (Glossosomatidae) *Drunella grandis* (Ephemerellidae)	*G. verdona* mortality correlated with increase in periphyton biomass (they got tangled in filamentous algae and died).	*G. verdona* removed more periphyton at fast velocity. *D. grandis* showed no preference reducing periphyton at all densities and velocities.	*G. verdona* was facilitated by *D. grandis* in slow treatment as it reduced the biomass of periphyton so that *G. verdona did not get tangled.*	

1.6.1 Simulated Drought in Mesocosms

In addition to modifying flow, mesocosms can be used to simulate longer term drying which gives the ability to study the effects of drying on ecology in controlled circumstances. Large experimental channels were used to test drought effects on algae and macroinvertebrates in a two year experiment (Ledger et al., 2006; Ledger et al., 2008; Ledger et al., 2011; Woodward et al., 2012; Ledger et al., 2013a; Ledger et al., 2013b; Lancaster and Ledger, 2015). Algal communities were found to change from green encrusting algae to diatom mats after de-watering (Ledger et al., 2008), although the response of the diatom mats was patchy. In Ledger et al. (2006), three remnant species were put into three artificial channels in single species treatments, the freshwater shrimp *Gammarus pulex*, mayfly *Serratella ignita* and the snail *Radix balthica*. When the mesocosms were opened to the inlet to the nearby stream allowing colonisation of macroinvertebrates and algae from the river water, each treatment had a different result, with *R. balthica* having the strongest effect on macroinvertebrate community following twenty one days of colonisation. This study showed that remnant species can have a strong or weak effect on the resulting macroinvertebrate communities after disturbance depending on their characteristics.

During a long-term dewatering experiment in Dorset, UK monthly drying disturbance events were found to make significant changes to the macroinvertebrate communities, whereas quarterly drying disturbances have no effect (Ledger et al., 2012). Macroinvertebrates with a larger body mass were more likely to be lost (Ledger et al., 2011) and smaller macroinvertebrates with faster life-cycles (r-selected) were favoured and this was linked to changes in the food web which included losses of predators and less trophic interactions over all (Ledger et al., 2013b). Woodward et al. (2012) identified that large predatory species were lost from the food chain, but also found that species which were ‘rare for their size’ were lost showing that drying events can change the shape of aquatic food webs. The changes in food-webs structure in these experiments suggested potential effects on ecosystem functioning, although changes to grazing rates were not known.

1.7 Summary

Despite knowledge of stream functioning, algal processes and invertebrate feeding and behaviour, research on these processes during drought are less extensive. Studies in streams during drought are, for obvious reasons, difficult and limited, therefore this shows a gap in the literature. Chapter three of this thesis is a study of dewatering areas of three streams during the 2011 drought, the information taken from this will aid the understanding of the effects of dewatering on macroinvertebrate communities.

Studies of the recovery of macroinvertebrate communities during drought are also limited, how quickly a stream recovers its biomass and functionality will have an effect on the rest of the ecosystem. Chapter four investigated the algal biomass and macroinvertebrate communities in the four months after the drought broke, following the recovery of the ecosystem.

Grazing macroinvertebrates have shown changes in feeding behaviour under different flows but this has not been specifically linked to drought, and dewatering events have not been included in grazing studies. Chapter five looked at grazing in the streams during the drought and recovery period, giving a chance to look at the functioning of the streams during drought which has not been done before. Chapter six investigated grazing relationships in mesocosms re-enacting drought conditions to gain detailed information about common grazers and how their grazing and mortality are effected by drought conditions.

The effect of supra-seasonal drought on invertebrate communities and functioning has been studied but more information is needed in temperate regions where droughts are predicted to become more common. The effects of drought on the invertebrate community and functioning and the recovery process are only just beginning to be understood. Considering drought and recovery as a whole ecosystem, including ecosystem functioning, allows for a comprehensive approach to understanding drought effects. Chapter seven takes the evidence from this thesis in all of these topics and connects the conclusions of each chapter to provide a synthesis which furthers the understanding of drought in chalk streams.

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CHAPTER 2

SITE DESCRIPTIONS AND DESCRIPTION OF THE DROUGHT USED IN THIS STUDY.

2.1 Site Descriptions

All three rivers lie within the North Wessex Downs Area of Outstanding Natural Beauty (Dunlop and Greenaway, 2011), within the counties of West Berkshire or Wiltshire (Figure 2.1). Three sites were chosen on each stream (Table 2.1). 1: a perennial site which was used as the control, this was far enough downstream to ensure drying would never occur and is referred to as perennial (P), 2: a site that was dewatering at the beginning of the study and may have dried if the drought persisted and is referred to as dewatering (D), 3: a site that was dry at the beginning of the study and rewetted in late May to early June 2012 and is referred to as rewetted (R).

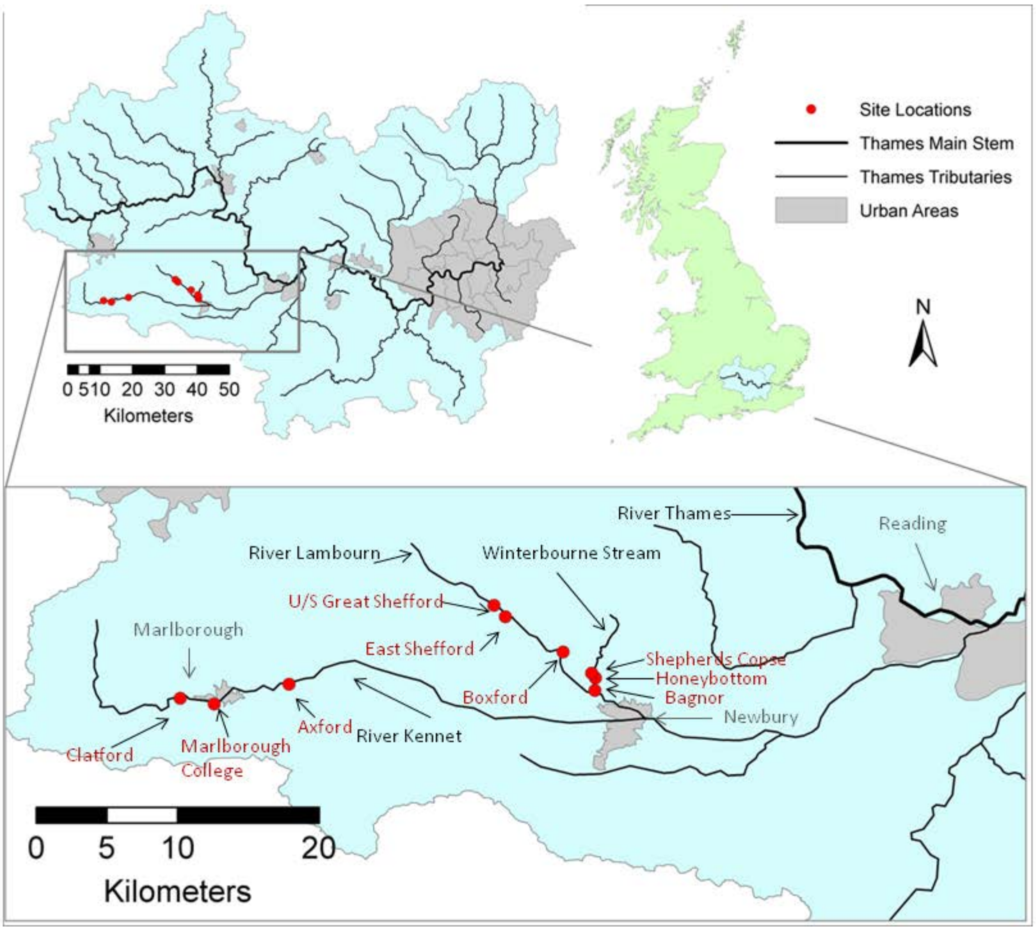

Figure 2.1. Map of sites

Table 2.1. Distance from source and altitude of each site. Catchment size was taken from the nearest gauging station to each site. Status is the code by which water permeability is ranked, P= Perennial, D = Dewatering and R = Rewetting. Upstream great Shefford is abbreviated to USGS.

Stream	Length of Stream (km)	Status	Site Name	Distance from Source (km)	Altitude (m)	Catchment Size km^2
River Lambourn	25	P	Boxford	15.395	116.65	176
River Lambourn	25	D	East Shefford	9.758	126.15	154
River Lambourn	25	R	USGS	8.429	133	105
Winterbourne Stream	8	P	Bagnor	6.939	90.45	49.2
Winterbourne Stream	8	D	Honeybottom	5.903	103.25	43
Winterbourne Stream	8	R	Shepherds Copse	5.515	108.15	42
River Kennet	72	P	Axford	31.718	80	295
River Kennet	72	D	Marlborough College	25.153	84.5	142
River Kennet	72	R	Clatford	22.272	86.1	128

2.1.1 The River Lambourn

The River Lambourn is a groundwater fed chalk stream which is a winterbourne in its headwaters, it lies on a mostly rural catchment of arable and grassland. The rich chalk soil has meant that the area around the river has been farmland for thousands of years (Dunlop and Greenaway, 2011). The river runs from its spring in Lynch Wood (51.512° N, 1.529° W) near the town of Lambourn, to where it joins the river Kennet in Newbury. The perennial part of the river starts upstream of Great Shefford at Maidencourt Farm (51.481° N, 1.464° E). The river Lambourn is a Site of Special Scientific Interest (SSSI) due to its good condition lacking pollution.

Boxford – Perennial Control Site

Boxford is positioned approximately 15 km from the source at 51.447° N, 1.384° E (See Figure 2.1). Boxford is located on a meander in the River Lambourn which means that there are frequent floods and there is a wetland meadow in the vicinity, the water depth ranges from 30 to 60 cm on average (Old et al., 2014).

The site at Boxford is currently owned by the Centre for Ecology and Hydrology (CEH) as part of the River Lambourn Observatory which covers approximately 600m of river and 10 ha of wetland. Weed cuts are carried out at the site approximately three times a year to reduce flood risk to surrounding houses (Old et al., 2014).

The area is only accessible by nearby land owners and fishermen and is a popular fishing spot and has populations of trout, bullhead, sticklebacks, brook lampreys and graylings. (Figure 2.2)

Figure 2.2. The River Lambourn at Boxford. May 2012 during the drought.

East Shefford – Dewatering Site

East Shefford is positioned approximately 10 km from the source at 51.469° N, 1.441° E

The site at East Shefford was owned by a private estate, the area was used for sheep farming (Figure 2.3). The area directly above the site was kept undisturbed as a nature reserve for water fowl. The site itself was in a field which was used much of the year to keep a small number of sheep. The upstream site is shallow and consists mostly of riffles. Further downstream the site had been modified and dug out to become deeper. At the beginning of the current study the top end of the site was too shallow to place bricks into for the grazing experiments, and hence they were placed into the deeper end. Once the water levels rose this downstream end became deeper, around 80cm. The area had many breeding wildfowl as well as a population of Canada Geese which were present for a few months of the year and resided in the field near the river. The area upstream of the site had been deepened in the past to reduce flood risk. This site became very shallow during this drought, and was also very shallow in the drought of 1976 but did not dry in that year (Personal communication with land owner).

Figure 2.3. The River Lambourn at East Shefford. May 2012 during drought.

U/S Great Shefford – Rewetted Site

Great Shefford was positioned approximately 8.5 km from the source at 51.476° N, 1.453° E

This site was surrounded on one side by a crop field and on the other by a church yard, there was a road with a bridge over the site which was only used by farm traffic and was not open to the public. There was a popular walking path which follows the river around 5 metres away from the bank. The site was dry and pooled until June 2012 when the water returned. The substrate was mainly gravel but contained boulders. During the drought the site became heavily vegetated with macrophytes and this persisted for 5-6 months post drought (Figure 2.4), the site is shown one year following the drought (Figure 2.5) for comparison.

There was a high density of molluscs and leeches on this site compared to the other sites on the Lambourn. *Ancylus fluviatilis* were particularly prolific, some of which were large which may suggest that a few remnant pools survived drying at this site.

Figure 2.4. The River Lambourn Upstream of Great Shefford in July 2012, three months after the drought.

Figure 2.5. The River Lambourn at US Great Shefford May 2013, one year after the drought. Note that the water level was higher and there was less edge vegetation than July 2012.

2.1.2 The Winterbourne Stream

The Winterbourne Stream is a small stream which is the only major tributary of the River Lambourn. It has a small rural catchment consisting of arable and grassland. The majority of its length is a winterbourne with only 2 of the 8km length being perennial. The Winterbourne joins the Lambourn at Bagnor and is known as an important spawning area for trout. The stream was studied in the 1970' and 1980's before, during and after the supra-seasonal drought of 1976 (Berrie & Wright 1984;, Wright 1992) and found that the intermittent reaches in non-drought years had a distinct macroinvertebrate community. During the 1976 drought many perennial sites dried but after the drought macroinvertebrate diversity and abundance recovered rapidly.

Bagnor – Perennial Control Site

Bagnor is positioned approximately 7 km from the source (Table 2.1) at 51.422° N, 1.351° E

The Winterbourne joins the Lambourn in Bagnor, the site in this study was around 10m upstream from the confluence. The banks of this site are managed by the land owner with grass being regularly mowed to allow the area to be used for recreation (Figure 2.6). There is a bridge 1m upstream of the site and a nature reserve on the opposite bank.

The River Lambourn at Bagnor was intensively studied in the 1970s and early 1980s. The studies and found a rich biodiversity of macrophytes and invertebrates (HAM et al., 1981; Wright et al., 1981; Wright et al., 1982; Wright et al., 2004) and Berrie & Wright (1986) looked at Bagnor on the Winterbourne stream and found similar results. The channel is narrow and during the summer vegetation growth restricts the width further.

Figure 2.6. The Winterbourne Stream at Bagnor, May 2013, one year after the drought.

Honeybottom – Dewatering Site

Honeybottom is positioned approximately 6 km from the source (Table 2.1) at 51.429° N, 1.351° E. The site is owned by a farm, however the area directly next to the stream was not farmed at the time of the study. On one side of the channel there was a 5 metre wide section of scrub woodland, and beyond this was crop farming. On the other side of the channel there was 1m of grassland and scrubland between the river and a minor single track road. With trees and scrub on both sides of the channel, this area was shaded for a large proportion of the year. This site was very shallow and the substrate mostly consisted of cobbles. In April during the drought the site was very shallow (Figure 2.7) it slowly recovered to its full wetted width by the following year (Figure 2.8).

Figure 2.7. The Winterbourne Stream at Honeybottom, April 2012, during the drought.

Figure 2.8. The Winterbourne Stream at Honeybottom, May 2013, one year after the drought.

Shepherds Copse – Rewetted Site

Shepherds Copse is positioned approximately 5 km from the source (Table 2.1) at 51.432^{o} N, 1.354^{o} E. The channel was very narrow and the site was dry from the beginning of the study until June 2012. The site has a road on one side and a steep bank leading to a crop farm on the other (Figure 2.9). There was a small bridge two metres downstream of the site leading to the farm. At the edges of the channel the water was pooled and there was very little flow. The sediment was a mixture of cobbles, sand and silt.

Figure 2.9. The Winterbourne Steam at Shepherds Copse, May 2013, one year after the drought.

2.1.3 The River Kennet

The River Kennet is a groundwater fed chalk stream which was designated as a Site of Special Scientific Interest (SSSI). The catchment is mostly rural, but was under threat from abstraction and invasive species such as the American Signal Crayfish. The river has a large sewage treatment plant which discharges treated effluent downstream of Marlborough. Historically there was a high phosphorous load in this river, however since sewage treatment was improved in the late 1990's phosphorus concentrations have remained low (Flynn et al., 2002).

Axford – Perennial Control Site

Axford is positioned approximately 32 km from the source at 51.427° N, 1.662° E. This site is upstream of Marlborough and hence has no sewage input. The site is owned by Ramsbury Estate, who manage the site. At the time of the study, one bank was improved grassland mixed with scrubland and the other bank was scrubland and unmanaged (Figure 2.10). There is a bridge 1m downstream of the site. There was a high density of American signal crayfish *Pacifastacus leniusculus* at this site which were often seen but were not found in the Surber samples. The site had abundant macrophytes in July, August and September especially near the banks. This site had the most stable depths and widths of all the study sites (Table 2.1). This may be because the site was naturally wide and so changes in flow are less apparent.

Figure 2.10. The River Kennet at Axford, June 2012 as the drought was ending.

Marlborough College – Dewatering Site

Marlborough College is positioned approximately 25 km from the source at 51.414^{o} N, 1.738^{o} E**.** The site is owned by Marlborough College. The banks on either side are lined with 2-5 metres of trees and scrub, (Figure 2.11). One bank has a sporting lake 5 metres beyond the bank, the other bank has a steep hill which then leads to managed grassland and some buildings.

Figure 2.11. The River Kennet at Marlborough College, May 2013, one year after the drought.

Clatford Bridge – Rewetted Site

Clatford is positioned approximately 22 km from the source at 51.418° N, 1.773° E. The site was downstream of Clatford Bridge which is used by mainstream traffic (roughly one vehicle every 5 minutes). The banks on either side were scrubland for at least 10m (Figure 2.12). Beyond this were fields used for arable farming.

A thick mat of filamentous algae covered the entire site for the first few months of the study (Figure 2.13), but declined by the end of the study in October and was all but gone by the following year (Figure 2.14). The sediment at the site was mostly silt with very few exposed rocks. The silt levels slowly reduced through the study.

Figure 2.12. The River Kennet at Clatford June 2012, two months after the drought. Note the coverage of filamentous algae

Figure 2.13. The River Kennet at Clatford July 2012, three months after the drought. This picture showed the thick mat of filamentous algae and silted substrate which covered the site for around 6 months after rewetting occurred.

Figure 2.14. The River Kennet at Clatford, May 2013, one year after the drought. Note how there was now no sign of filamentous algae.

2.2 The effect of the drought of 2010-2012 on the streams.

The drought that this study covers lasted for two years. The origins of the drought were in 2009 when a wet autumn was followed by a winter with little precipitation, there were then a further two dry winters in 2010/11 and 2011/12 (Kendon et al., 2013). By early spring 2012 the UK had a pronounced groundwater deficit (Kendon et al., 2013) Figure 2.15 showed the rainfall data from the UK Met Office between 2010 and 2012 as a percentage of the average between 1981 and 2012; the south east of England had less than 65% of the average rain in this time period. The low precipitation levels in winter led to low water levels in the aquifers which are the main source of water supply to the surrounding areas (Kendon et al., 2013; National Hydrological Monitoring Programme, 2012). It was found that the amount of water stored in the chalk was less than that in 1976 which was the worst UK drought on record (Kendon et al., 2013; National Hydrological Monitoring Programme, 2012)

The drought of 2010-2012 led to large areas of the streams remaining dry for two winters, this allowed terrestrial plants to grow on the river bed (Figure 2.16) which were then under water by June 2012 when the streams rewetted (Figure 2.17). Sites which were normally perennial dried and most reaches were much shallower than normal. All three of the 'rewetted' sites in this study are normally perennial but dried during the drought.

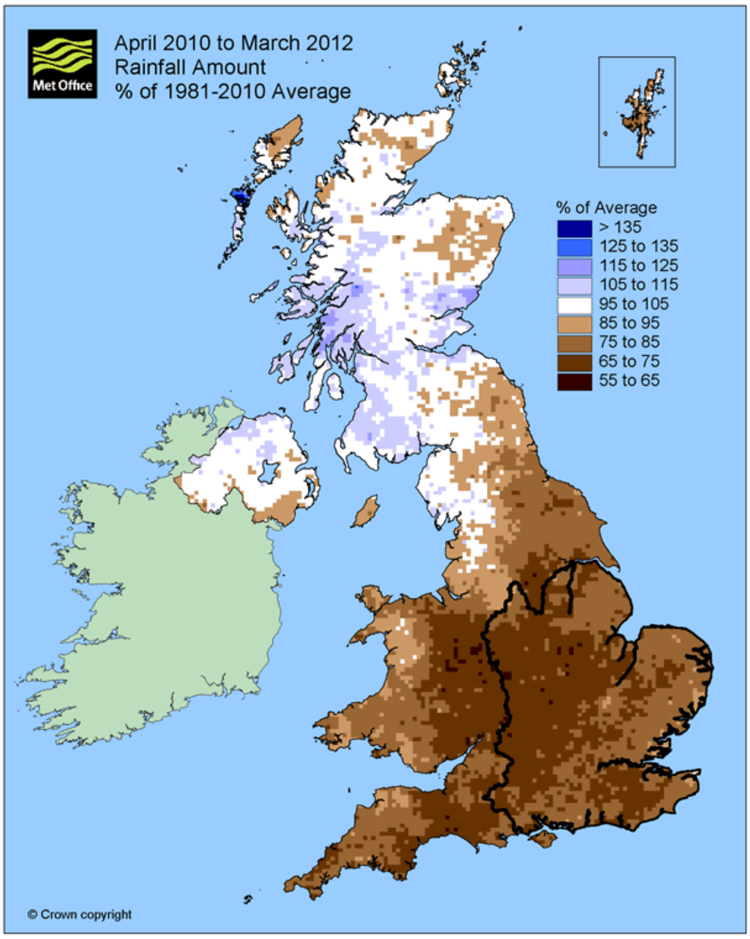

Figure 2.15. **Rainfall map from the Met Office (Met Office, 2012) showing rainfall amount as an average of rainfall from 1981-2010.**

Figure 2.16. The River Lambourn, upstream of East Shefford. November 2011 during the drought.

Figure 2.17. The River Lambourn at East Garston just upstream of the field site US East Shefford 23.108 N 48.996 W in May 2012 just as the site rewetted. This site was normally intermittent but had been dry for two years. Terrestrial plants had grown on the riverbed which were then flooded when the site rewetted

2.3 Comparing sites throughout the drought

2.3.1 Physical Changes

The Kennet is the largest of the three rivers and the study sites are the furthest from the source. The Axford site has the largest catchment size and the lowest altitude (Table 2.1). The Winterbourne is a very short stream with a small catchment size and the size of the Lambourn is in-between the other two streams, and it has the highest altitude (Table 2.1).

The wetted widths and depths of the streams changed during and after the drought. Most streams became wider and deeper after the drought broke in spring (Table 2.2), except at the Winterbourne perennial site.

Table 2.2. The wetted width and mid-channel depth measurements of the perennial and dewatering sites. The site with the highest flow permanence was shown first for each river. P = perennial, D = dewatering and R = rewetting, Sp= spring, Su- summer, A=autumn.

Stream	Site	Widths (m)			Depth Mid Channel (cm)		
		Sp	**Su**	**A**	**Sp**	**Su**	**A**
Lambourn	P	7.5	8.5	9	61	56	63
Lambourn	D	9	11	10.5	20	36	31
Lambourn	R	-	8.6	8.7	-	19	19
Winterbourne	P	8	6	7	23	20	38
Winterbourne	D	3	3.5	3	7	10	9
Winterbourne	R	-	4.1	4.3	-	13	20
Kennet	P	12	15.5	16	21	36	54
Kennet	D	8	8	9	11	33	35
Kennet	R	-	8.6	9.3	-	45	52

2.3.2 Chemistry data during and after the drought

Data was collected from Boxford on the River Lambourn (Figure 2.18) and Woolhampton on the River Kennet (Figure 2.19) as part of the CEH Thames Initiative. There is a peak in soluble reactive phosphorus (SRP) in January and February 2012 probably caused by heavy rainfall and run off. See section 5:3 for more analysis. Nitrate (NO3), and boron (B) which is a signifier for sewage effluent, do not fluctuate significantly over the drought or recovery period. Suspended chlorophyll *a* has a peak on both streams in spring. However, the sites which these samples were taken at were perennial and the chemical status of dewatering and rewetted sites is not known.

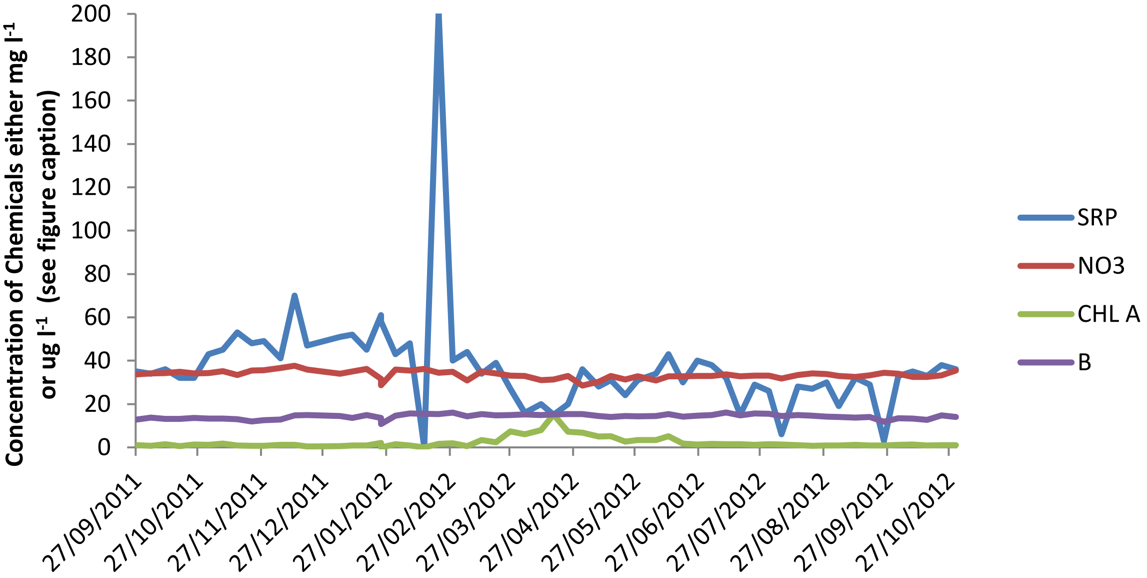

Figure 2.18. Water chemistry results of the River Lambourn at Boxford, the perennial site in this study. Chemicals shown are: bio-available soluble reactive phosphorus (SRP) in µg l^{-1}; Nitrate (NO3) in mg/l; Chlorophyll *a* (CHL A) in ug l^{-1} and Boron (B) in µg/l. Boron is used as a tracer for sewage treatment effluent and so would show changes in inputs of nutrients from sewage treatment effluent.

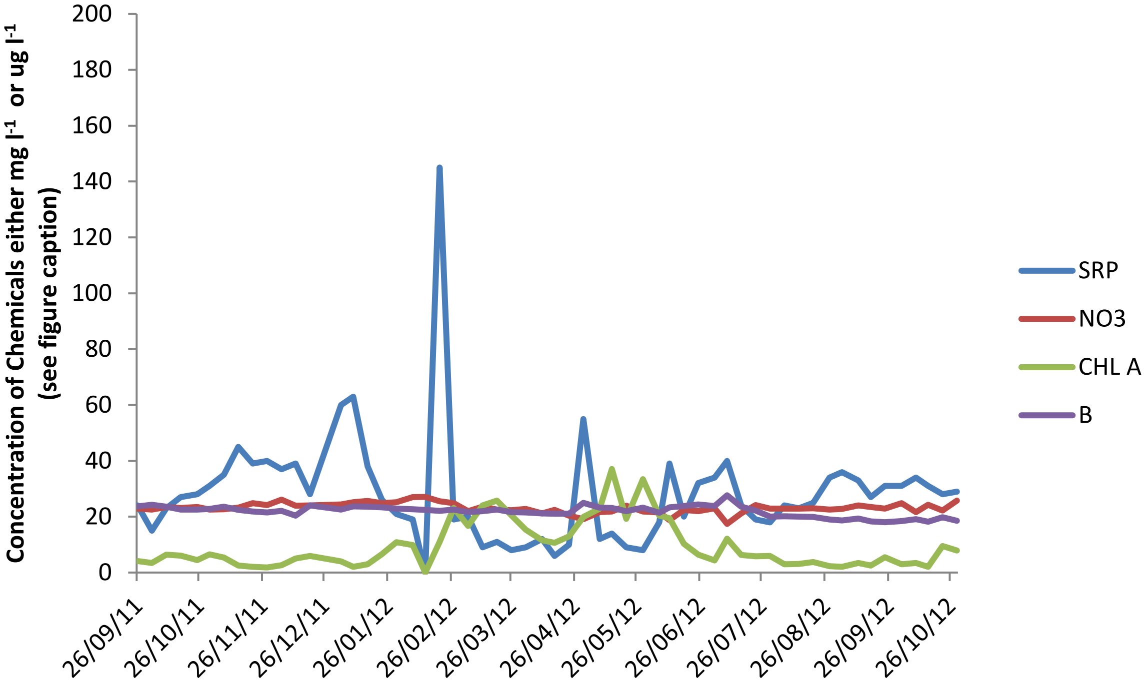

Figure 2.19. Water chemistry results of the River Kennet at Woolhampton, downstream of all sampling sites. Chemicals shown are: bio-available soluble reactive phosphorus (SRP) in µg l^{-1}; Nitrate (NO3) in mg/l; Chlorophyll *a* (CHL A) in µg l^{-1} and Boron (B) in µg l^{-1}. Boron is used as a tracer for sewage treatment effluent and so would show changes in inputs of nutrients from sewage treatment effluent.

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CHAPTER 3

THE EFFECTS OF LOW FLOWS ON MACROINVERTEBRATE COMMUNITIES AND ALGAL BIOMASS

3.1 Introduction

Climate change is expected to increase the frequency and intensity of meteorological drought in many regions, with potentially profound implications for river flows (Beniston et al., 2007; IPCC, 2007; IPCC, 2013; Wada et al., 2013; Van Loon, 2015). Low river flows can arise naturally as a result of precipitation deficits but these impacts could be exacerbated by global climate change (Wright and Berrie 1987; Rolls et al., 2012) and human activities such as water extraction (Soley et al., 2012; Bradley et al., 2014) and flow regulation (Acreman et al., 2008). In the future, increasing water usage will pressurise water resources, with potentially far-reaching consequences for the biodiversity and functioning of freshwater ecosystems (Walther et al., 2002; Smith, 2011; Wernberg et al., 2013).

Low flows can have marked impacts on a wide range of aquatic organisms, including benthic algae and macrophytes (Suren and Riis, 2010). Suren and Riis (2010) modelled the effects of low flow on aquatic plants and algae and found increased growth of both groups at low flow, with macrophytes often dominating the substratum. The extent of algal growth at low flow depends on water quality, and is often most marked in streams that are rich in nutrients such as nitrogen and phosphorus (Suren and Riis, 2010). These changes in plant abundances directly and indirectly affect macroinvertebrates that rely on them for food and habitat. For instance, filamentous algae are not as readily ingested as diatoms (Lamberti, 1996) and macrophyte dominance can reduce benthic algae by shading, constraining food availability to herbivores. Thus, low flows can have long-lasting effects on aquatic plants, with far-reaching consequences for the whole stream community.

The effect of low flows on macroinvertebrate community structure depends on the extent of channel drying (Covich et al., 2003; Dewson et al., 2007a). Complete drying of the substratum can severely reduce animal abundances and cause local extinction of vulnerable species (Suren et al., 2003a; Arscott et al., 2010), but where free surface water remains, impacts can be weak or absent (Dewson et al., 2007a) and difficult to detect (Rader and Belish, 1999). White et al. (2012) showed in Australian streams that experimentally reducing stream flow by two thirds reduced macroinvertebrate taxon richness. Under low flow, they observed that abundances of Oligochaeta and Diptera increased and Ephemeroptera, Plecoptera and Trichoptera decreased. Oligochaeta and Diptera larvae (mainly from the Chironomidae family) are opportunists that exploit a range of disturbances including drought (Lugthart and Wallace, 1992; Whiles and Wallace, 1992; Otermin et al., 2002). Siltation caused by drought can also have a marked effect on macroinvertebrate communities (Wright and Berrie, 1987; Wright and Symes, 1999). Some taxa are highly sensitive to siltation (e.g. Simuliidae) whereas others (Oligochaeta) are less affected or increase (Extence et al. 2013). Suren and Jowett (2006) compared the effect of low flows on macroinvertebrates to that of floods in New Zealand and found floods to have the greater effect on community structure, with no taxa apparently lost during low flows.

Low flow can elicit changes in the behaviour of macroinvertebrates, including drift (Dewson et al., 2007b; Kennedy et al., 2014), crawling (Lancaster et al., 2006) and foraging (Poff et al., 2003; Poff and Zimmerman, 2010; Wellnitz and Poff, 2012). Feeding behaviour can differ from species to species over flow gradients, for example Poff et al. (2003) showed grazing by two taxa (*Baetis* and *Glossosoma*) decreased with decreasing velocity whereas feeding by a third taxon (*Drusus*) was unaffected. Such contrasting responses to low flow conditions within functional groups could have implications for the functioning of the macroinvertebrate community during drought.

The effects of low flow on individuals and assemblages is likely to have consequences for the rate of key processes in drying streams, but studies are still needed to in chalk streams. Research on leaf litter decomposition – a key process in stream ecosystems – in northern Spain (Arroita et al. 2015) has revealed that drought can suppress leaf litter breakdown rates, especially in the winter months, and reduce the abundance of macroinvertebrate shredders Dewson et al. (2007b) assessed the effect of low flows on algal primary production in New Zealand streams during changes of flow and found that there was little if any change in chlorophyll *a* production between the control and low flow sites. It must be noted that other factors may be affecting these sites such as nutrient enrichment, for example, Suren et al. (2003b) found that low flows only increased biomass of algae in areas which had nutrient enrichment. Secondary production has been shown to change during drought, smaller short-lived species of macroinvertebrate dominated during experimental drought disturbances (Ledger et al., 2011; Ledger et al., 2013). Ledger et al. (2013) also found changes in functional feeding group during the mesocosm drought experiment, less shredders and engulfers were found in frequently dewatered treatments whereas grazers showed a more complex response, with molluscan species declining but Orthoclad Chironomidae increasing. Functioning data from natural droughts are rare and difficult to obtain due to the unpredictability of events and thus understanding of river ecosystem functioning during drought is still relatively poor.

Chalk streams contain a wide variety of aquatic organisms, many of which are protected by environmental legislation (Bennett, 2007; Wright, 1992). Chalk streams are scarce – there are fewer than 200 worldwide, 85% of which are located in England, often in areas with relatively high population densities (O'Neill and Hughes, 2014). Chalk streams are threatened by water extraction from the river channels and from the chalk aquifers that sustain them, 70% of the water used in England comes from chalk aquifers (O'Neill and Hughes, 2014). These pressures on chalk stream flows can be exacerbated during supra-seasonal drought (Kendon et al., 2013), when flows in normally perennial and intermittent reaches can decline, leading to periods of low flow and stream drying (Berrie and Wright, 1984).

A number of studies report the ecological effect of low flows in chalk streams (Ladle and Bass, 1981; Berrie and Wright, 1984; Wright and Symes, 1999; Wood and Petts, 1999; Wright et al., 2004). Wood and Petts (1999) showed that the effect of drought may depend on event duration, with multiyear events (1989-1992) having greater impacts on macroinvertebrate assemblages than seasonal events (1995). Wood and Armitage (2004) also studied two droughts (1992 and 1996-1997) that reduced macroinvertebrates abundances, with Gammaridae numbers negatively correlated to water velocity. Berrie and Wright (1984) studied chalk streams during the 1976 drought. They observed little change in ecology of the areas of the stream retaining water, but reported a reduction in taxon richness at the site where dewatering occurred. During drought, taxa associated with slow flowing or still water can become more prevalent while those that require fast flows can perish (Feminella, 1996; Dewson et al., 2007a). Such shifts in macroinvertebrate community structure could in theory alter the rate of key ecosystem processes, but research on the functional implications of drought is still scarce.

Overall there is uncertainty as to how low flows affect the macroinvertebrate communities and associated processes in streams. This chapter reports the results of a study that evaluated the impact of a supra-seasonal two year drought on three chalk streams in south east England which reduced flows markedly for at least 15 months (Kendon et al., 2013). The aim of this study was to determine how low flows occurring during a supra-seasonal drought altered benthic macroinvertebrate communities in these chalk streams. Three streams were sampled at perennial and dewatered sites in the month preceding the end of the 2012 drought.

Hypotheses were:

H_1: Dewatering sites will contain a greater biomass of algae than perennial sites

Rationale: The dewatering site will contain less grazing invertebrates (see hypothesis 4) and less sloughing of algae will occur allowing a greater build-up of biomass

H_2: Macroinvertebrate community structure will alter, with declines in Ephemeroptera, Trichoptera and Plecoptera and increases in Oligochaeta and Chironomidae in drying sites.

Rationale: Ephemeroptera, Trichoptera and Plecoptera are flow-sensitive species which should decline with reduction in flow. Oligochaeta and Chironomidae are disturbance-resistant species often found in areas of disturbance.

H_3: Densities of macroinvertebrates will rise in dewatering sites but biomass will change little.

Rationale: Large numbers of Oligochaeta and Chironomidae exploit drying conditions, however community biomass was expected to change very little as these abundant opportunistic species typically have a small body mass

H_4: Functional feeding groups (FFG) will differ between dewatering and perennial sites with less predators and scrapers and more shredders and deposit feeders

Rationale: Many of the flow-sensitive species are predators and scrapers whereas Oligochaetes are deposit feeders. Chironomids are varied in FFG so this may depend on the species which flourish in the dewatering sites.

3.2.1 Site Descriptions

Three chalk streams in Berkshire and Wiltshire were used in this study: River Lambourn, Winterbourne Stream and the River Kennet. Two sites were investigated on each stream during the supra-seasonal drought of 2010-2012, one which was a perennial control and the other was dewatering (very shallow and at risk of drying). On each river or stream, the control sites were compared with the dewatering site to determine how low flows had affected macroinvertebrate communities and algal biomass. Each site was visited once during the drought (May 2012) and again as the drought broke (June 2012). See Chapter 2 for full descriptions of streams, sites and the drought.

The during-drought samples were limited as the drought broke 6 weeks after sampling began. Therefore only one or two months of data exist for the different samples. This chapter therefore is looking at a snapshot of the samples comparing perennial sites with the dewatering site within the same river.

3.2.2 Physical measurements in streams

Water depth was measured using a metre rule at 0.5m intervals along the same transect, and water velocity measured at a) 40% depth and b) 2.5 cm above the substratum using a Doppler flow meter.

3.2.3 Macroinvertebrate sampling and processing

At each site, three macroinvertebrate samples were collected using a standard Surber net (area $0.0625m^2$, mesh size 500µm). The samples were preserved in 5% formaldehyde in the field. In the laboratory, macroinvertebrates were sorted from debris, identified and counted. Macroinvertebrates were identified to the lowest practicable taxonomic unit, typically species, excepting Oligochaeta, Ostracoda and Copepoda (order) and Chironomidae (sub-family). Body length, maximum lengths of animals with shells or head width (depending on taxa) was measured to the nearest 0.1mm and converted to biomass using published length mass regression equations (Smock, 1980; Meyer, 1989; Towers et al., 1994; Burgherr and Meyer, 1997; Benke et al., 1999; Cressa, 1999; Johnston and Cunjak, 1999; Gonzalez and Chaneton, 2002; Sabo et al., 2002; Edwards et al., 2009).

3.2.4 Macroinvertebrate metrics

Three metrics were calculated using family-level macroinvertebrate data. The proportion of sediment sensitive macroinvertebrates (PSI) is an index of sedimentation impact (Extence et al., 2013). The Whalley Hawk Paisley Triggs (WHPT) metric is an index of poor water quality, principally organic pollution (SNIFFER 2007). The lotic macroinvertebrate flow evaluation score (LIFE) is an index of low flow effects (Extence et al. 1999). Each index assigns a score to each taxon and the appropriate equation is used to calculate the index at the sample level. For each metric, high values indicate low levels of impacts on the macroinvertebrate communities.

3.2.5 Algal biomass determination

At each sample site, epilithic biofilm was collected from the upper surfaces of five cobbles in May 2012. A Five cobbles (Wentworth scale Wentworth, 1922) were sampled at each site. Using a 5cm^2 template, algae were scraped from upper surface of each stone using a toothbrush. The resulting slurry washed into a sterile 250ml plastic bottle using a funnel and wash bottle containing stream water. On return to the laboratory, the volume of the sample was standardised to 300ml using deionised water. Aliquots of 200 ml were frozen at -20^{o}C and processed for chlorophyll *a* and biomass determination (American Public Health Association, 2005). For chlorophyll analyses, samples were defrosted in the dark and homogenised. Aliquots of 100ml were filtered using grade GF/C 0.47 um thickness glass fibre filter paper and placed into a vial with 20 ml of 90% (v/v) acetone. Chlorophyll was extracted overnight in a dark refrigerator. The absorbance of the extract was measured at wavelengths of 665 and 750 using a spectrophotometer (model Beckman DU520), against a 90% acetone blank in a cuvette with a path length of 1cm. The concentration of chlorophyll *a* in the sample was then calculated using equations (American Public Health Association, 2005).

Biofilm ash-free dry mass (AFDM) was determined by defrosting the 100ml aliquot, filtered onto an ashed and pre-weighed G/FC glass fibre filter, dried at 70^{o}C overnight, and then cooled in a desiccator and weighed. Each dried sample was then ashed in a furnace at 500 C for one hour, then cooled to room temperature and reweighed. Ash-free dry mass was calculated as the difference in mass (mg) between the oven-dried and ashed sample (Ledger & Hildrew, 1998).

3.2.6 Autotrophic Index

The autotrophic index is used as an indicator of the quality of the biofilm, and reflects the extent to which biofilms consist of heterotrophic organisms (bacteria, fungi, microinvertebrates) and detritus versus autotrophic pigment-containing algae and cyanobacteria. It is calculated by dividing the total AFDM μg-cm^2 by chlorophyll-*a* μg-cm^2.

Numbers over 400 are considered to be poor quality and usually from rivers with high nutrient load (American Public Health Association, 2005).

Autotrophic Index = AFDM (µg cm^{-2})/Chlorophyll-*a* concentration (µg cm^{-2})

3.2.7 Data Analysis

Water Velocity Data

Data was assessed for normality and QQ plots showed no sign of deviating from normal distributions, however, histograms and boxplots showed one site – Winterbourne dewatering – had extreme values which meant the samples did not have homogeneity of variance (Figure 3.1) (levenes test p+>0.05). Therefore non-parametric tests were chosen for this analysis. Kruskal Wallis tests were used to compare flow rate between sites and flow rate between site types (perennial or dewatering).

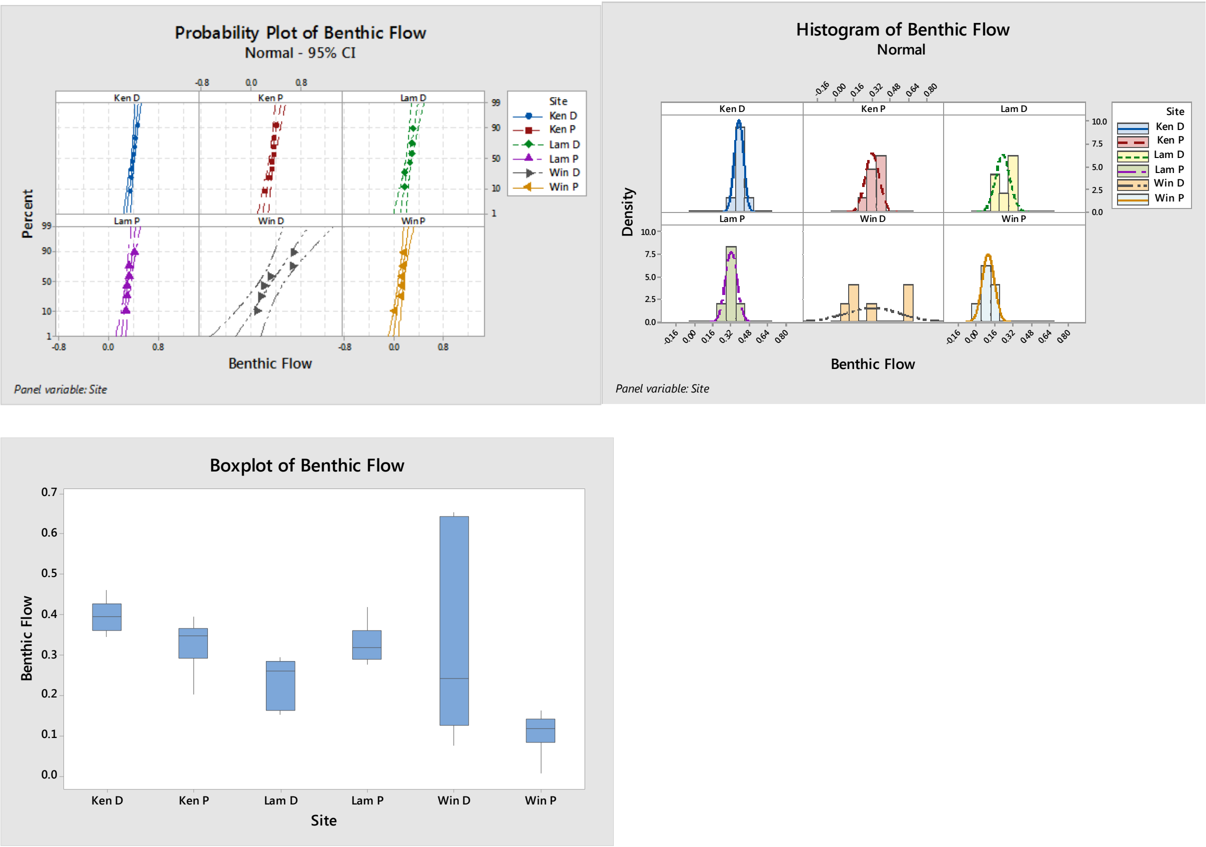


Figure 3.1: Data exploration for flow data. Lam = Lambourn. Ken = Kennet, Win = Winterbourne, P = perennial and D = dewatering. Probability plots all sites had p values over 0.05 indicating data is likely to be normally distributed. Histograms and boxplot show one site Winterbourne dewatering site has outliers and a larger range.

All statistical tests were carried out in Minitab 16$^{(R)}$ Flow for the benthic surface was analysed in a one-way ANOVA testing for differences between perennial and dewatering sites, with flow as the response and site as the factors. This test was also performed on the River Lambourn for measurements at 0.4 depth which the other two streams did not have.

Algal chlorophyll and AFDM were deemed to be not normally distributed and non-parametric tests were used to analyse this data (figure 3.2). The data were analysed to determine differences between perennial and dewatering sites. Kruskal Wallis tests were performed on chlorophyll *a*, AFDM and AI data separately with each as the response, to test for differences between chlorophyll *a* and site for each river.

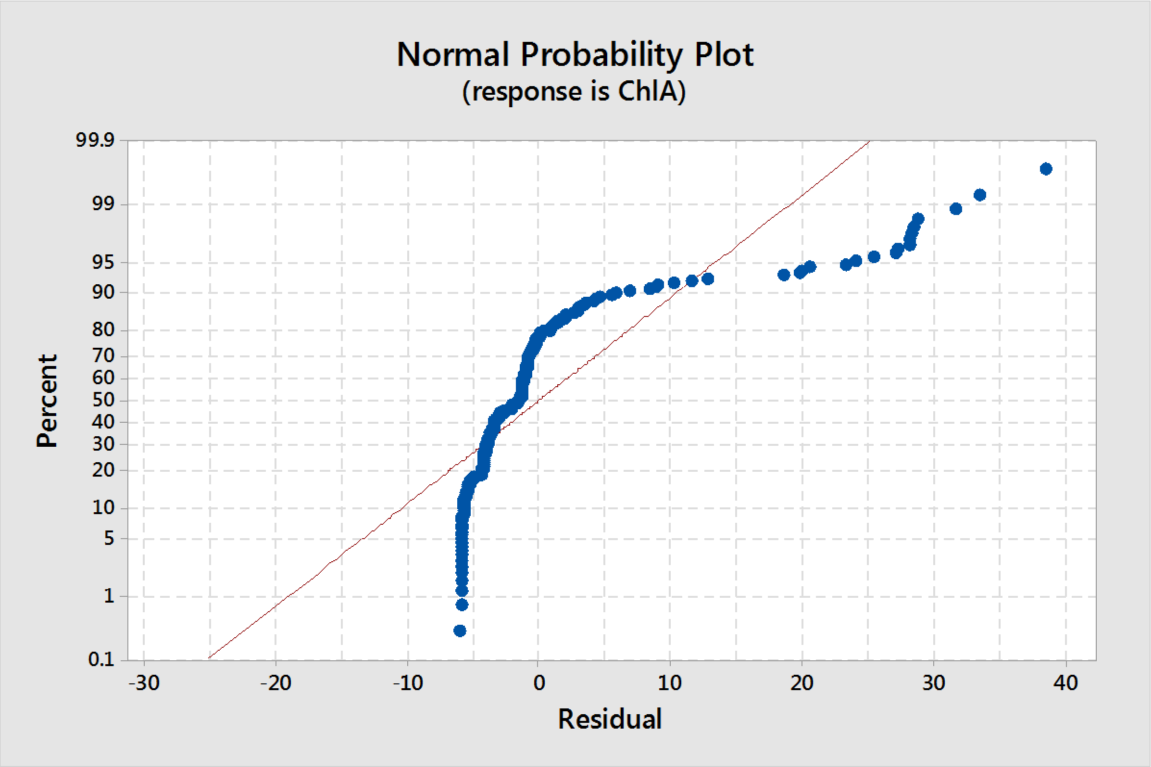


Figure 3.2. QQ Plot of Chlorophyll *a* data showing curve indicating data were not normally distributed

Macroinvertebrate density and biomass data were collated to allow analysis on various different groups. For each Surber the combined densities and biomasses of all macroinvertebrates were compared. One-way ANOVA tests were performed on each river to test for differences between perennial and dewatering sites where density and biomass were the responses and river and site were the factors. One-way ANOVAs were selected due to only one factor differing between responses. All tests used the 95% confidence interval.

Macroinvertebrate density and biomass data was summarised by family to allow family level analysis and biometrics to be analysed. A functional feeding group (FFG) was assigned to each species using the Macroinvertebrate Traits Database (Usseglio-Polatera, 1991; Chevene et al., 1994; Tachet et al.). In this database species are given a number of 0-5 for each trait, the feeding habit with the highest number was picked as the main FFG. If two feeding habits had an equal number in the database, the food category was then referenced, for example if an macroinvertebrate was a three for both shredding and scraping, but a five for algae and a three for detritus, it was assumed algae was its main food source and so scraping was chosen as its FFG. Taxa in the database were a mixture of species, genus, family and sub-family. If only genus, family or subfamily was given in the database, it was assumed all species of that group had the same traits.

Macroinvertebrate data in functional feeding groups was analysed for normality, homogeneity of variances and outliers (Figure 3.3). It was found the data was skewed due to outliers on the left, it was decided not to remove the outliers as they showed true variability of the data – a large amount of one FFG on one site which could be a response to the drought. It was therefore decided to transform the data. Different transformations were trailed, and Box Cox allowed the data to show normal distribution and homogeneity of variances. This data was then used in an ANOVA model as follows: biomass of macroinvertebrates as the response, FFG, site (nested within river), site type (perennial or rewetted) and surber sample as a nested random sample were used as factors.

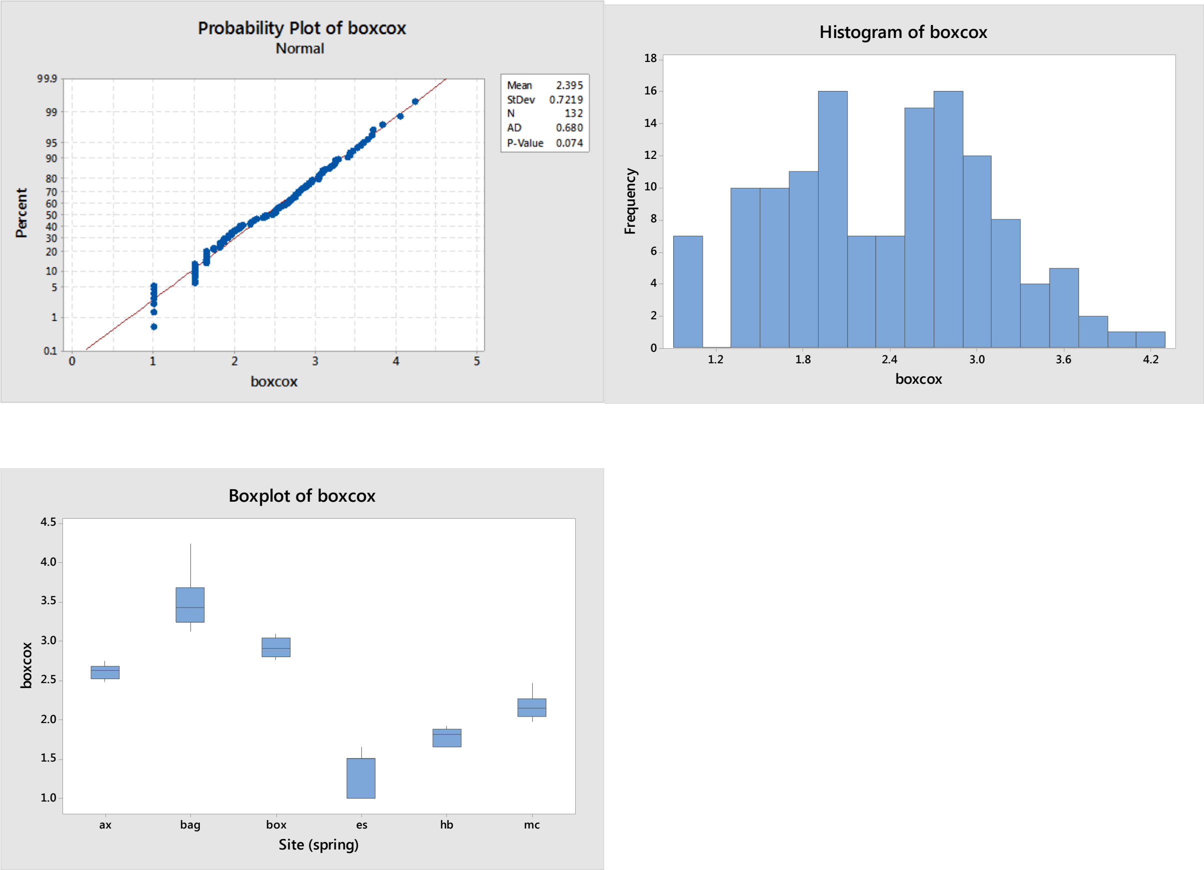


Figure 3.3. Plots of macroinvertebrate biomass showing QQ plot and histogram over overall data and boxplots separated by site.

Macroinvertebrate data for family group was treated in the same manner as FFG data, one-way ANOVA tests were conducted on functional feeding groups as the response and site as the factor to test differences between individual feeding groups between perennial and rewetted sites of the same stream. The macroinvertebrate density data was formatted and Canoco (Ter Braak and Smilauer, 2002) was used to perform Principal Component Analysis (PCA).

3.3 Results

3.3.1 Stream flow

In the Winterbourne Stream and the River Kennet, the dewatering site had higher water velocity (Figure 3.4) although the River Kennet was not significantly different (Table 3.1) and was shallower than the perennial site, but the opposite was the case in the River Lambourn and this was significant (Table 3.1).

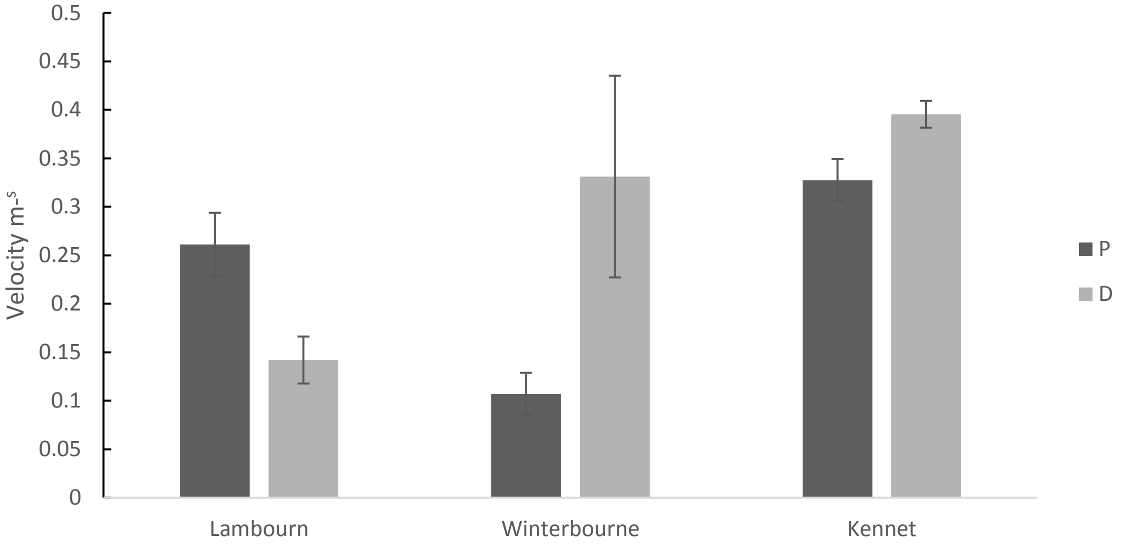


Figure 3.4. A Mean (± 1 SE) water velocity at benthic depth (2.5 cm above substratum) of both the perennial and dewatering site. Statistical significance between sites (AVOVA p<0.05) is marked with an asterisk.

Table 3.1. Kruskal Wallis testing for differences in water velocity between perennial and dewatering sites on each stream. DF = Degrees of freedom.

River	P Value	H Value	DF
Lambourn	0.018	5.63	1
Winterbourne	0.055	3.69	1
Kennet	0.036	4.41	1

3.3.2 Algal biomass

The density of chlorophyll *a* was significantly lower in the dewatering site than in the perennial sites on the Winterbourne and significantly higher in the dewatering site on the Lambourn (Figure 3.5), but differences between sites on the Kennet were not statistically significant ($p>0.05$, Table 3.2). AFDM followed the same pattern (Figure 3.6; Table 3.2). The autotrophic index was higher at the perennial site on in the Winterbourne Stream, but not on the River Lambourn or Kennet (Figure 3.7, Table 3.2).

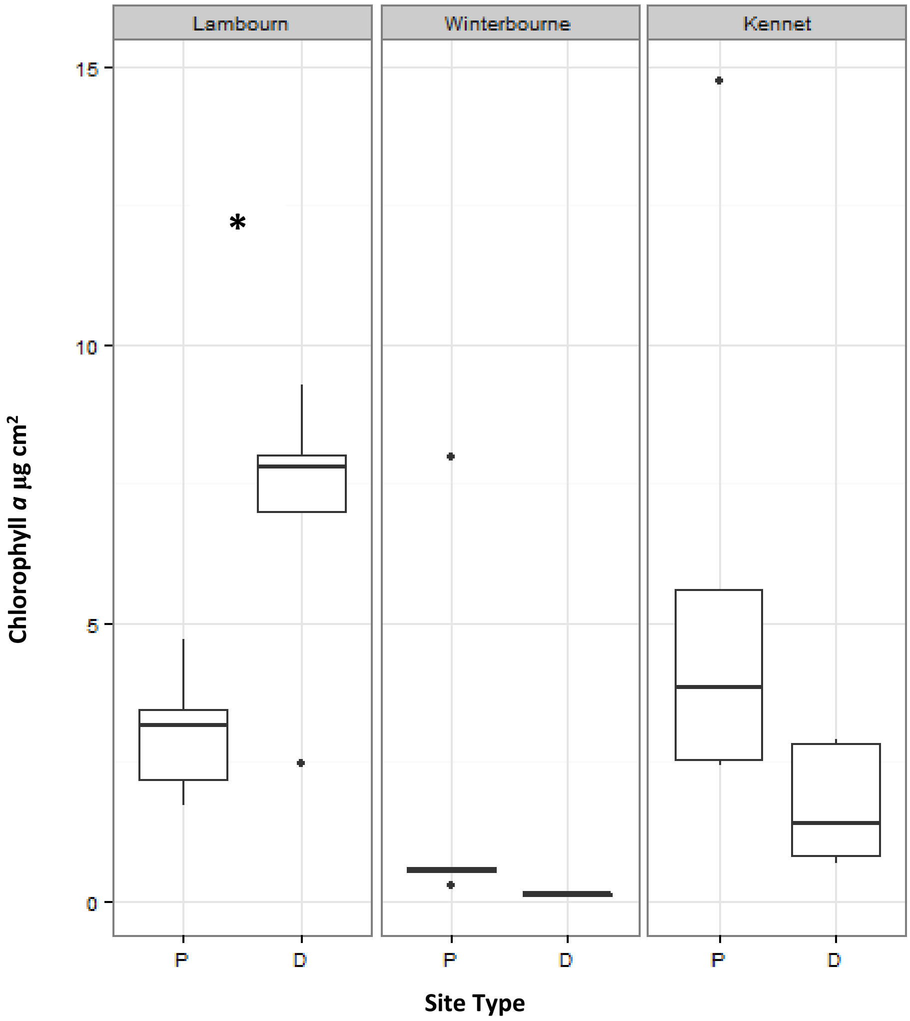


Figure 3.5. Boxplot depicting median with interquartile ranges of chlorophyll *a* in perennial and dewatering sites in each stream. D: dewatering; P: perennial; significant ($p<0.05$) effects are asterisked.

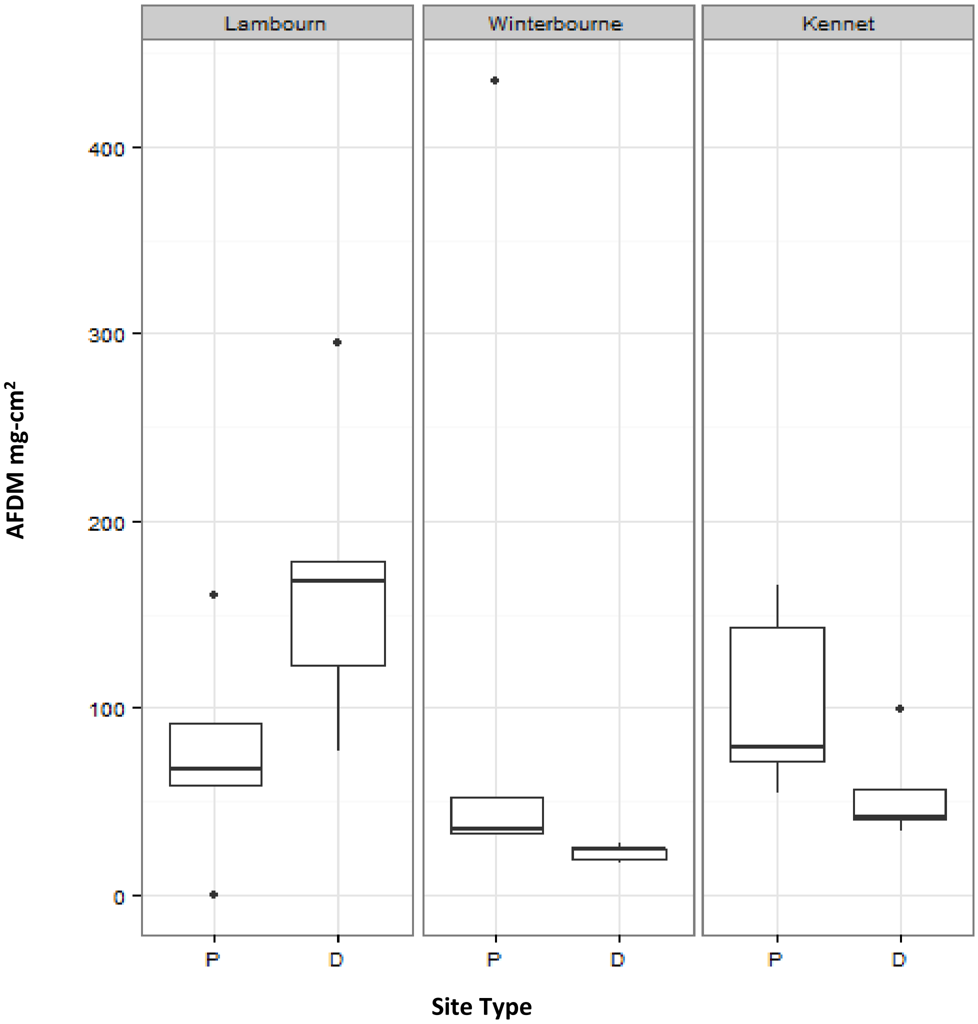


Figure 3.6. Boxplot depicting median with interquartile ranges of biofilm ash free dry mass (AFDM) in perennial (P) and dewatering (D) reaches of three streams.

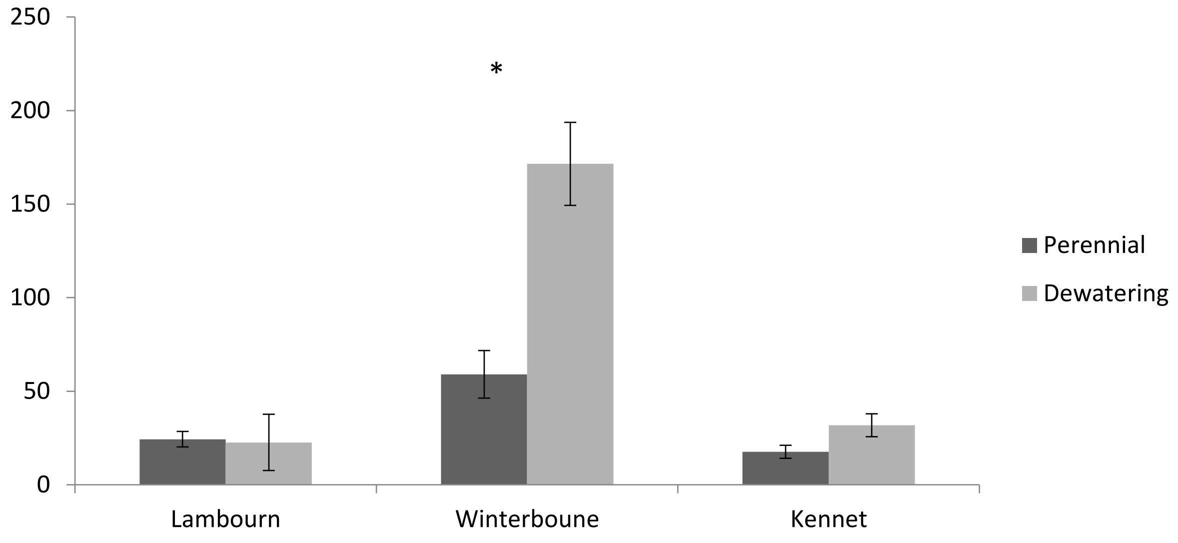


Figure 3.7. Mean (± 1 SE) autotrophic index of epilithic biofilm in perennial and dewatering reaches of three chalk streams. Significance is marked with an asterisk.

Table 3.2. Kruskal Wallis tests were used to test the effects of site on the chlorophyll *a* (Chl *a*), ash free dry mass and the autotrophic index. DF = Degrees of freedom.

River	Data	P Value	H Value	DF
Lambourn	Chl *a*	0.047	3.94	1
Winterbourne	Chl *a*	0.009	6.82	1
Kennet	Chl *a*	0.076	3.15	1
Lambourn	AFDM	0.047	3.94	1
Winterbourne	AFDM	0.009	6.82	1
Kennet	AFDM	0.076	3.15	1
Lambourn	AI	0.602	0.27	1
Winterbourne	AI	0.009	6.82	1
Kennet	AI	0.076	3.15	1

3.3.3 Macroinvertebrate Data

There was no statistically significant difference in total macroinvertebrate densities between dewatering and perennial sites in any of the study streams (ANOVA, p>0.05 in all cases) (Figure 3.9). There was no consistent trend in total macroinvertebrate biomass among perennial and dewatered sites of the three streams; drying sites had a higher (Winterbourne, F=9.72, DF=1, p>0.05) lower (Kennet, (F=29.56, DF=1, p>0.01) or similar (Lambourn, p<0.05) biomass of macroinvertebrates than perennial sites, depending on the study stream.

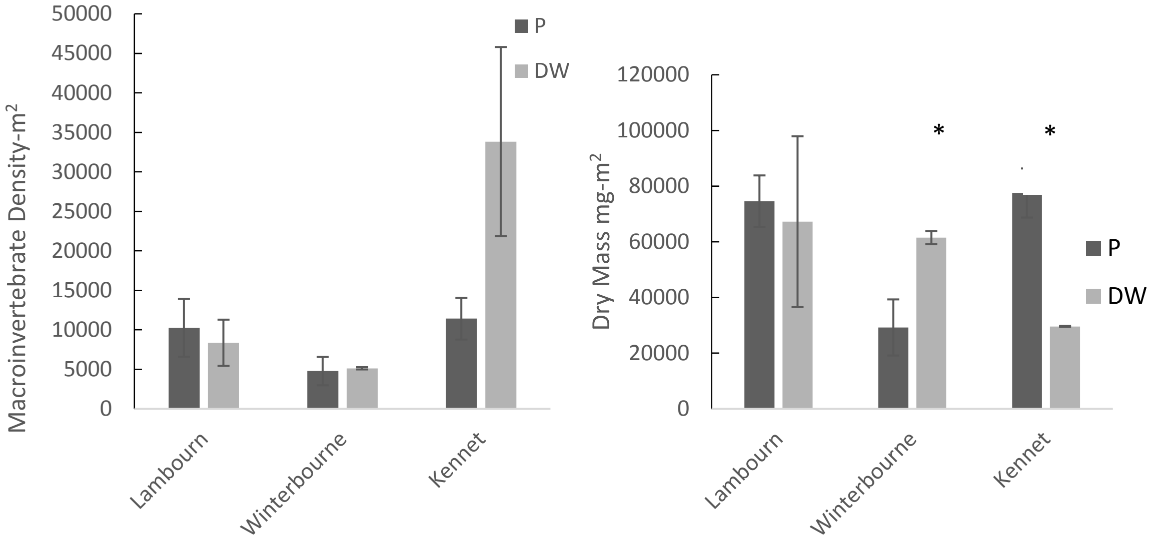


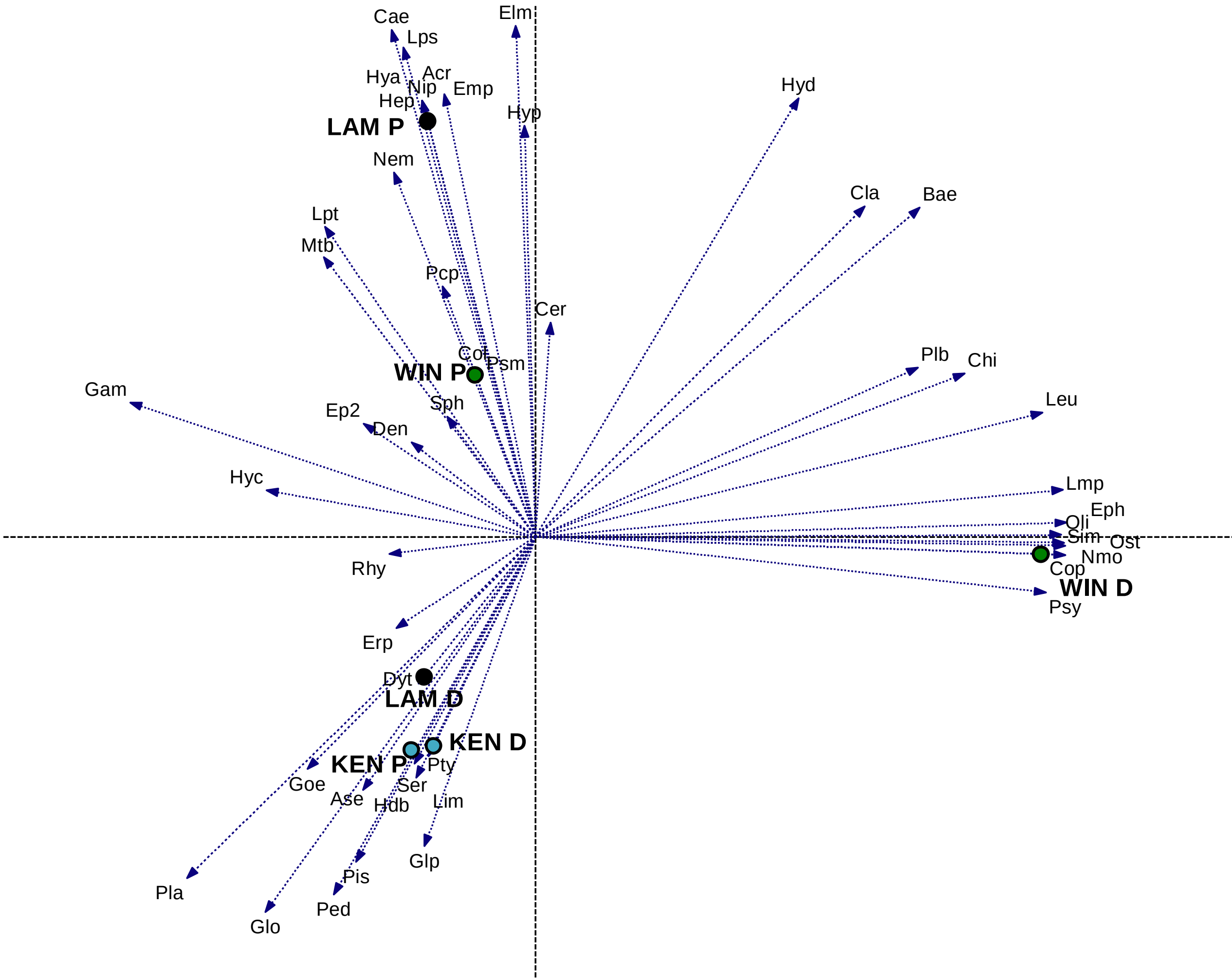
Figure 3.9. Mean (±1 SE) density (number m^{-2}) and biomass (mg m^{-2}) of macroinvertebrates in perennial and dewatering reaches on three chalk streams. Statistical significance among treatment means ($p<0.05$) is denoted by asterisks.

3.3.3.1 Macroinvertebrate Community Analysis

The macroinvertebrate communities of dewatered and perennial sites differed markedly in the Winterbourne Stream and River Lambourn, whereas similar communities were found in the River Kennet's sites (Figure 3.10). The River Kennet sites were most similar taxonomically, especially across the Limoniidae, Hydrobiidae, Asellidae and Glossiphoniidae. For the River Lambourn and Winterbourne Stream, large distances in ordination space between the perennial and dewatering site suggest more marked effects of the drought. The Winterbourne Stream's dewatering site community reflects responses of on Ostracoda, Oligochaeta, Simuliidae and Psychodidae among others. The River Kennet and River Lambourn had similar dewatering communities, sharing taxa such as Glossosomatidae, Pedicidae and Asellidae (Figure 3.10). The number of taxa in the perennial sites in the River Lambourn and River Kennet was higher both for total taxa and families, the Winterbourne Stream showed a similar taxa richness between perennial and dewatering sites (Table 3).

Table 3.3. Total taxa and family numbers from the three Surber samples for each site from the samples taken on the May sampling occasion. P=perennial site and D= Dewatered site.

Site	Number of Taxa	Number of Families
Lam P	56	32
Lam D	44	29
Win P	39	26
Win D	40	27
Ken P	49	32
Ken D	42	25



Cladocera (Cla), Collembola (Col), Copepoda (Cop), Dendrocoelidae (Den), Dytiscidae (Dyt), Elmidae (Elm), Empididae (Emp), Ephemerellidae (Eph), Ephemeridae (Eh2), Erpobdellidae (Erp), Gammaridae (Gam), Glossiphoniidae (Glp), Glossosomatidae (Glo), Goeridae (Goe), Heptegeniidae (Hep), Hydracarina (Hyc), Hydraenidae (Hya), Hydridae (Hyd), Hydrobiidae (Hdb), Hydroptilidae (Hyp), Lepidostomatidae (Lps), Leptoceridae (Lpt), Leuctridae (Leu), Limnephilidae (Lmp), Limoniidae (Lim), Microturbullaria (Mtb), Nematoda (Nem), Nemouridae (Nmo), Niphargidae (Nip), Oligochaeta (Oli), Ostracoda (Ost), Pediciidae (Ped), Piscicolidae (Pis), Planariidae (Pla), Planorbidae (Plb), Polycentripodidae (Pcp), Psychodidae (Psy), Psychomyiidae (Psm), Ptychopteridae (Pty), Rhyacophilidae (Rhy), Sericostomatidae (Ser), Simuliidae (Sim), Sphaeriidae (Sph)

Figure 3.10. Principle Component Analysis (PCA) of the perennial and dewatering sites at all three waterbodies. The analysis is on density data. L= Lambourn, K= Kennet, W= Winterbourne, P=Perennial and DW = Dewatered. Key showed name of taxa alongside code used in the figure as: Taxa (code).

Functional feeding group analysis showed changes in proportions of groups in all streams. In the Lambourn and Winterbourne shredders were the most numerous group in both the perennial and dewatering site, although the biomass of shredders was higher in the dewatering site in both waterways (Figure 3.11). In the River Lambourn there was a reduction in scrapers (One-way ANOVA, F=169.92, DF=1, p<0.01) and deposit feeders (One-way ANOVA, F=39.17, DF=1, p<0.01) in the dewatering site. Predators numbers did not vary significantly with site (One-way ANOVA, F=5.43, DF=1, p=0.08). In the Winterbourne Stream there was no change in the order of groups in terms of biomass, however the dewatering site had a higher biomass of shredders, although this is not significant (One-way ANOVA, F=6.68, DF=1, p=0.061), a higher biomass of predators (ANOVA, F=46.51, DF=1, p<0.01) and similar biomass of the other feeding groups. The perennial and dewatering sites of the River Kennet differed most markedly, with the former having a higher biomass of deposit feeders (One-way ANOVA, F=763.34, p<0.01) and a lower biomass of scrapers (ANOVA, F=693.5, DF=1, p<0.01) and filter feeders (ANOVA, F=8.64, DF=1, p<0.05).

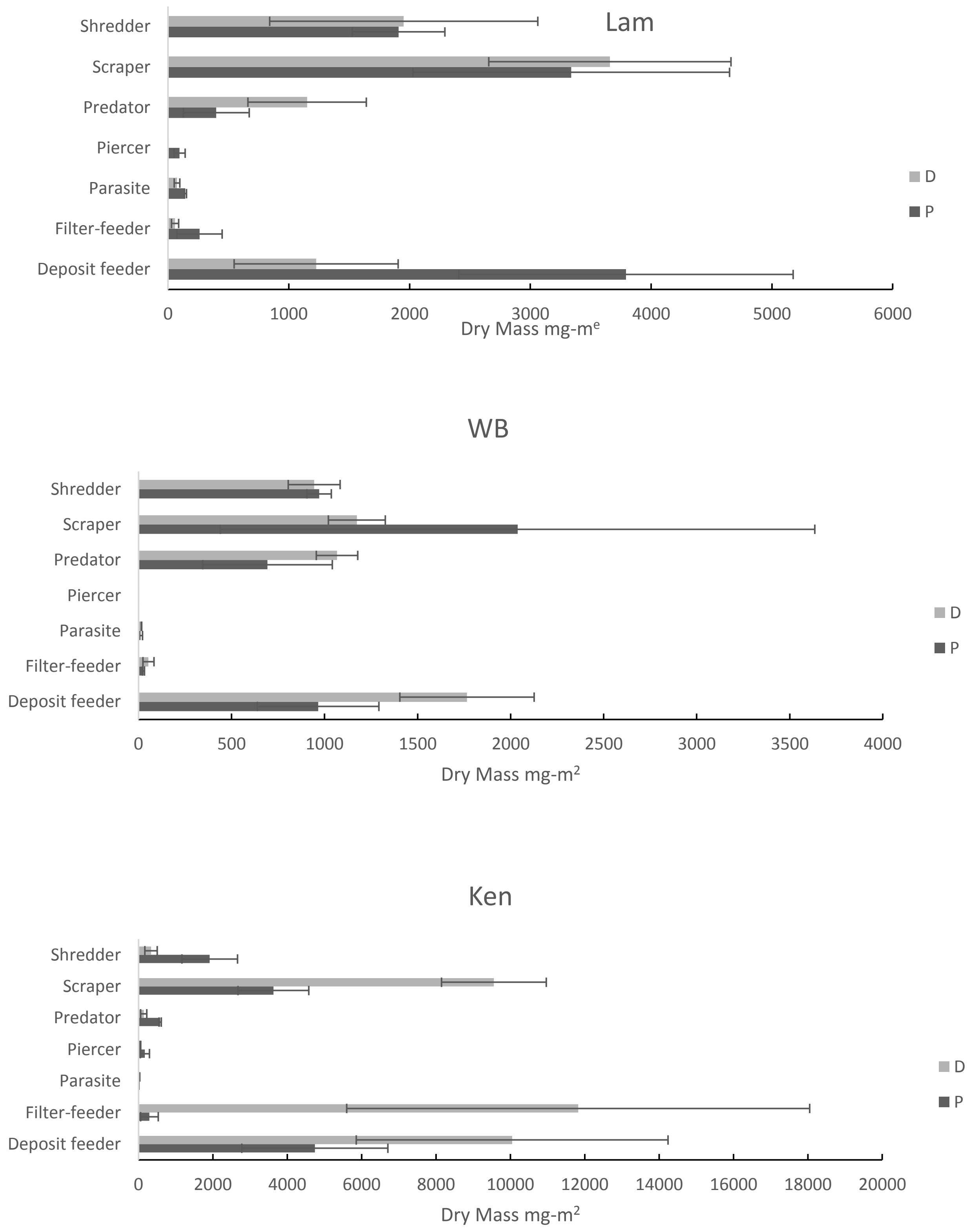


Figure 3.11. Biomass of functional feeding group (FFG) showing comparison of dewatering (D) and perennial (P) sites in Lambourn (Lam) Winterbourne (WB) and Kennet (Ken)

3.3.3.2 Macroinvertebrate Family Biomass and Densities

Analysis at the taxonomic family/class level showed that the biomass of Chironomidae, Oligochaeta and Simuliidae were higher in dewatering sites (Figures 3.12, 3.13 & 3.14). The Ostracoda in all sites were higher ranking in densities than in biomass, and Gammaridae were higher ranked biomass than densities.

In the River Lambourn the rank abundance of Chironomidae increased with dewatering (Table 3.4). Families in the perennial site that were absent in the dewatering site were: Acroloxidae, Caenidae, Cladocera, Ephemeridae, Heptageniidae, Hydaenidae, Hydridae, Hydroptilidae, Lepidostomatidae, Niphargidae and Polycentropodidae. Families present in the dewatering site which were not found in the perennial site were: Asellidae, Dytiscidae, Erpobdellidae, Glossiphoniidae, Pedicidae, Psychodidae and Sphaeridae.

In the Winterbourne Stream the highest ranking prevalent families according to biomass differed markedly from the highest ranking families according to densities (Table 3.3, Figure 3.13). Families present in the perennial site which were not found in the dewatering site were: Ceratopogoniidae, Leptoceridae and Microturbularia. Families found within the dewatering site which were not found in the perennial site were: Asellidae, Ephemeridae, Limoniidae, Polycentropodidae and Ptychopteridae.

In the River Kennet the biomass of the top ranked families in the dewatering site is very high compared with the perennial site (Figure 3.14) although overall biomass is lower than the perennial site (Figure 3.9). Families which were present in the perennial site which were missing from the dewatering site were: Asellidae, Caenidae, Collembola, Dendrocoelidae, Erpobdellidae, Lepidostomatidae, Planariidae, Polycentropodidae and Sericostomatidae, Families present in the dewatering site which were not found in the perennial site were: Copepoda, Glossiphoniidae, Nemouridae and Psychodidae.

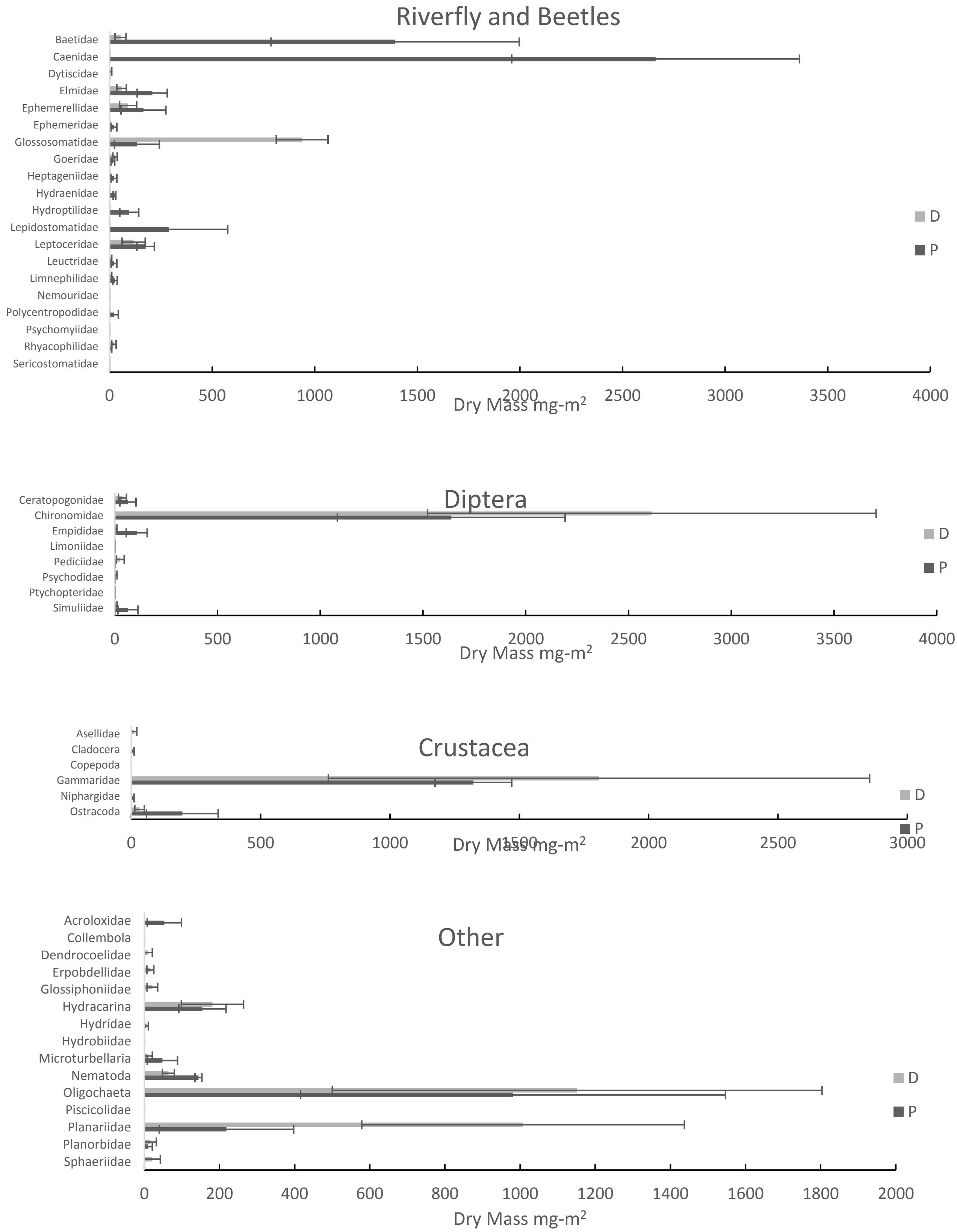
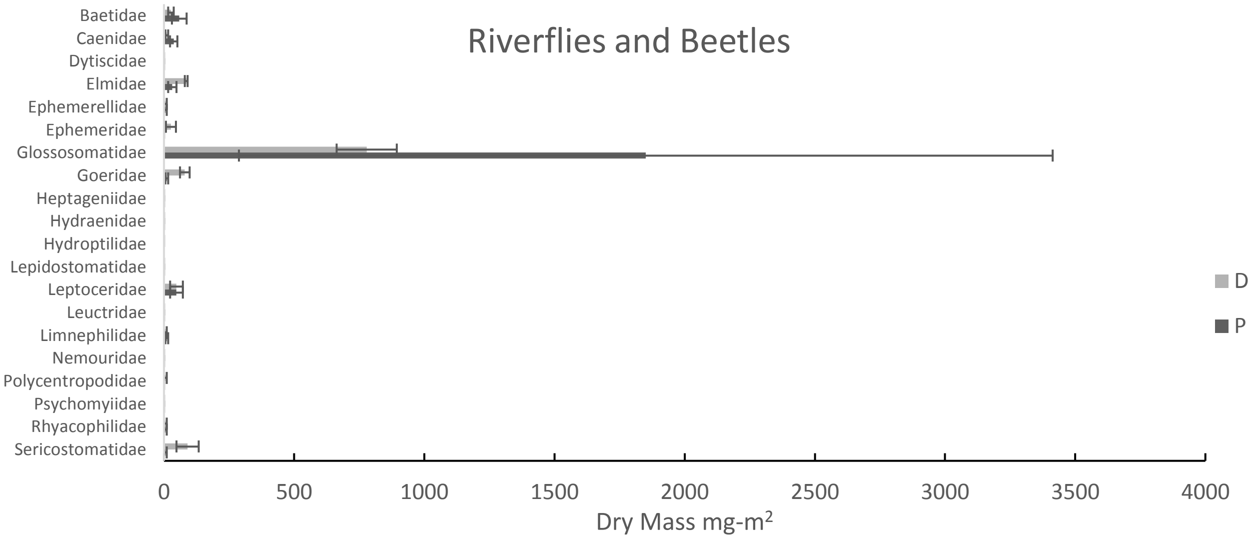
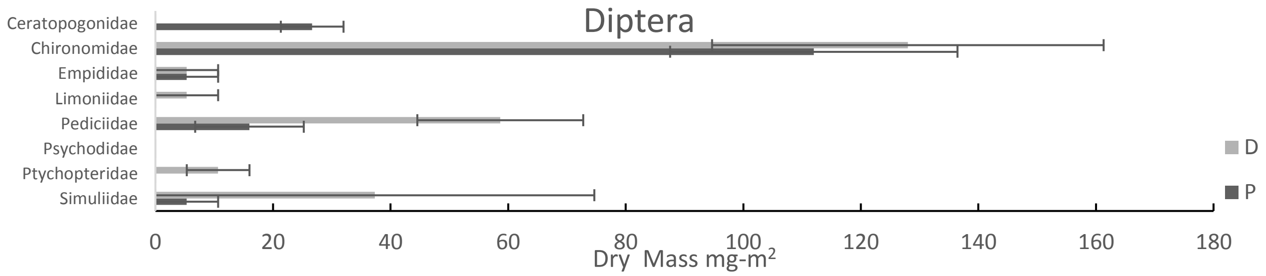
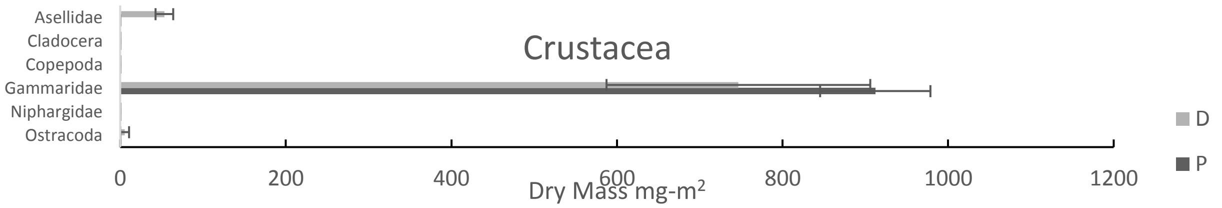


Figure 3.12. Biomass mg-m² ± 1 SE of the families of macroinvertebrates in the River Lambourn in perennial and dewatering sites in taxonomic groups. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs.







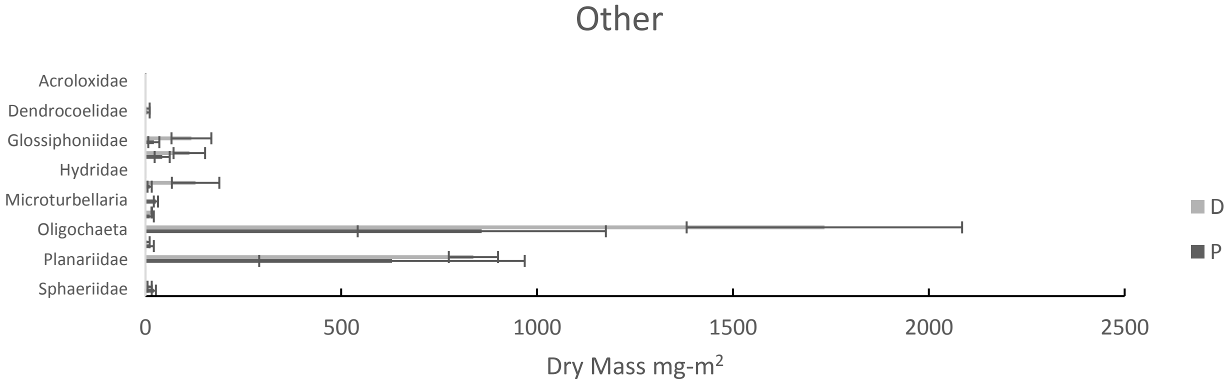


Figure 3.13. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in the Winterbourne Stream in perennial and dewatering sites in taxonomic groups. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs.

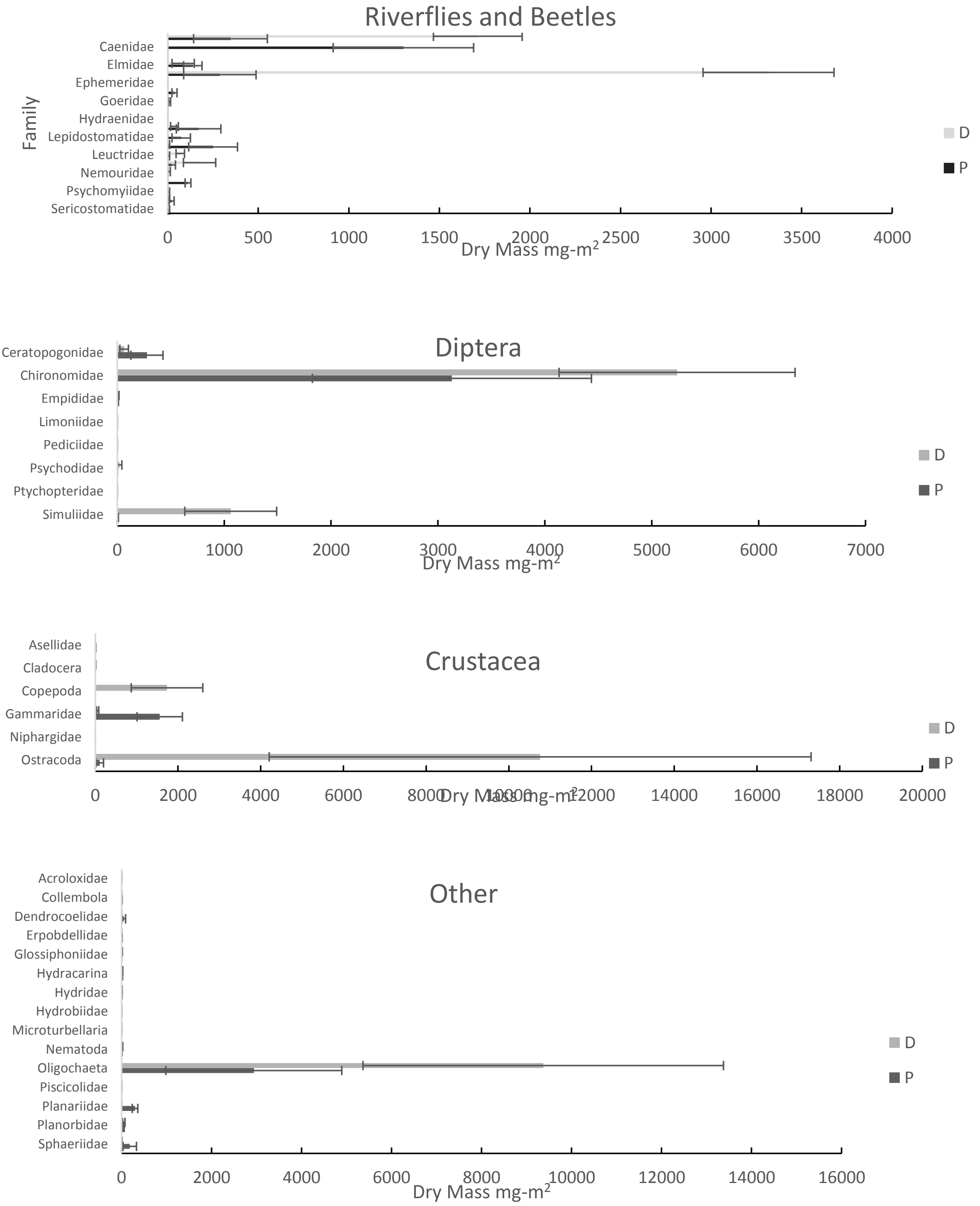


Figure 3.14... Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in the River Kennet in perennial and dewatering sites in taxonomic groups. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs.

Table 3.4. Rankings of family data for densities and biomass for each site, family with 1 is the densest or has the most mass, higher numbers indicate less density or mass L= River Lambourn, W= Winterbourne, K= Kennet, P= Perennial and D= Dewatering. Some families were present in density data but not biomass due to no biomass formula being available

	Density						Biomass					
Family ↓, Site →	LP	LD	WP	WD	KP	KD	LP	LD	WP	WD	KP	KD
Acroloxidae	19	-	-	-	-	-	9	12	-	-	-	-
Asellidae	-	21	-	13	23	-	-	-	-	12	25	-
Baetidae	3	11	6	15	5	6	3	9	13	15	16	1
Caenidae	1	-	9	18	4	-	2	-	8	20	2	-
Ceratopogoniidae	17	12	11	-	8	11	19	13	16	-	13	8
Chironomidae	2	1	5	5	1	3	5	3	12	16	8	5
Cladocera	29	-	-	-	-	21	-	-	-	-	-	-
Collembola	-	-	-	-	24	-	-	-	-	-	-	-
Copepoda	-	-	-	-	-	5	-	-	-	-	-	-
Dendrocoelidae	-	22	21	21	16	-	-	18	20	21	18	-
Dytiscidae	-	24	-	-	-	-	-	20	-	-	-	-
Elmidae	8	10	10	10	12	9	10	15	15	13	19	9
Empididae	15	25	22	22	25	18	12	21	21	-	-	15
Ephemerellidae	11	8	23	23	7	4	8	10	24	22	12	4
Ephemeridae	23	-	-	16	-	-	13	-	-	7	-	-
Erpobdellidae	-	19	-	-	26	-	-	8	-	-	11	-
Gammaridae	4	2	2	4	3	12	1	1	1	1	1	7
Glossiphoniidae	-	16	13	7	-	19	-	11	5	5	-	11
Glossosomatidae	14	5	1	3	18	-	18	5	3	4	17	-
Goeridae	27	14	16	11	21	-	-	22	10	10	7	-
Heptageniidae	24	-	-	-	-	-	18	-	-	-	-	-
Hydracarina	12	6	8	8	22	16	11	6	9	11	25	16
Hydraenidae	22	-	-	-	-	-	24	-	-	-	-	-
Hydridae	30	-	-	-	27	22	29	-	-	-	-	20

Hydrobiidae	-	-	17	6	-	-	-	-	6	6	-	-
Hydroptilidae	16	-	-	-	11	14	23	-	-	-	20	14
Lepidostomatidae	6	-	-	-	15	-	6	-	-	-	6	-
Leptoceridae	10	7	7	-	9	23	14	7	14	-	14	21
Leuctridae	25	26	-	-	28	10	27	26	-	-	26	13
Limnephilidae	21	27	18	24	19	8	15	-	11	25	10	6
Limoniidae	-	-	-	25	-	-	-	-	-	25	-	-
Microturbellaria	20	23	12	-	-	-	22	25	19	-	-	-
Nematoda	13	9	19	17	29	17	25	24	25	27	-	22
Nemouridae	-	-	-	-	-	20	-	-	-	-	-	17
Niphargidae	31	-	-	-	-	-	28	-	-	-	-	-
Oligochaeta	5	3	3	1	2	2	4	4	4	3	3	2
Ostracoda	9	13	-	26	14	1	30	27	-	28	28	23
Pedicidae	-	15	25	12	-	-	-	16	18	17	-	-
Pisciolidae	-	-	20	27	-	-	-	-	7	18	-	-
Planariidae	7	4	4	2	6	-	7	2	2	2	5	-
Planorbiidae	28	20	-	-	17	13	21	19	-	-	4	10
Polycentropodidae	26	-	-	28	13	-	20	-	-	19	9	-
Psychodidae	-	28	-	-	-	15	-	-	-	-	-	12
Psychomyiidae	-	-	-	-	30	-	-	-	-	-	21	-
Ptychopteridae	-	-	-	19	-	-	-	-	-	9	-	-
Rhyacophilidae	32	17	24	29	20	24	26	14	23	26	24	19
Sericostomatidae	-	-	25	9	31	-	-	-	-	8	22	-
Simuliidae	18	29	26	14	32	7	17	23	22	14	27	3
Sphaeridae	-	18	14	20	10	25	-	17	17	23	15	18

3.3.3.3 Macroinvertebrate metrics

PSI suggests that moderate sedimentation has occurred in the dewatered site of the River Lambourn and the Winterbourne Stream (Table 3.5). Life scores show little change between sites, WHPT scores were similar between sites and each dewatering site has a slightly higher value than the perennial site.

Table 3.5. Biological metrics of the 6 sites from this study. Sedimentation status codes are SS which stands for Slightly Sedimented, and MS which codes for Moderately Sedimented. WHPT scores are given as average scores per taxon (ASPT)

Site	PSI	Sedimentation Status	Life	WHPT
Lam P	65.38	SS	7.046	5.45
Lam DW	58.33	MS	7.118	5.51
Ken P	62.26	SS	7.108	5.505
Ken DW	67.5	SS	7.123	5.514
Win P	72.5	SS	7.016	5.411
Win DW	54.90	MS	7.016	5.417

3.4 Discussion

The rare opportunity to study a drought as it was occurring allowed a comprehensive study of how dewatering affected macroinvertebrates and algae within a river to be carried out. This study found changes in the macroinvertebrate densities, biomass and communities in dewatering sites compared to the perennial control sites (H_4). The density and biomass of pioneer species such as Chironomidae and Oligochaeta increased in the dewatering sites (H_1), whereas Caenidae, Baetidae, Leptoceridae and other Trichoptera, and Ephemeroptera tended to decrease (H_2), indicating that the low flows were acting as a disturbance on the community. Functional feeding groups showed differences in dewatering and perennial sites with more shredders and predators in dewatering sites (H_3) The last opportunity to study chalk streams during a drought of this magnitude was in 1976 where and Berrie and Wright (1984) and Wright and Berrie (1987) found the number of taxa in dewatering sites remained relatively stable until it was almost dry. In addition taxa indicative of normally intermittent sites were found in areas which were previously perennial, however, there was no analysis of sites as they were drying.

The drought had little impact on the taxonomic richness of the communities whereas there were clear differences in density, biomass and community structure of macroinvertebrates between perennial and dewatering sites. The most abundant families were very different between dewatering and perennial sites, and biomass showed similar trends. Taxa which are typically pioneer taxa such as Chironomidae and Oligochaeta, were far more common in dewatering sites. This agrees with the conclusions of Suren and Riis (2010) and White et al. (2012) who both found reduction in Trichoptera and Ephemeroptera and increases in

Chironomidae and Oligochaeta, and it is similar to Suren and Jowett (2006) who found increases in Chironomidae and Oligochaeta but did not find any species loss.

There are drawbacks to the statistical method used in this chapter, replicates of site and river can be argued to be psuedoreplicates due to the connected nature of the river system (as seen in chapter 2). It is understood that this adds a source of covariation to the design of the experiments and this was dealt with as much as possible by nesting site into river in statistical analysis.

The River Lambourn had the most differences between communities, showing that the dewatering community had gone through significant changes, which were probably due to the slow flows in the dewatering site. This is further verified by examining the families of macroinvertebrates present in the River Lambourn sites. Chironomidae was the most numerous taxon in the dewatering site with almost twice as many per m^2 than in the perennial site. In the River Kennet, Ostracoda was the most abundant taxa in the dewatering site, this is a taxa particularly associated with slow flows and was also found by Suren et al. (2003a) and Suren and Jowett (2006) in two separate investigations into the effects of low flows as well as in other studies (Rader and Belish, 1999). The other most abundant taxa included Oligochaeta, Chironomidae, and Copepoda which are taxa which can often be abundant in disturbed habitats as pioneer species and are commonly associated with low flows (Rader and Belish, 1999; Suren et al., 2003a; Suren and Jowett, 2006; Stubbington et al., 2015). The River Kennet had an unusual result where the communities were similar and perennial site's two most numerous families were Oligochaeta and Chironomidae, which as mentioned earlier are commonly associated with disturbance, this may suggest that this site had suffered a different disturbance, perhaps organic pollution, increased sediment or flow changes.

The Winterbourne Stream dewatering site had a distinct macroinvertebrate community consisting of species associated with slow flowing or still water such as Ostracoda and Psychodidae. This may be explained by the physical structure of this stream, the Winterbourne Stream is very narrow, shallow and slow flowing in the upstream reaches compared to the other two streams in this study. This may mean that it naturally has different taxa even without disturbance although Berrie and Wright (1984) studied the stream before and during the 1976 drought, they found little differences between the non-perennial sites out-with the drought period, or that drought disturbance effects this small stream more severely than larger streams. Berrie and Wright (1984) studied the Winterbourne Stream before and during the 1976 drought, they found many taxa were restricted either to intermittent sites or to perennial sites. The dewatering site in the current study is one of the perennial sites in Berrie and Wright (1984), and in 1976 at the height of the drought, this site became the head of the stream. At this point the number of taxa in this site decreased compared to the perennial site but until that point the two sites had been very similar, which matches what is found in the current study.

The River Kennet was the only stream to show higher macroinvertebrate densities in the dewatering site, although this was not significant due to large variability between samples. The huge densities were due to large numbers of Ostracoda in the dewatering site which had a very patchy distribution. The other streams showed no change in macroinvertebrate densities between dewatering and perennial sites, which was not what was expected. The ranking of macroinvertebrate densities between dewatering and perennial sites differs between streams, therefore in the River Lambourn and Winterbourne Stream, the densities of flow sensitive species in the perennial site is replaced with pioneer species in the dewatering site. However the Kennet showed a large abundance of pioneer taxa in the dewatering site, supporting the theory that pioneer species can proliferate in disturbed habitats (Wali, 1999).

It was predicted that biomass would remain constant between perennial and dewatering sites due to the small size of pioneer species and this was true in the River Lambourn. However, differing results were found in the Winterbourne Stream where there was a significantly higher biomass in the dewatering site, and the River Kennet where there was a significantly higher biomass in the perennial site. In the Winterbourne Stream, there was twice the biomass of Gammaridae and Planariidae in the dewatering site compared with the perennial site, this showed resilience to slow flows in these taxa. This is contrary to Wood and Armitage (2004) who found a significant reduction in the numbers of Gammaridae in drought conditions when compared with non-drought conditions. However, the River Kennet dewatering site had very few Gammaridae, this was also the site with the lowest flow out of all the sites in this study. It is probable that there is a flow limit under which Gammaridae can no longer thrive. The higher biomass in the perennial site of the River Kennet may be due to the taxa present being larger, Ostracoda were the top ranked taxa in density at the dewatering site, and yet the lowest in the biomass due to this taxa's small size. There were also seven fewer taxa and families present in the dewatering compared to perennial site in the River Kennet which were large biomass taxa such as Polycentropodidae and Limnephilidae.

Predicting an overall change to biomass in low flow conditions is therefore a difficult process, as taxa identity can change the outcome drastically.

The macroinvertebrate community changed between perennial and dewatering site principally as expected. The perennial and dewatered sites of both the River Lambourn and River Kennet were extremely dissimilar, the Winterbourne Steams sites are more similar. Differences within streams were almost as large as differences between streams, showing the major differences in the macroinvertebrate community at these sites. The taxa which create these differences were those which are associated positively or negatively with disturbance, hence disturbance was the factor creating community changes. Trichoptera and Ephemeroptera were more abundant in the perennial sites, in the River Lambourn perennial site there were large numbers of Caenidae, Baetidae, Lepidostomatidae and Ephemerellidae, in the River Kennet there were similar results with many Caenidae, Baetidae, Ephemerellidae and Leptoceridae. The Winterbourne Stream had differences but they were less clear-cut, there were more Glossosomatidae, Baetidae, and Leptoceridae in the perennial site than the dewatering site. This is similar to the findings of Suren and Riis, (2010) and showed that these taxa are sensitive to the changes occurring during dewatering.

The River Lambourn and Winterbourne Stream had an increase in the biomass of shredders and predators in the dewatering site, this seems to be due to the increase in Gammaridae which are shredders and Planariidae which are predators. The River Kennet does not have this pattern, and in fact the biomass of shredders and predators were reduced significantly but this agrees with Ledger (2011) who found that shredders and predators reduced in number during drought. In the Kennet the families with highest biomass in the dewatering site were Baetidae – a scraper, Oligochaeta – a detritivore and Simuliidae – a filter feeder. This showed that the ecosystem function of the stream can be substantially changed depending on the resilient taxa within that stream. Predicting the functioning of a dewatering site is therefore difficult. As this study showed, differences between flow rate can be the difference between an abundance of Gammaridae or very few of them. There will be many other factors which affect the abundance of individual taxa, the balance of factors needed to create a fully functioning river ecosystem are not known and may differ depending on the stream and species in question. It is unlikely ecosystem functioning of disturbed habitats could be accurately predicted without investigating the individual taxa present in each individual stream. However changes in community and species abundances occur rapidly in freshwater ecosystems and ecosystem functioning will change too. Ecosystem functioning should stabilise when the apex community is reached.

The changes which occur during dewatering relate to the physical parameters of the stream, the chemistry and the food sources available for macroinvertebrates (Dahm et al., 2003; Dewson et al., 2007a; Suren and Riis, 2010). The reduction of flow and depth of water in the dewatering sites clearly had an effect on the biota. In this investigation the Winterbourne Stream and River Kennet had less algae in the dewatered site although not significantly different, and the River Lambourn had significantly more algae in the dewatered site. The Winterbourne Stream was the only stream to show a change in autotropic index with a higher index in the dewatering stream indicating a lower quality of algae. This is usually associated with higher nutrient input, however other factors can cause this response such as increased organic matter or sedimentation (Collins and Weber, 1978). The River Lambourn dewatering site was deeper than the other two, being the only one deep enough to carry out a 0.4 depth flow measurement. The shallowness of the water may have affected the growth of algae in the Winterbourne Stream and River Kennet as algal growth needs constant flow to be stimulated to grow (Biggs et al., 1998). The data from the Winterbourne Stream and River Kennet streams of this study concurs with that of Suren and Riis (2010), where only high-nutrient streams displayed changes in algal growth. The changes in the River Lambourn were unlikely to be due to nutrient concentrations as the River Lambourn had a lower nutrient concentration than the River Kennet (Chapter 2), consequently, flow or another mechanism such as siltation must be driving this difference. Changes in algal biomass are likely to have effects on the rest of the food web so it is important to understand why some sites have differing responses for future droughts.

PSI scoring showed that the dewatering sites of the River Lambourn and the Winterbourne Stream had taxa which are associated with sedimentation. This fits with the idea that slower flows increases sediment deposition of rivers (Wood and Armitage, 1997), and this changes the macroinvertebrate community (Extence et al., 1999). WHPT scores were high at all sites, showing little evidence of organic pollution, however scores at dewatering sites were universally higher than perennial sites, although the sensitivity of the index is not high enough to pick out fine differences and was not designed for drought conditions and so may not show changes in communities in this situation.

3.4.1 Conclusions

The macroinvertebrate community, density and biomass differed in the dewatering site in all cases, more so in the larger streams. This change in macroinvertebrate community needs to be investigated to assess function within the environment. It is possible the pioneer species will have differing traits to the stable apex community, changing the balance of functioning within the river system.

Algal relationships to low flows were less predictable, studies linking nutrient content, flow, grazing pressure and grazer identity are needed to unpick the reasons behind the variation in responses of algae to low flows.

It is clear low flows have stronger effects on macroinvertebrates than previously shown in other studies, it may be that recovery is rapid after the drought period, however, if the drought period is extensive it is important to understand how these changes affect the food web and functioning of the river.

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CHAPTER 4

MACROINVERTEBRATE RECOVERY FROM SUPRA-SEASONAL DROUGHT IN CHALK STREAMS.

4.1 Introduction

Complete drying, where all water is lost and no pools remain, is a severe disturbance (Lake, 2011) and in temperate regions only occurs likely during drought (Boulton, 2003). Climate change is expected to increase the frequency and duration of drought (Beniston et al., 2007; IPCC, 2007; IPCC, 2012; Watts et al., 2015). Furthermore effects on UK rivers will be intensified by an increasing human population (Office for National Statistics, 2010) resulting in increased water abstraction (Chessman, 2009; Poff and Zimmerman, 2010), particularly in the driest parts of the UK (Hess et al., 2010). This makes supra-seasonal drought in UK streams more likely.

Perennial pools have been found to be the most effective refuge in drying streams with other refuges such as damp sediment, or beneath stones harbouring very few species in Australian rivers (Chester and Robson, 2011). If pools do remain, macroinvertebrates can survive for a period of time (Ledger and Hildrew, 2001; Boulton, 2003; Acuna et al., 2005; Beche et al., 2006; Boersma et al., 2014; Verdonschot et al., 2015), although connectivity and oxygen levels are important to maintain high density and diversity of macroinvertebrates (Lake, 2003; Robson et al., 2013). The majority of freshwater macroinvertebrates do not survive complete drying unless they can migrate from the area (Acuna et al., 2005). Even within desert streams where invertebrates are adapted it is unusual to find any individuals surviving after ten days of drying (Stanley et al., 1994).

The length and severity of a drought affects the recovery time by macroinvertebrates, the longer the drying episode persists the fewer pools will remain in the river bed (Datry et al., 2012). And with fewer pools there are fewer refuges for macroinvertebrates to survive the drought. Terrestrial plants will grow on the river bed (Salinas and Guirado, 2002) accumulating organic matter (Dewson et al., 2007; Ylla et al., 2010) which will influence recovery on rewetting (Madsen et al., 2001; Clarke, 2002).

4.1.1 Resistance and resilience to drought.

Macroinvertebrates in streams are adapted to frequent disturbance, including resistance traits enabling persistence in disturbed habitats (Townsend and Hildrew, 1994; Fritz and Dodds, 2004) or resilience through recovery, such as dispersion traits (Bonada et al., 2007a). As the river dries and pools decrease, macroinvertebrate survival varies by species and resistant traits can be passed to the next generation (Bonada et al., 2007a; Chester and Robson, 2011; Robson et al., 2011). Resistant traits are only common where drought is frequent. Mediterranean and arid streams are well studied in the effect of drought on macroinvertebrates as drought is a common occurrence. Research includes studies of traits of macroinvertebrates in drought conditions (Bonada et al., 2007a; Bonada et al., 2007b; Gaudes et al., 2010; Robson et al., 2011; Garcia-Roger et al., 2013; Elias et al., 2015); resilience and resistance studies (Acuna et al., 2005; Bonada et al., 2007b; Beche et al., 2009; Gaudes et al., 2010; Robson et al., 2011) and recovery of macroinvertebrate communities after drought (Acuna et al., 2005; Beche et al., 2009; Boix et al., 2010). Bonada et al. (2007a) compared the taxonomic and trait richness of hundreds of Mediterranean and temperate river sites, they found that local taxon richness did not differ between the regions, however the Mediterranean sites had higher trait richness, which is linked to the constant fluctuation of environmental conditions including frequent droughts. Therefore resistance and resilience traits are likely to be rarer among macroinvertebrates in the UK, although few studies exist (Culp et al., 2011), and thus resistance and resilience to drought is unknown.

In the UK winterbourne streams have intermittent reaches and species possess some resistant traits, although it is more likely that they drift downstream to perennial areas when drying occurs. Intermittent reaches of streams tend to have different macroinvertebrate communities. In New Zealand intermittent reaches supported less species richness than perennial reaches (Arscott et al. 2010) with similar findings in Brazil (Rocha et al., 2012), Venezuela (Ely Rincon, 2010) and South Africa (Arab et al., 2004). However very few studies have been carried out in intermittent streams in the UK, Berrie and Wright (1984) studied the Winterbourne stream before and during the 1976 drought and found even out-with the drought the intermittent reaches had a unique macroinvertebrate community including a greater abundance of Coleoptera, Chironomidae and Diptera. The sites in this study which rewetted were normally perennial and only dried due to the severe nature of the drought in 2010-2012.

Therefore the sites would not have a macroinvertebrate community which was characteristic of intermittent sites under normal circumstances.

4.1.2 Recolonisation

As the dry substrata rewets following drought, recolonisation begins to occur. Studies of the recovery of dewatered sites are limited due to the infrequency of drought, and the few studies that do exist are from precipitation-dependant streams, which are not directly comparable with chalk ground-water streams (Cowx et al., 1984; Covich et al., 2003; Churchel and Batzer, 2006; Lake, 2011). Most studies found similar taxa during recolonisation, common among post-drought communities were: Chironomidae; Simuliidae; Oligochaeta and Ostracoda. Previous studies of UK droughts have shown rapid recovery of macroinvertebrate density and diversity within three months to two years (Ladle and Bass, 1981; Wood and Petts, 1999; Morrison, 1990; Boulton, 2003). The differences in dates may be due to differences in reporting recovery, some studies claimed recovery when the densities of macroinvertebrates were equivalent to perennial sites or pre-drought data and others looks specifically at the species which were present. A few studies have examined recovery at dewatered sites, for example Wood and Petts (1999) studied the River Stour during and after the 1992 drought, two sites were dry during the drought and these were sampled annually after rewetting for two years. However the infrequent sampling may have missed the initial recovery cycle of the rewetted sites. Wood and Armitage (2004) extended this study with a further year of data and found interesting patterns of macroinvertebrate abundance such as *Gammarus pulex* during the drought, however, the rewetting sequence was again not studied in detail. The study of the Winterbourne Stream by Berrie and Wright (1984) did follow the rewetting of dried stream reaches, however as this was not the focus of the study little data were provided. If droughts become more frequent as predicted (IPCC, 2007) it is important to understand the recovery process in more detail to predict changes in the macroinvertebrate communities which may cause problems for the river as a whole.

Few studies have investigated the macroinvertebrate recovery after supra-seasonal droughts, and this is especially rare in temperate regions. This study was carried out on sites which had dried during the severe drought of 2010-12 and compares these sites with perennial controls after rewetting. Macroinvertebrate communities, biomass, functional feeding groups (FFG) and algal mass were investigated. It is predicted that the maximum differences in communities will be after the initial rewetting in June and that communities will become more similar each month. Macroinvertebrate biomass is predicted to peak in June or July in rewetted sites as pioneer species appear in great numbers and the biomass should become more similar to the perennial sites by October. The functional feeding groups are predicted to differ from perennial sites initially as advantageous species exploit resources which may differ from perennial sites (such as a peak or organic matter or algal growth), it will become more similar to the perennial site through the months. The algal biomass is predicted to peak after the rewetting and then reduce to become equal to the perennial sites quickly after the first month.

The following hypotheses were tested;

H_1: Macroinvertebrate communities will differ in rewetted and perennial sites in June.

H_2: Macroinvertebrate communities will be more similar between rewetted and perennial sites in the months after June.

H_3: Macroinvertebrate biomass will peak in June or July in rewetted sites.

H_4: FFG’s will differ most in June between rewetted and perennial sites.

4.2 Methods

4.2.1 Drought description

The two year drought ended in late spring 2012. The streams began to rewet after two weeks of rain in early June 2012. The sites were sampled mid-June 2012 and monthly until October 2012 see Chapter 2 for full description of the drought event.

4.2.2 Site Descriptions

Samples were collected over five months on three chalk streams in southeast England. The three streams were: The River Lambourn, The Winterbourne Stream and The River Kennet. The perennial sites on these streams were: Boxford on the River Lambourn, Bagnor on the Winterbourne Stream and Axford on the River Kennet and these were sampled as the control site. The sites which were originally dry during the drought but rewetted were: Upstream Great Shefford on the Lambourn, Shepherds Copse on the Winterbourne Stream and Clatford on the Kennet were sampled as the rewetted sites. The sites will be labelled as P for perennial and R for rewetted from this point onwards. Rewetted sites are assumed to have been completely dry without perennial pools, however the survey of these sites was brief as we were still awaiting land-owners permissions to use the site when the drought broke. For more detailed information about the streams see Chapter 2 for full site descriptions

4.2.3 Physical Measurements in Streams

Width, depth and flow measurements at 2.5 cm above the benthos and the hydrological standard 0.4 depth monthly. See chapter 3.2.2 for full description of physical measurements.

4.2.4 Macroinvertebrates

Five Surber samples were collected monthly for five months from June until October. See section 3.2.2 for more details.

4.2.5 Algae Rock Scrapes

Algal rock scrapes were taken monthly from June until October 2012. See section 3.2.5 for methods of sampling and chlorophyll, ash free dry mass and autotrophic index calculation.

4.2.6 Data Analysis

Macroinvertebrate density and biomass data were collated to allow analysis on various different groups. For each Surber the combined densities and biomasses of all macroinvertebrates were compared. Data was explored to determine if it met assumptions for ANOVA tests, it was found that the data had normal residuals and range (Figure 4.1). Minitab was used to perform multiple one-way ANOVA tests using a Generalised Linear Model (ANOVA) on each river to test for differences between perennial and dewatering sites as the factors on total density and total biomass as the response.

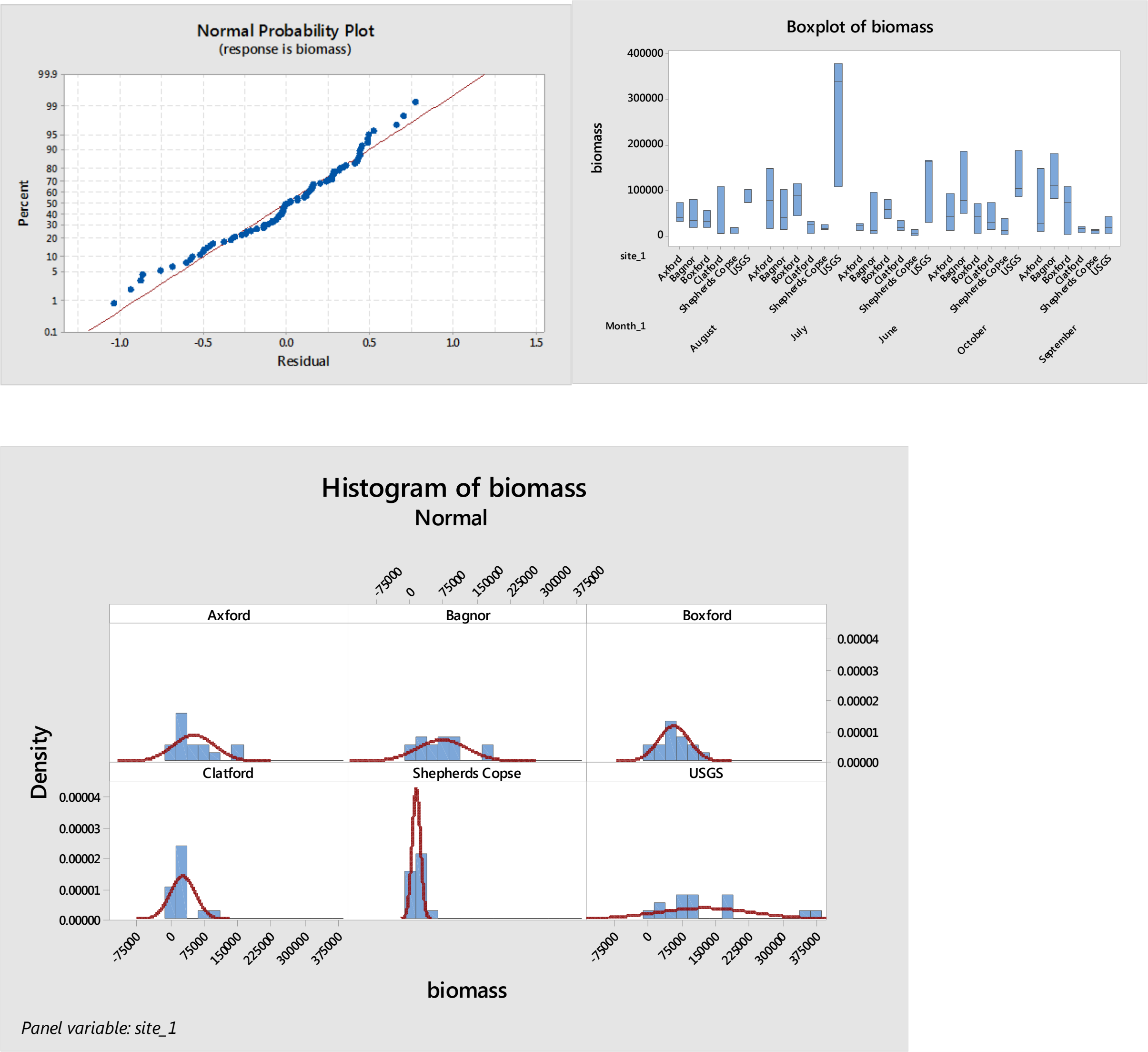


Figure 4.1. Data exploration of macroinvertebrate biomass data including QQ plot of all data, boxplots and histograms of each site.

Macroinvertebrate density and biomass data were summarised by family to allow family level analysis. A functional feeding group (FFG) was assigned to each species using the Macroinvertebrate Traits Database (Usseglio-Polatera, 1991; Chevene et al., 1994; Tachet et al., 2002). In this database species are given a number of 0-5 for each trait, the feeding habit with the highest number was picked as the main FFG. If two feeding habits had an equal number in the database, the food category was then referenced, for example if an macroinvertebrate was a 3 for both shredding and scraping, but a 5 for algae and a 3 for detritus, it was assumed algae was its main food source and so scraping was chosen as its FFG. Taxa in the database were a mixture of species, genus, family and sub-family. If only genus, family or subfamily was given in the database, it was assumed all species of that group had the same traits.

The macroinvertebrate family biomass data was used for community analysis. Each stream was analysed separately comparing perennial and rewetted sites over all five months in Canoco (Ter Braak and Smilauer, 2002) using a Principal Components Analysis (PCA) community analysis, the amount of variance which accounted for each family in the PCA model was ranked, and the top twenty families were retained.

Velocity for the benthic surface was analysed in Minitab using a one-way ANOVA testing (see appendix 1 figures 1, 2 & 3) for data exploration figures) for differences between perennial and dewatering sites where flow was the response and site was the factor, this test was also performed on measurements at 0.4 depth when the water was deep enough to do so. 0.4 depths were taken due to this being the hydrological standard for discharge calculations this was only possible in the Lambourn.

Algal data from chlorophyll and AFDM were analysed to determine differences between perennial and dewatering sites. Minitab was used to perform a two-way ANOVA with Tukey post-hoc tests on chlorophyll *a* data to test for differences between chlorophyll and river, chlorophyll and site and the interaction between river and site.

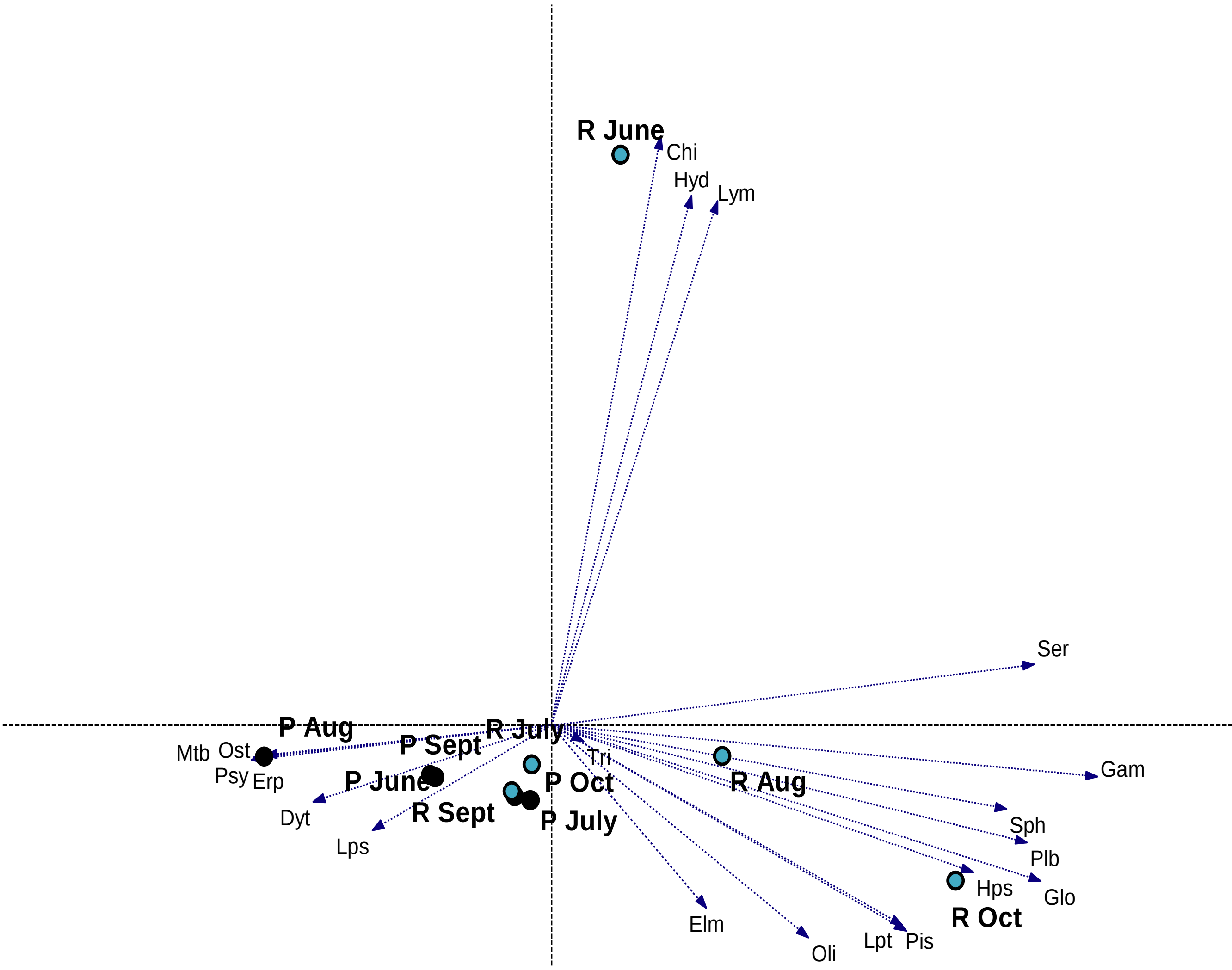
4.3 Results

4.3.1 Macroinvertebrate Community Results

Macroinvertebrate diversity of rewetted sites in the Lambourn and Winterbourne was higher than the perennial sites in June. The Lambourn rewetted site continued to support more taxa and families than the perennial site though all months whereas in September and October the Winterbourne contained less taxa (Table 4.1). The Kennet's rewetted site fluctuated between lower and higher numbers of taxa but consistently had fewer families than the perennial site particularly in October when there is a substantial reduction in taxa (28 in September to 18 in October) and families (21 in September to 14 in October) in the rewetted site (Table 4.1). The taxonomic composition of the rewetted site in every stream differed the in the rewetting month of June (Figures 4.1, 4.2 & 4.3). In the Lambourn the taxa characterising the rewetted site in June include Chironomidae, Hydridae and Lymnaeidae. The rewetted site differs less in July and following months, however there was a general pattern of the rewetted sites sharing certain taxa in all months including Gammaridae, Sphaeridae, Oligocheata and Planorbiidae whereas perennial sites are characterised by Lepidostomatidae, Microturbularia, Erpobdellidae and Dytiscidae. The taxonomic composition of the rewetted site in October was distinctive to that of the perennial site again with taxa such as Hydropsychidae and Glossosomatidae.

Table 4.1. Mean total macroinvertebrate taxon richness of each site (n = 3). Taxa is counted as species or lowest level taxa were identified this is mostly species but with some genera and families.

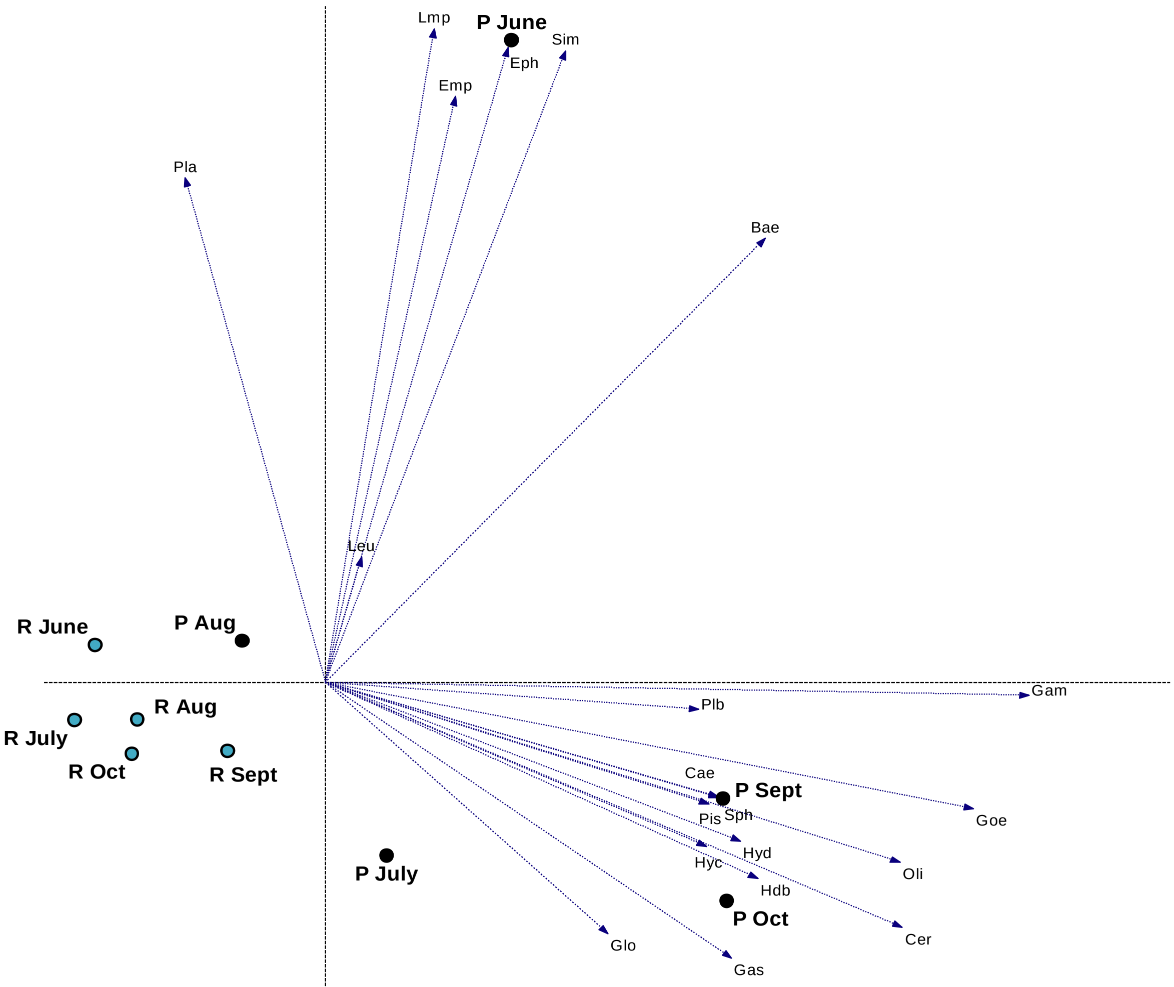
River	Flow permanence	Number of taxa					Number of families				
		June	July	Aug	Sept	Oct	June	July	Aug	Sept	Oct
Lambourn	Perennial	37	47	38	47	54	21	29	21	30	30
Lambourn	Rewetted	41	49	56	49	62	29	30	33	34	35
Winterbourne	Perennial	39	41	42	52	49	26	27	28	32	33
Winterbourne	Rewetted	46	44	46	28	43	29	33	32	23	31
Kennet	Perennial	36	41	31	39	48	25	28	27	26	26
Kennet	Rewetted	29	42	37	28	18	18	25	22	21	14



Invertebrate family codes Chi=Chironomidae, Dyt=Dytiscidae, Elm-Elmidae, Erp= Erpobdellidae, Gam=Gammaridae, Glo=Glossosomatidae, Hps=Hydropsychidae, Hyd=Hydridae, Leu=Leuctridae, Lym=Lymnaeidae, Lps= Lepidostomatidae, Lpt=Leptoceridae, Mtb=Microturbullaria, Oli=Oligochaeta, Ost=Ostracoda, Pis=Pisciolidae, Plb=Planorbiidae, Psy=Psychodidae, Ser=Sericostomadidae, Sph=Sphaeridae,

Figure 4.2. Ordination of the River Lambourn perennial (P) and rewetted (R) sites using the 20 top macroinvertebrate families accounting for the most variance in June to October. Eigenvalues axis 1: 0.636, 2: 0.261. Cumulative percentage variant of species data axis 1: 63.6, 2: 89.7

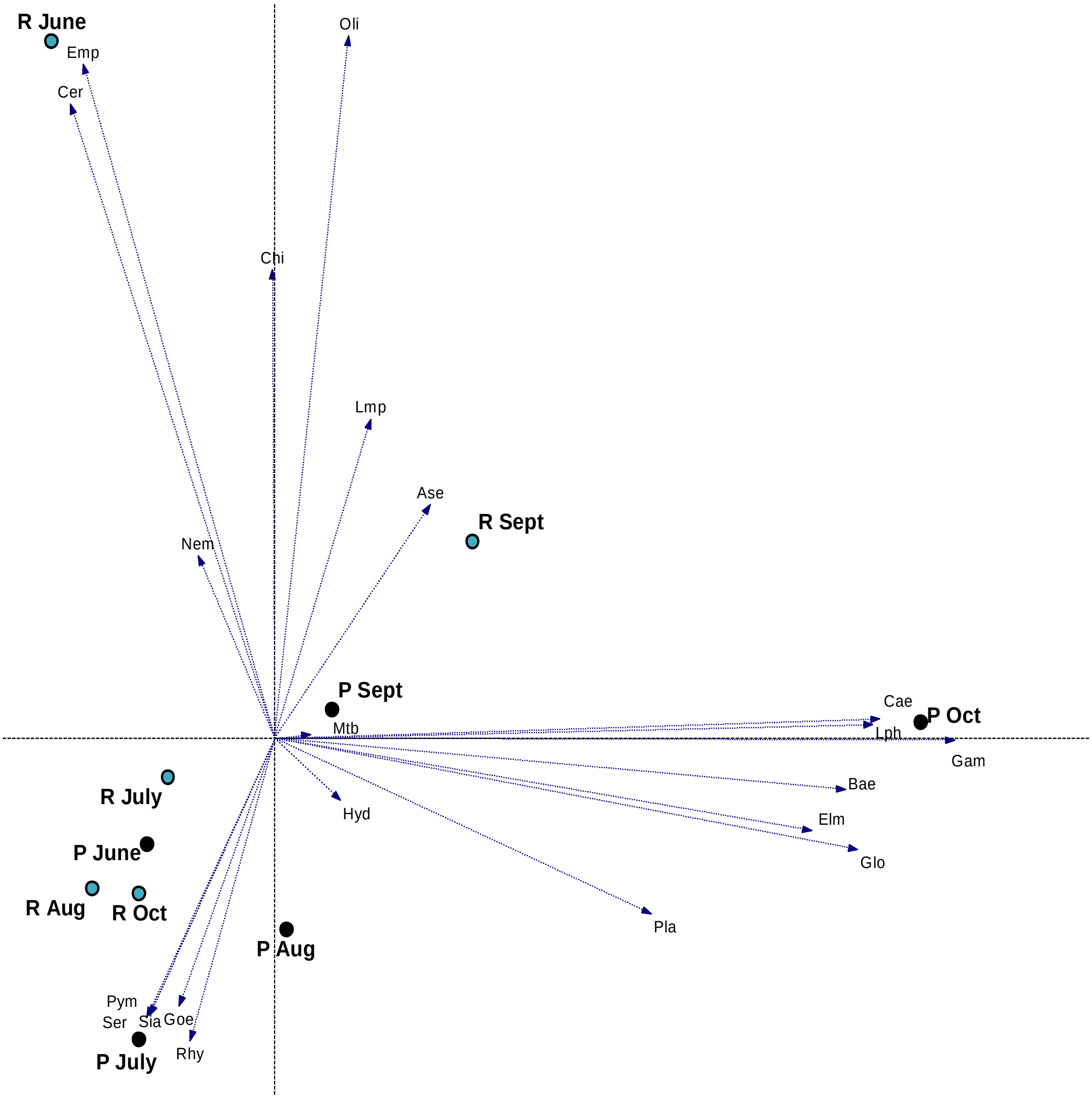
In the Winterbourne Stream the perennial site is on the right hand axis in every month except August showing a strong difference in taxonomic composition between the perennial and rewetted site (Figure 4.3). The rewetted site's macroinvertebrate community differs little across month. Taxa which characterise the perennial sites include Empididae, Ephemerellidae and Baetidae in June and Ceratopogoniidae, Goeridae and Gastropoda in other months.



Invertebrate family codes Bae=Baetidae, Cae =Caenidae, Cer = Ceratopogoniidae, Emp=Empididae Eph= Ephemerellidae, Gam=Gammaridae, Gas=Gastropoda, Glo=Glossosomatidae, Goe=Goeridae, Hdb=Hydrobiidae Hyc=Hydracarina, Hyd=Hydridae, Leu=Leuctridae, Lmp=Limnephilidae, Pla=Planadiidae, Pis=Pisciolidae, Plb=Planorbiidae, Sim-Simuliidae, Sph=Sphaeridae, Oli=Oligochaeta,

Figure 4.3. Ordination of the Winterbourne Stream perennial (P) and rewetted (R) sites. The analysis used top 20 macroinvertebrate families accounting for the most variance across the months of June to October. Eigenvalues axis 1: 0.922, 2: 0.060. Cumulative percentage variant of species data axis 1: 92.2, 2: 98.3.

The River Kennet showed a similar pattern as the River Lambourn in community differences (Figure 4.4). The rewetted site in June is characterised by Empididae and Ceratopogoniidae. By July the rewetted community showed similarities to the perennial site except in October when the perennial site was associated with Leptophlebiidae, Caenidae, Baetidae and Gammaridae.



Invertebrate family codes Ase=Asellidae, Bae=Baetidae, Cae =Caenidae, Cer = Ceratopogoniidae, Chi=Chironomidae, Elm=Elmidae, Emp=Empididae Eph= Ephemerellidae, Gam=Gammaridae, Glo=Glossosomatidae, Goe=Goeridae, Hyd=Hydridae, Lmp=Limnephilidae, Lph=Leptophlebiidae, Mtb=Microturbullaria, Nem=Nematoda, Pla=Planadiidae, Pym=Psychomyiidae, Rhy=Rhyacophilidae, Sia=Sialidae, Oli=Oligochaeta,

Figure 4.4. Ordination of the River Kennet perennial (P) and rewetted (R) sites. The analysis used top 20 macroinvertebrate families across the months of June to October. Eigenvalues axis 1: 0.962, 2: 0.025, 3: 0.010 and 4: 0.001. Cumulative percentage variant of species data axis 1: 96.2, 2: 98.7, 3: 99.7 and 4: 99.9.

4.3.2 Macroinvertebrate Biomass and Density

In the River Lambourn total biomass was generally higher in the rewetted site (Figure 4.5) although this difference was not significant ($p > 0.05$) there was also no difference between biomass between months ($p > 0.05$) and no interaction between site and month ($p > 0.05$). The density in the Lambourn was only higher in June and this was not significantly different ($p > 0.05$) but there was a significant different between site overall (ANOVA of differences between site on density $F = 4.48$, $DF = 1$, $p < 0.05$). Both biomass and density have large variation in the rewetted site in June which accounts for the non-significance.

The Winterbourne's perennial site has higher biomass throughout all months and this is significant (Figure 4.6) (ANOVA of differences between site, $F = 11.29$, $DF = 1$, $p < 0.01$), but monthly differences and the interaction between site and month were not significant ($p > 0.05$). The density data in the Winterbourne showed a very similar pattern and has similar statistical results (ANOVA on differences between site $F = 13.97$, $DF = 1$, $p < 0.01$, ANOVA on differences between month $p > 0.05$, ANOVA on interaction between month and site $p > 0.05$).

The Kennet supported higher biomass in the rewetted sites (Figure 4.7) although this was not significant ($p > 0.05$). Month and the interaction between month and site were both significant ($p < 0.01$). Tukey post-hoc tests showed a significant difference between the rewetted site in June compared to all sites and months with exception to the perennial site in October and the rewetted site in September. Macroinvertebrate abundance in the Kennet showed significant differences between site, month and interaction between the two (differences between site

F=9.71, DF=1, p<0.01, differences between month F=7.84, DF=4, p<0.01, interaction between month and site F=8.75, DF=4, p<0.001). Tukey post-hoc tests show that October and July were months with the most difference between them, and that the perennial site in October is significantly different to all other site and months apart from the rewetted site in September.

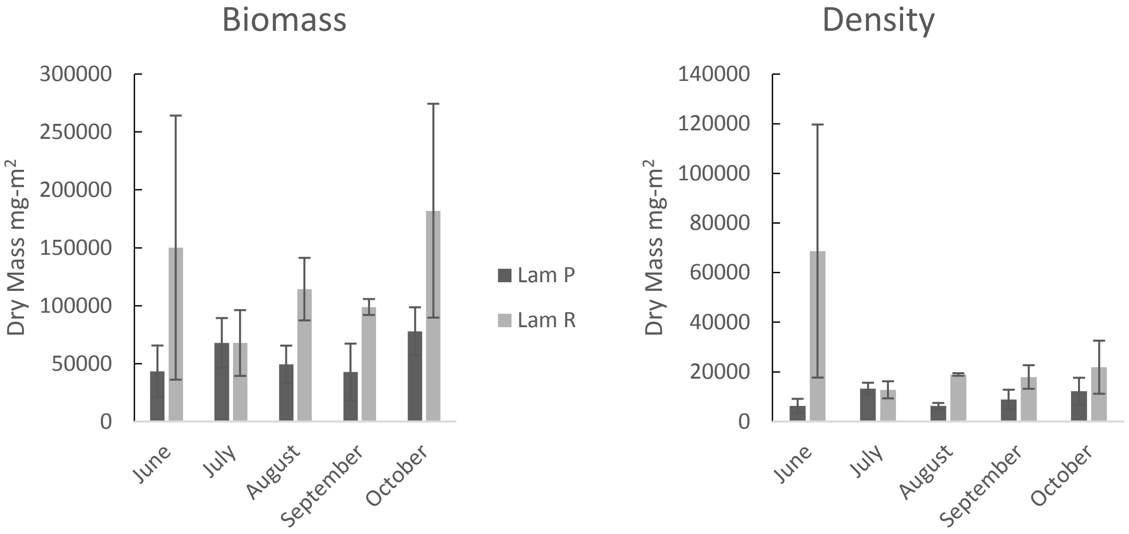


Figure 4.5. The River Lambourn total biomass and density data comparing perennial and rewetted sites from June to October ± 1 SE.

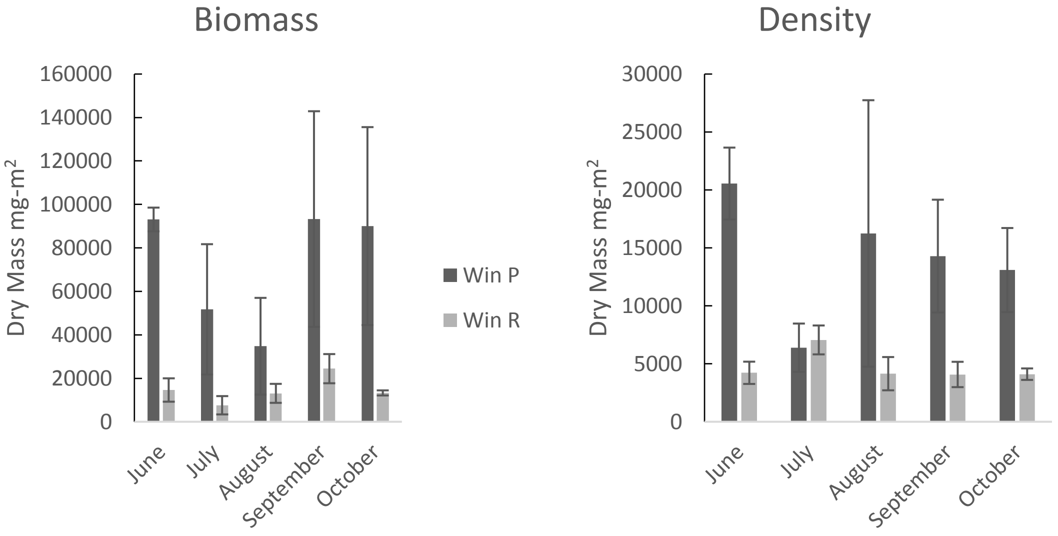


Figure 4.6. The Winterbourne Stream total biomass and density data comparing perennial and rewetted sites from June to October ± 1 SE.

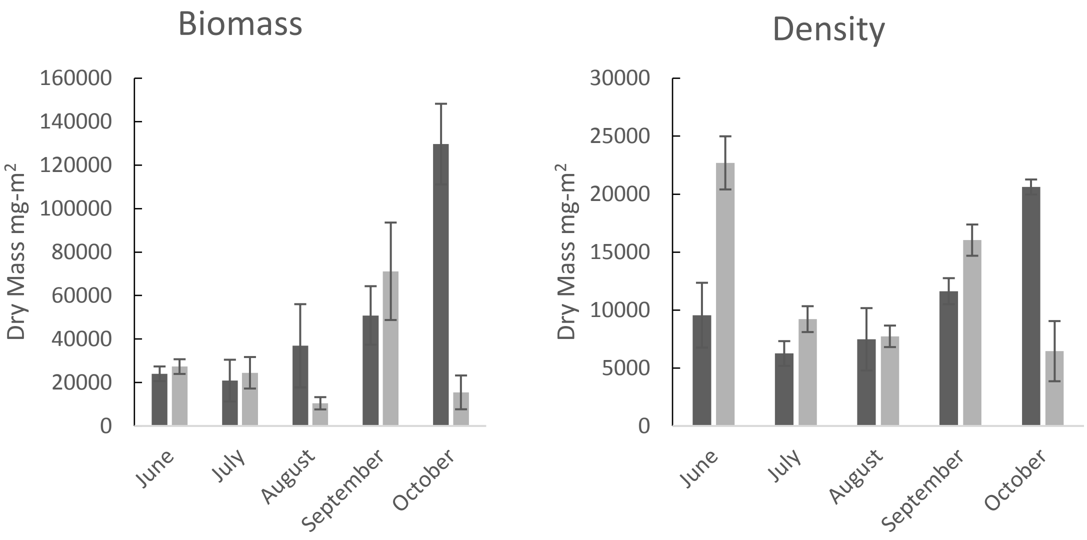


Figure 4.7. The River Kennet total biomass and density data comparing perennial and rewetted sites from June to October ± 1 SE.

4.2.3 Functional Feeding Groups

Scrapers was the most dominant FFG in June at the rewetted site in the River Lambourn whereas shredders dominated the perennial site (Figure 4.8). By July the most numerous FFG at both sites were shredders and this continued until October. The ranking of biomass of FFG's in the perennial site change little between months, the rewetted site changes readily in the first few months. In July the second most numerous FFG is predators and from August onwards was scrapers (Figures 4.8, 4.9 & 4.10).

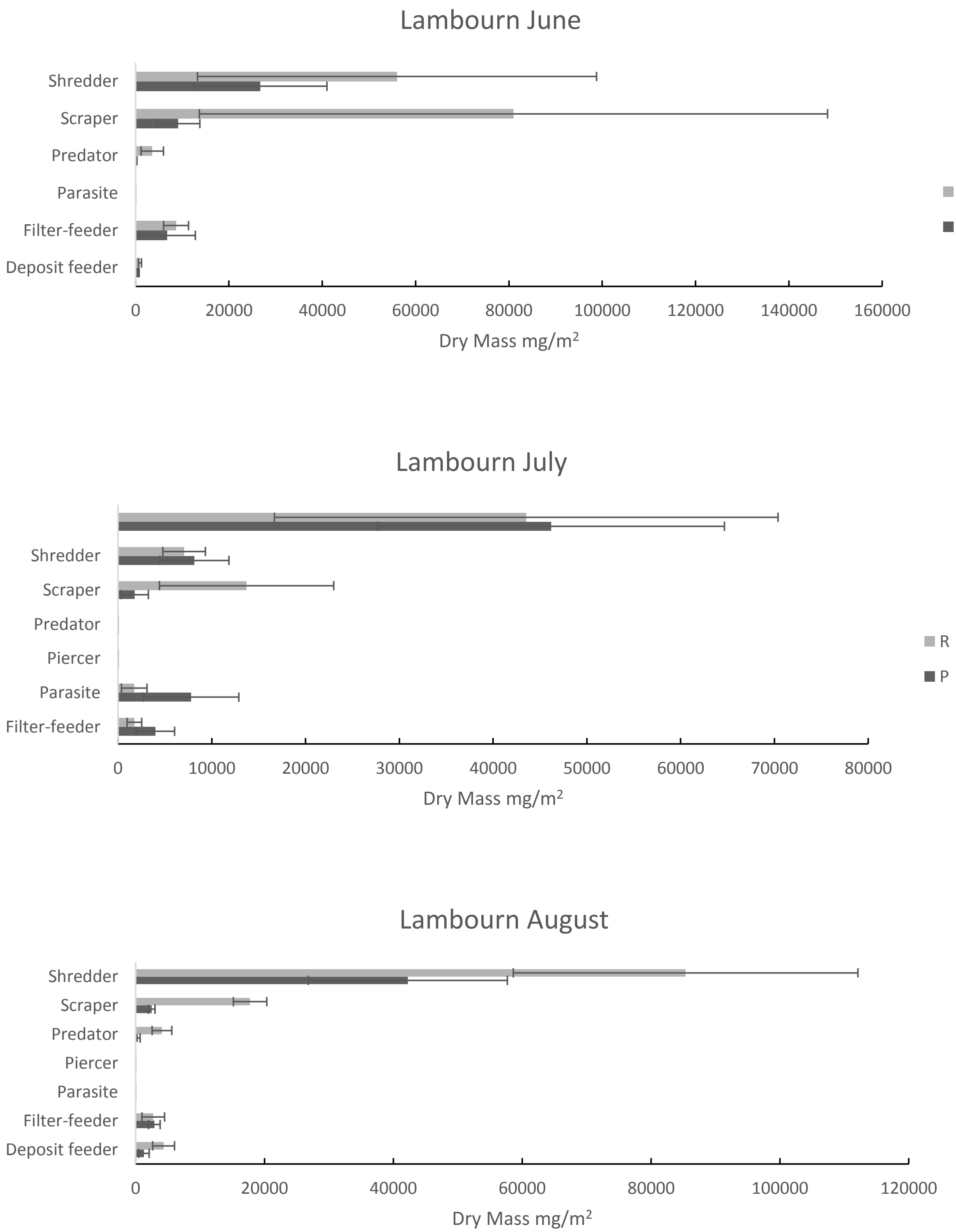
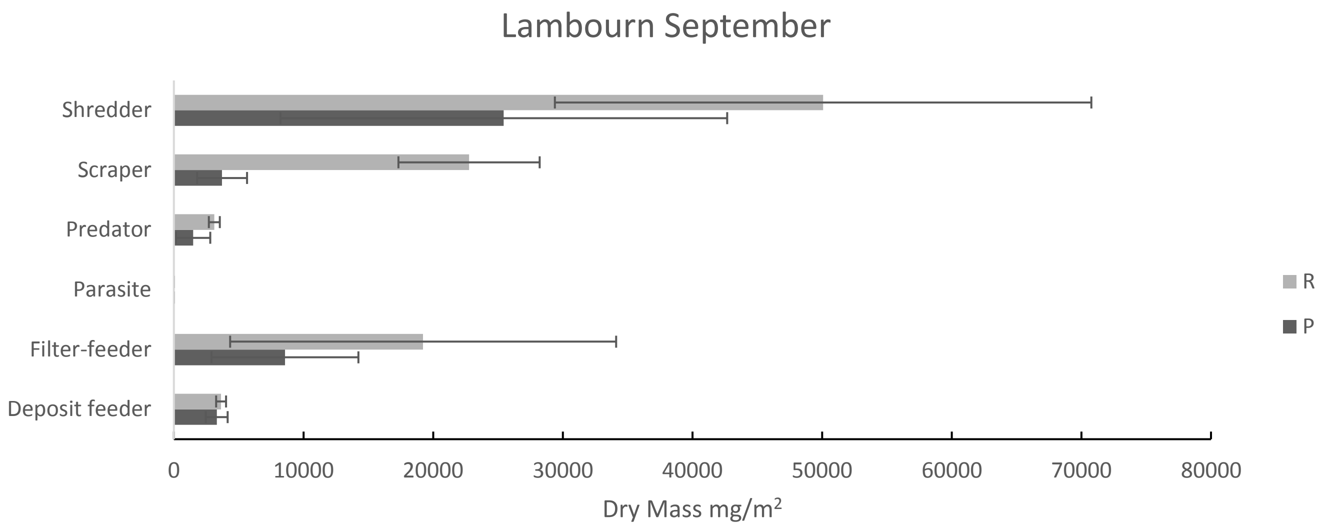


Figure 4.8 part 1. The River Lambourn macroinvertebrate biomass for functional feeding drought (FFG) in perennial (P) and rewetted (R) sites.



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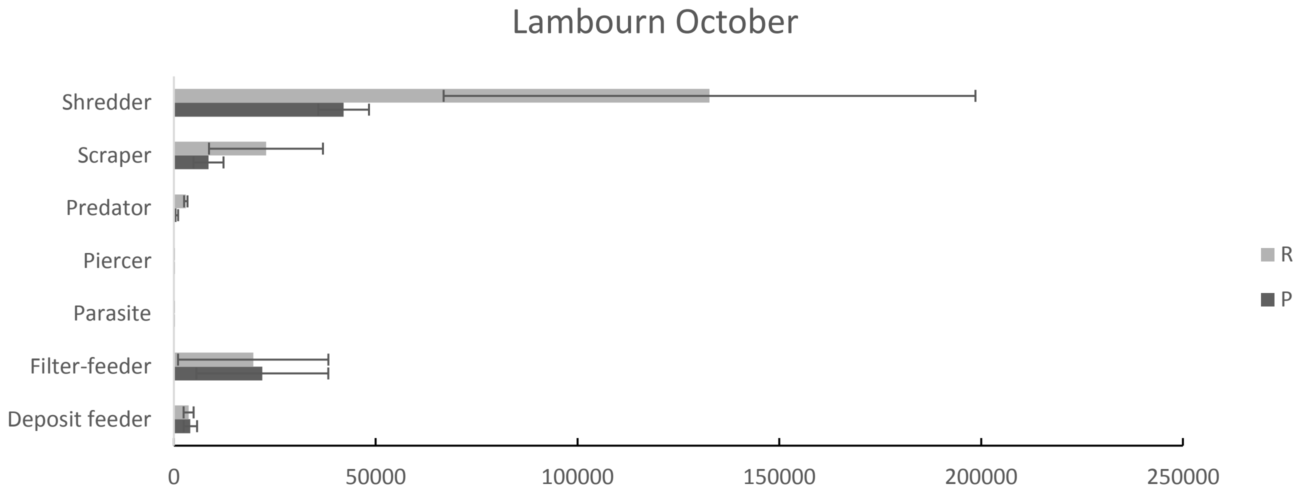
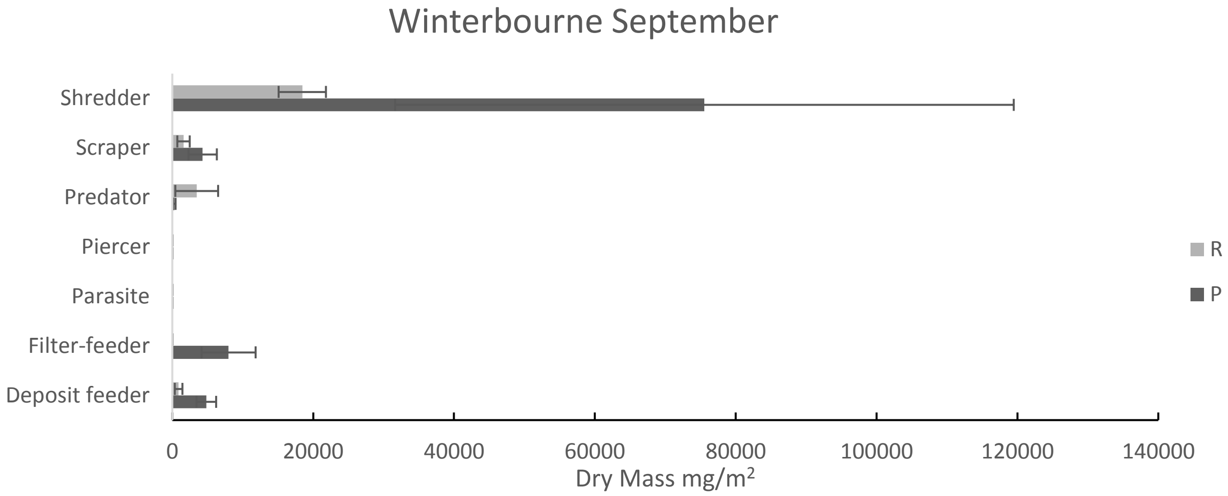


Figure 4.8 cont'd. The River Lambourn macroinvertebrate biomass for functional feeding drought (FFG) in perennial (P) and rewetted (R) sites.

In the Winterbourne Stream, filter-feeders were the most dominant FFG at the rewetted site whereas shredder dominated the perennial site the number of predators increased at both sites in July and August (Figure 4.9).

Figure 4.9 part 1. The Winterbourne Stream macroinvertebrate biomass for functional feeding drought (FFG) in perennial (P) and rewetted (R) sites.



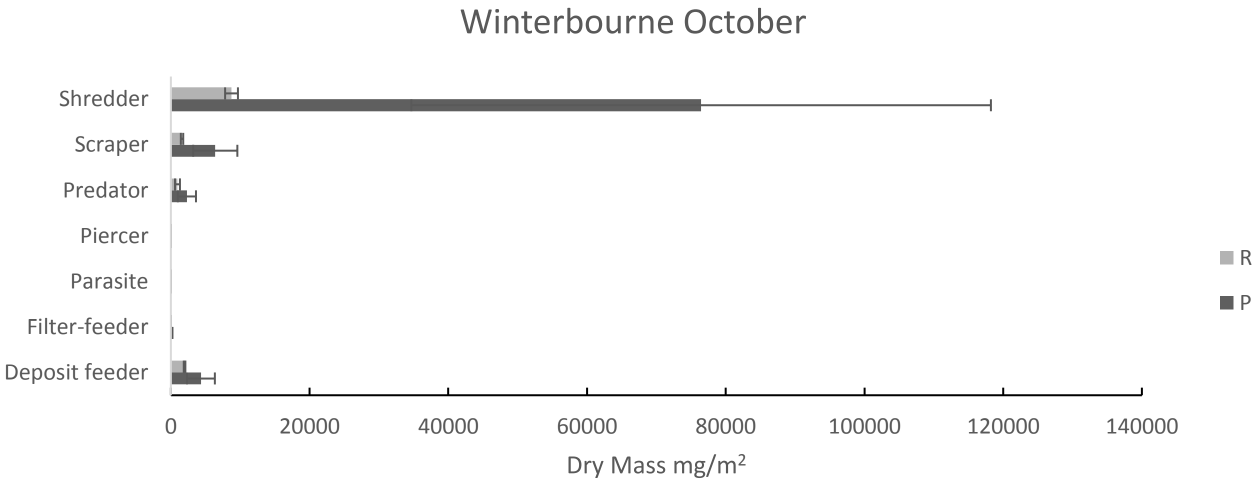


Figure 4.9 cont'd. The Winterbourne Stream macroinvertebrate biomass for functional feeding drought (FFG) in perennial (P) and rewetted (R) sites.

Filter feeders were the dominant FFG in rewetted site in June on the Kennet (Figure 4.10) compared with shredders in the perennial site and there were very few filter-feeders in the perennial site, the shredders dominated the perennial site and there were few in the rewetted site. From July onwards the shredders were the dominant FFG in both sites and deposit feeders and scrapers were also prominent. The perennial site has a small biomass of piercers in some months and they were never found in the rewetted sites.

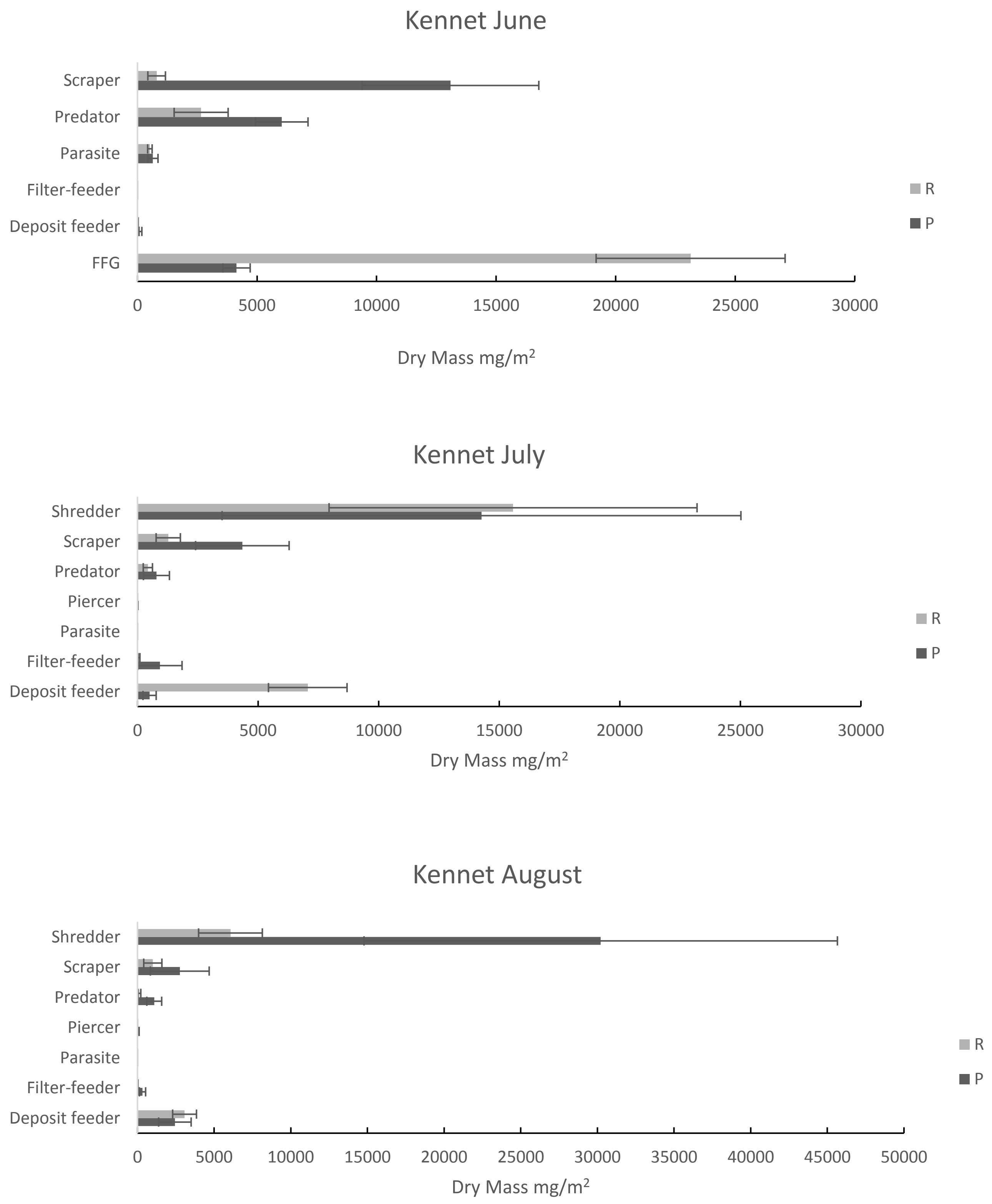
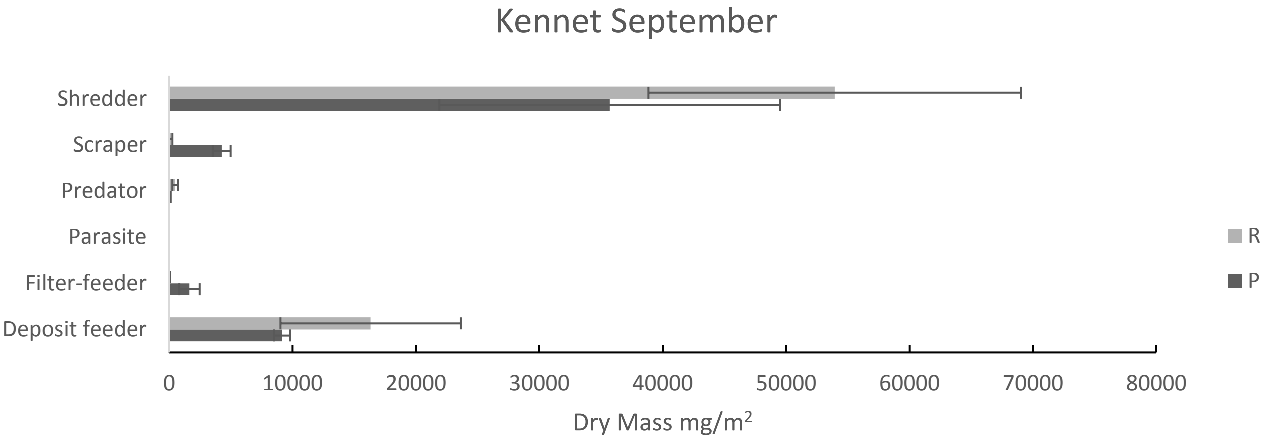


Figure 4.10 part 1. The River Kennet macroinvertebrate biomass for functional feeding drought (FFG) in perennial (P) and rewetted (R) sites.



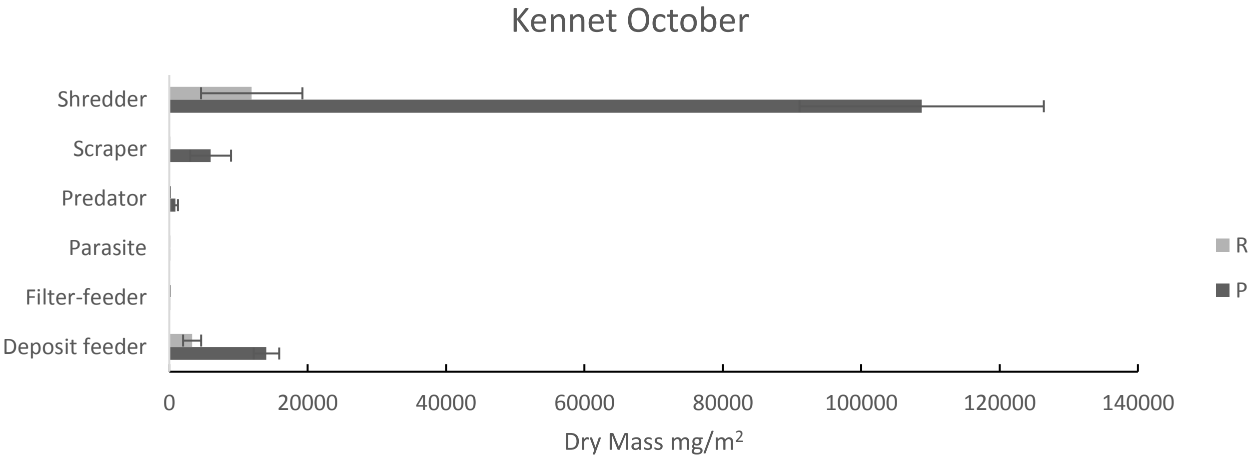


Figure 4.10 cont'd. The River Kennet macroinvertebrate biomass for functional feeding drought (FFG) in perennial (P) and rewetted (R) sites.

4.3.4 Biomass of individual macroinvertebrate families

Biomass showed high variation in the rewetting month of June. In the River Lambourn the rewetting site a high mass of Chironomidae was found compared to the perennial site. Other families present in high biomass including Asellidae, which was not present at the perennial site (Figure 4.11). The perennial site supported families which were not present in the rewetted site including Caenidae, Leptoceridae, Polycentropodidae and Planorbiidae and the rewetted site had families not found in the perennial site including Psychodidae, Dytiscidae, Dendrocoelidae and Glossiphoniidae. In July the mass of Chironomidae at the rewetted site was similar to the perennial site and the biomass of Gammaridae was the highest at both sites (Figure 4.12). Later months still show high biomass of pioneer families such as Chironomidae, Planariidae and Oligochaeta but an increasing biomass or riverflies and beetles as months pass (Figures 4.12, 4.13 and 4.14)

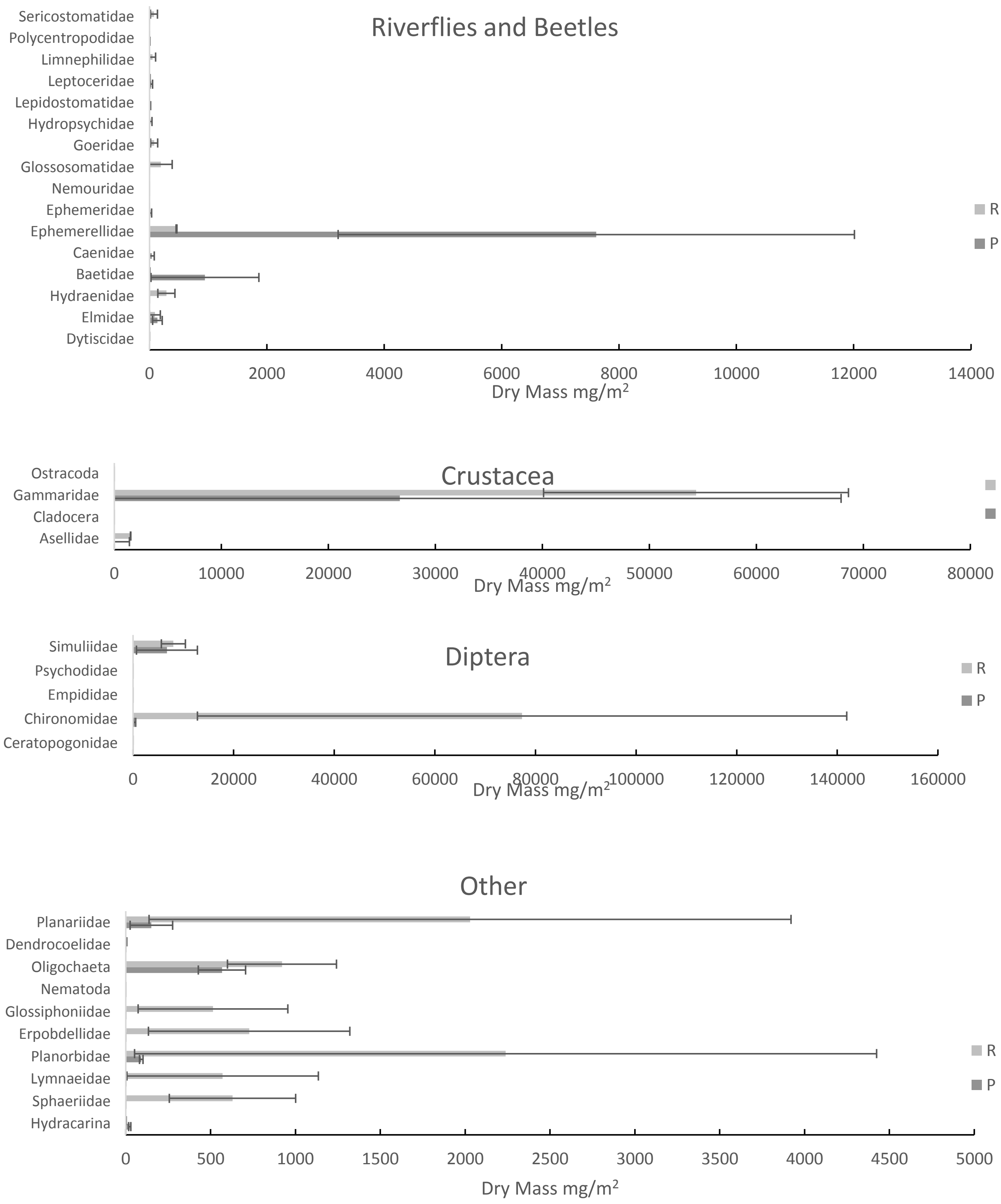
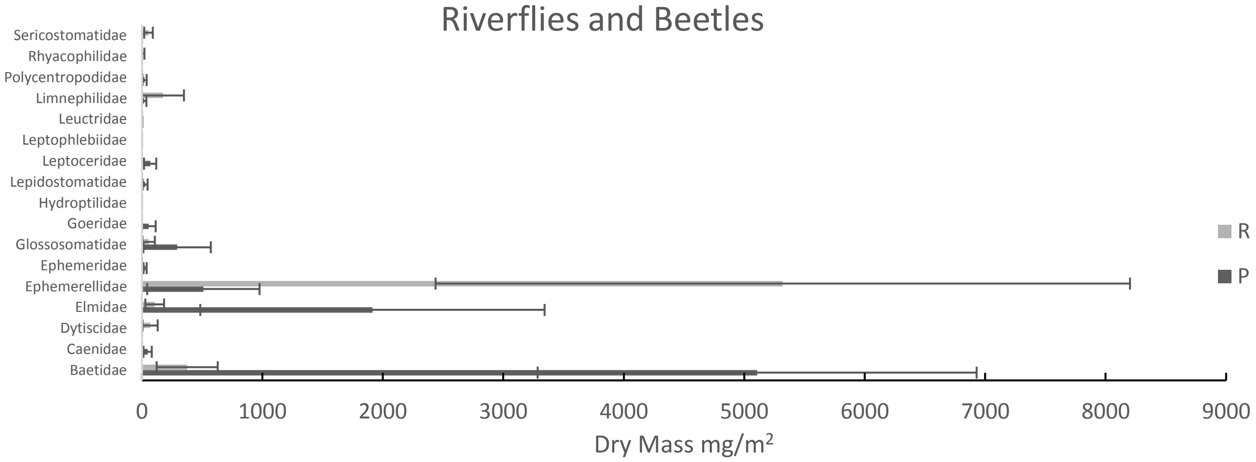
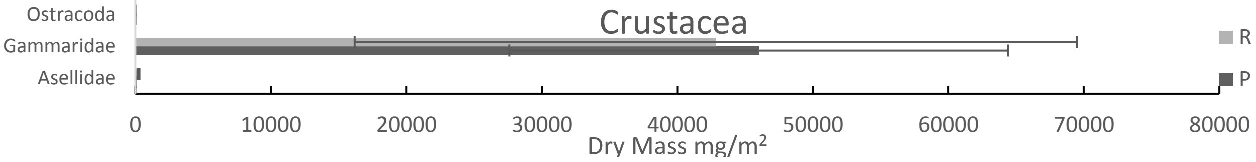
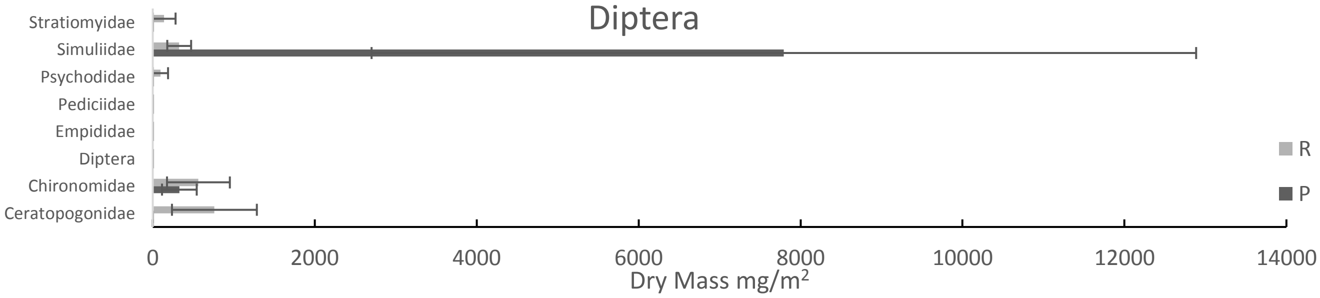


Figure 4.11. The River Lambourn June. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs







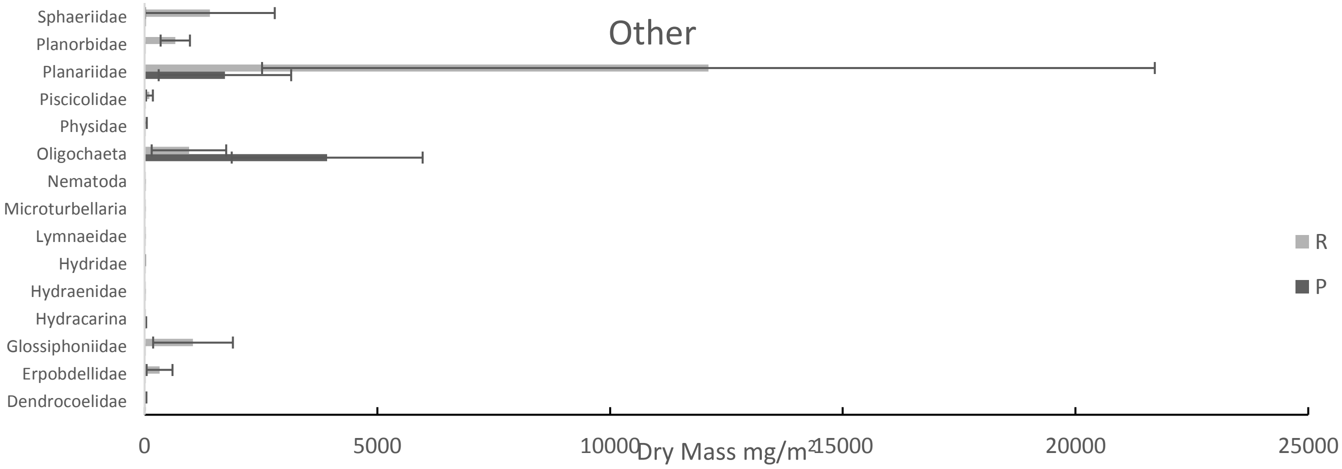


Figure 4.12. The River Lambourn July. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

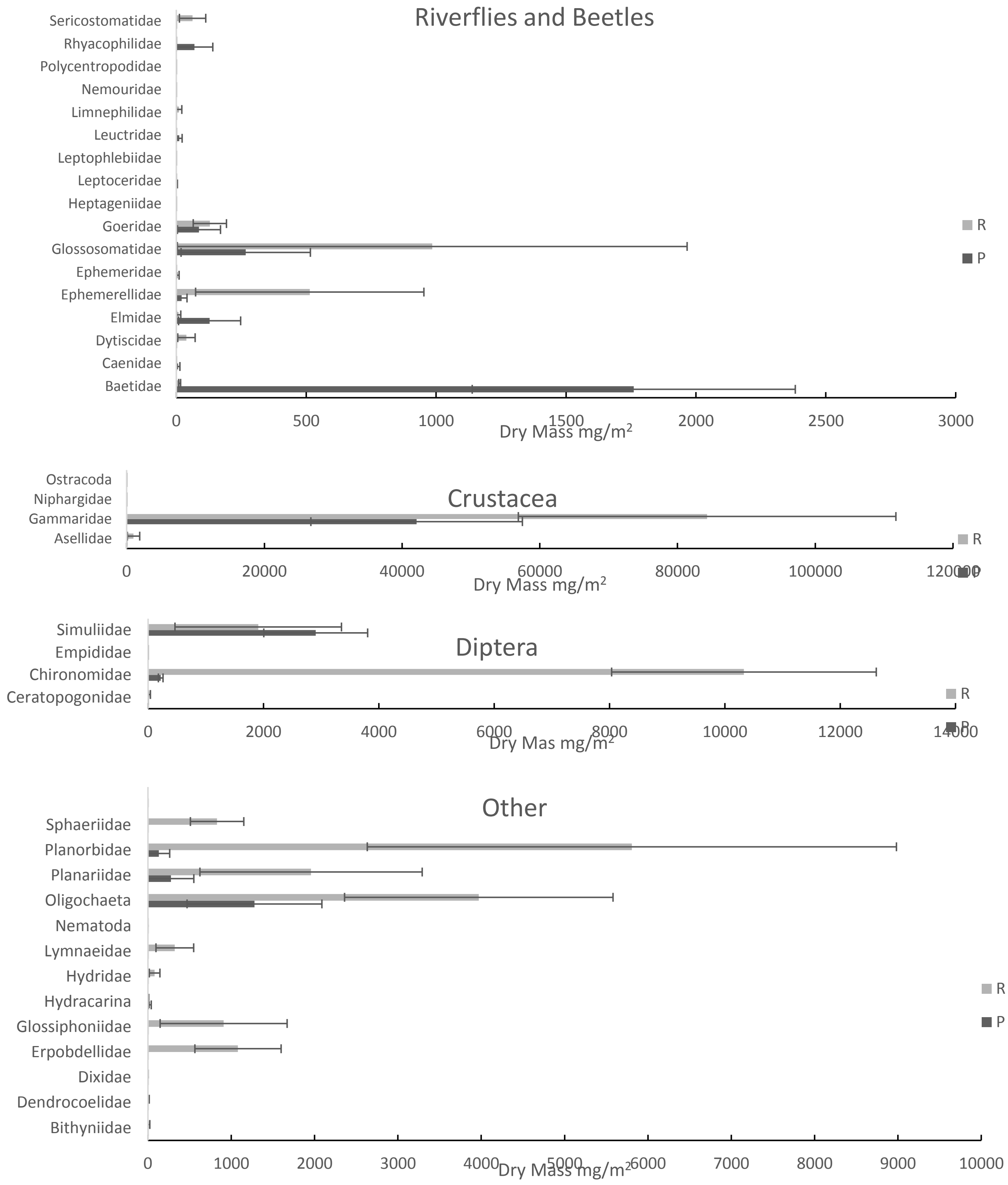


Figure 4.13. The River Lambourn August. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

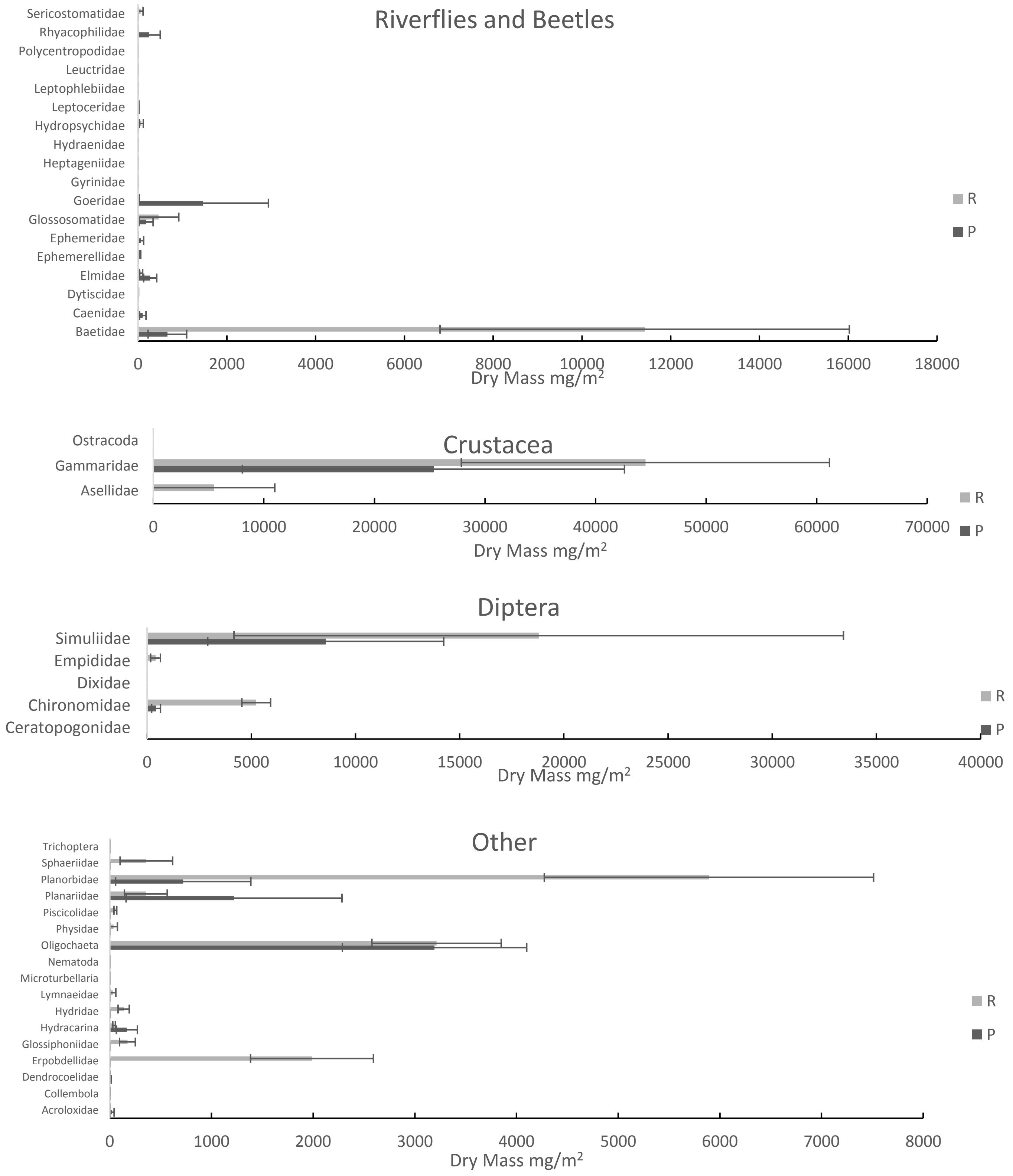


Figure 4.14. The River Lambourn September. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

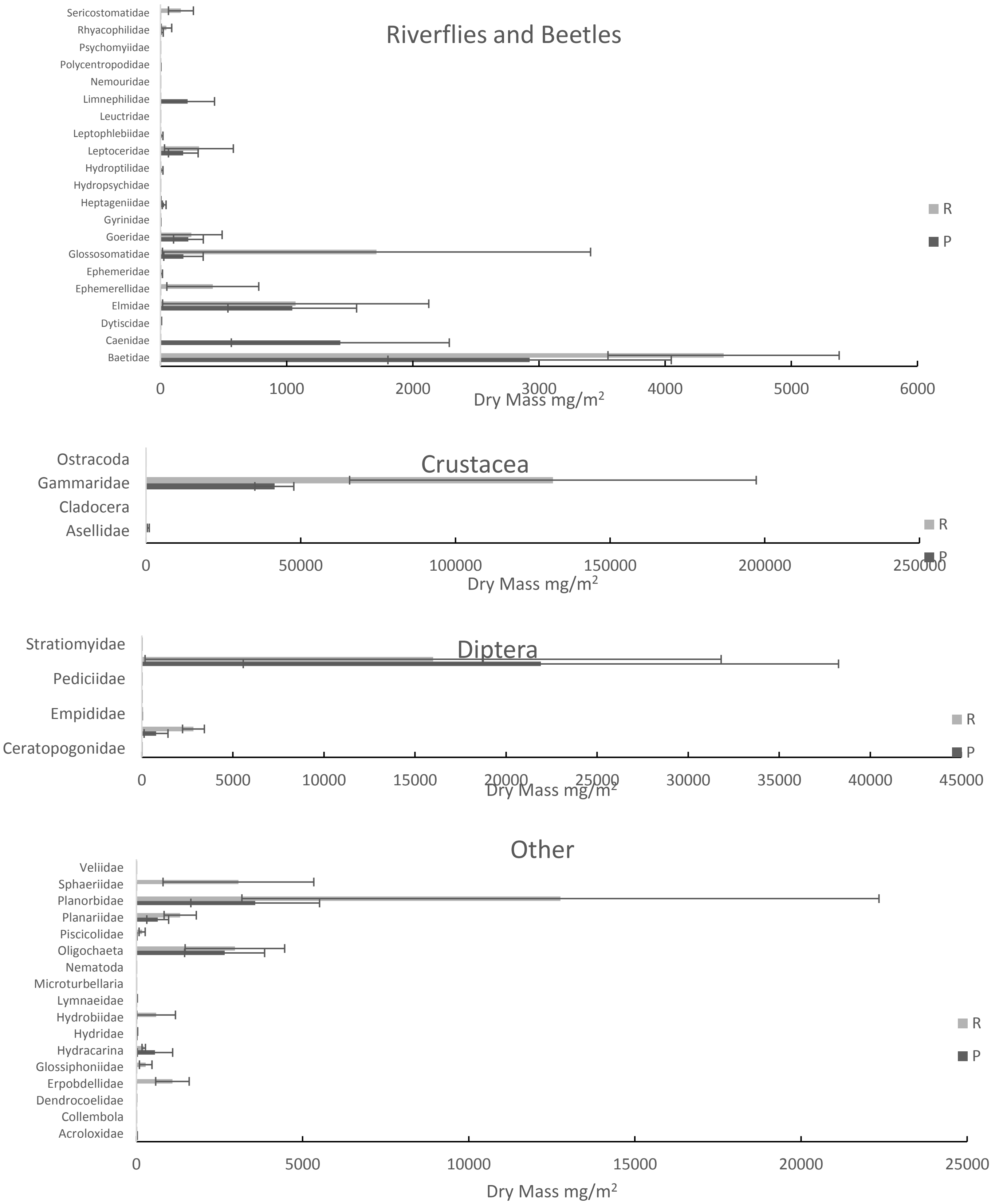


Figure 4.15. The River Lambourn October. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

The Winterbourne Stream had a lower overall biomass in the rewetted sites throughout all months (Figure 4.5) the individual families biomass was low in June (Figure 4.16) and July (Figure 4.17) although the most numerous species were similar to the perennial site. The rewetted site in June had families which were not in the perennial site including: Nemouridae, Sciritidae, Goeridae, Velidae and Dixidae. The perennial site supported families not found at the rewetted site including: Rhyacophilidae, Hydroptilidae, Leuctridae and Leptoceridae. In July the rewetted site Rhyacophilidae and Leptoceridae were present, making the community more similar to the perennial site in composition despite the low overall biomass. The rewetted site had an increase of Planariidae and Glossosomatidae which began in August and peaked in September and October (Figures 4.18-4.20). Most families continued to have a higher biomass in perennial sites (figures 4.18-4.20).

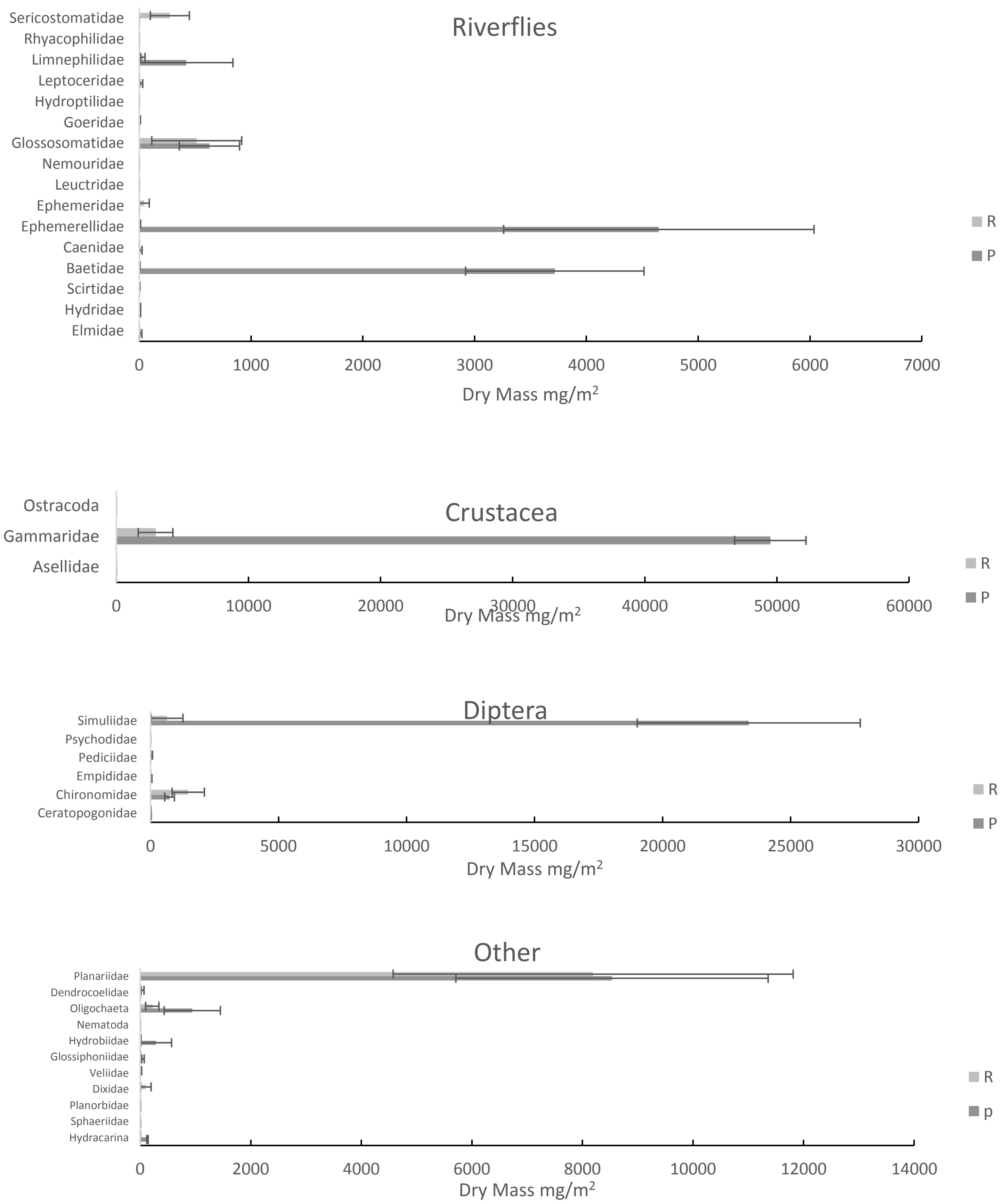


Figure 4.16. The River Winterbourne June. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

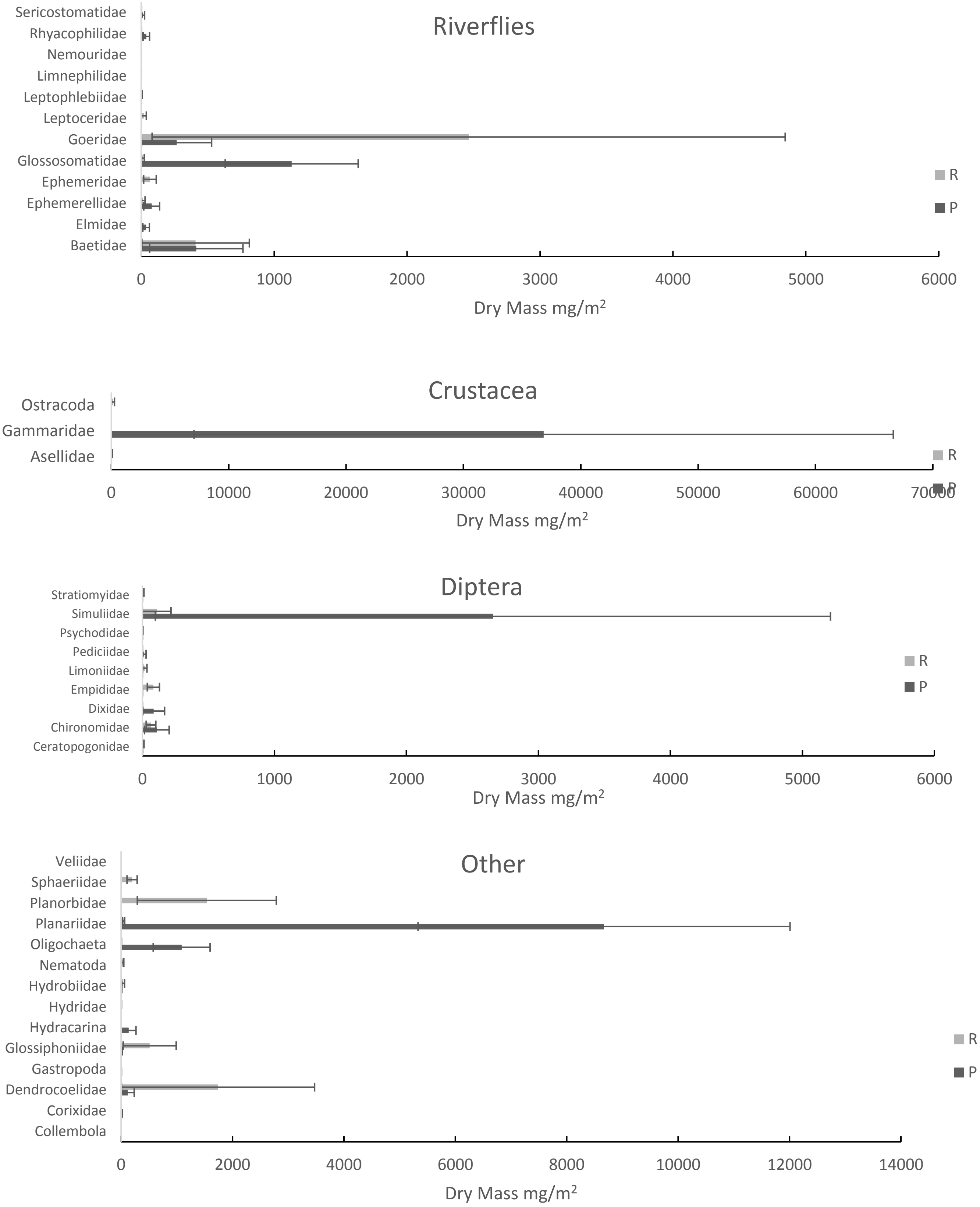


Figure 4.17. The River Winterbourne July. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

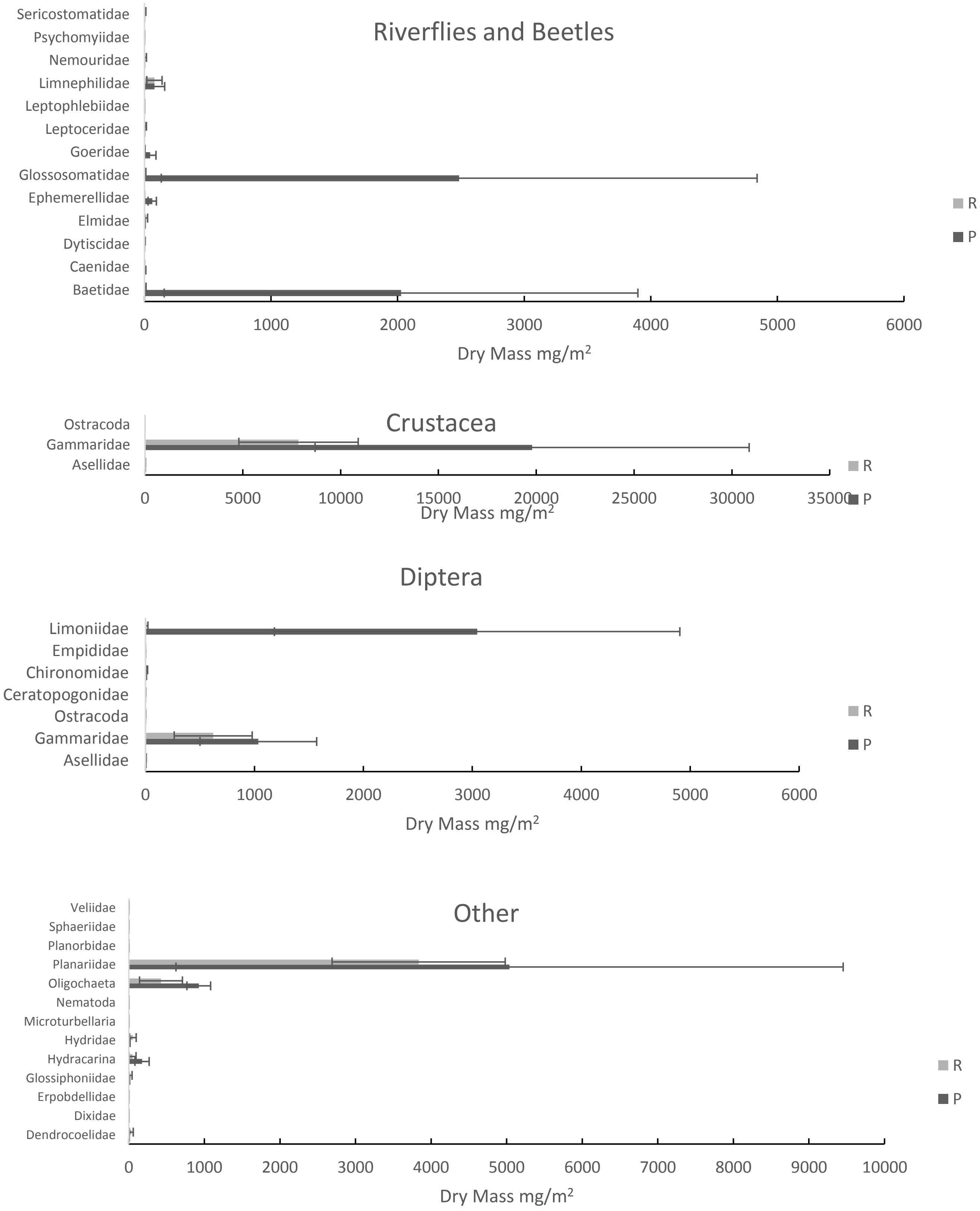


Figure 4.18. The River Winterbourne August. Biomass mg-m² ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

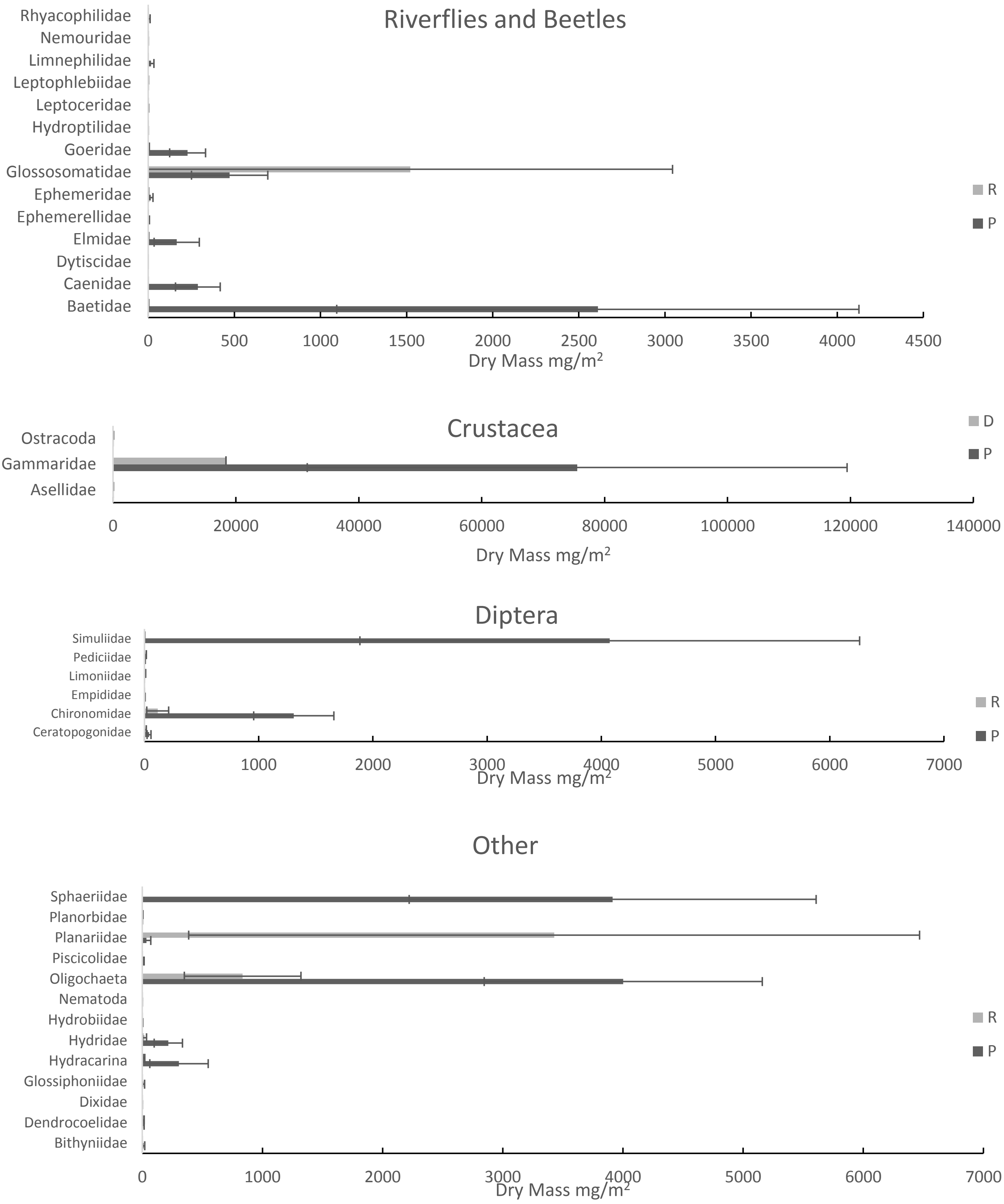


Figure 4.19. The River Winterbourne September. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

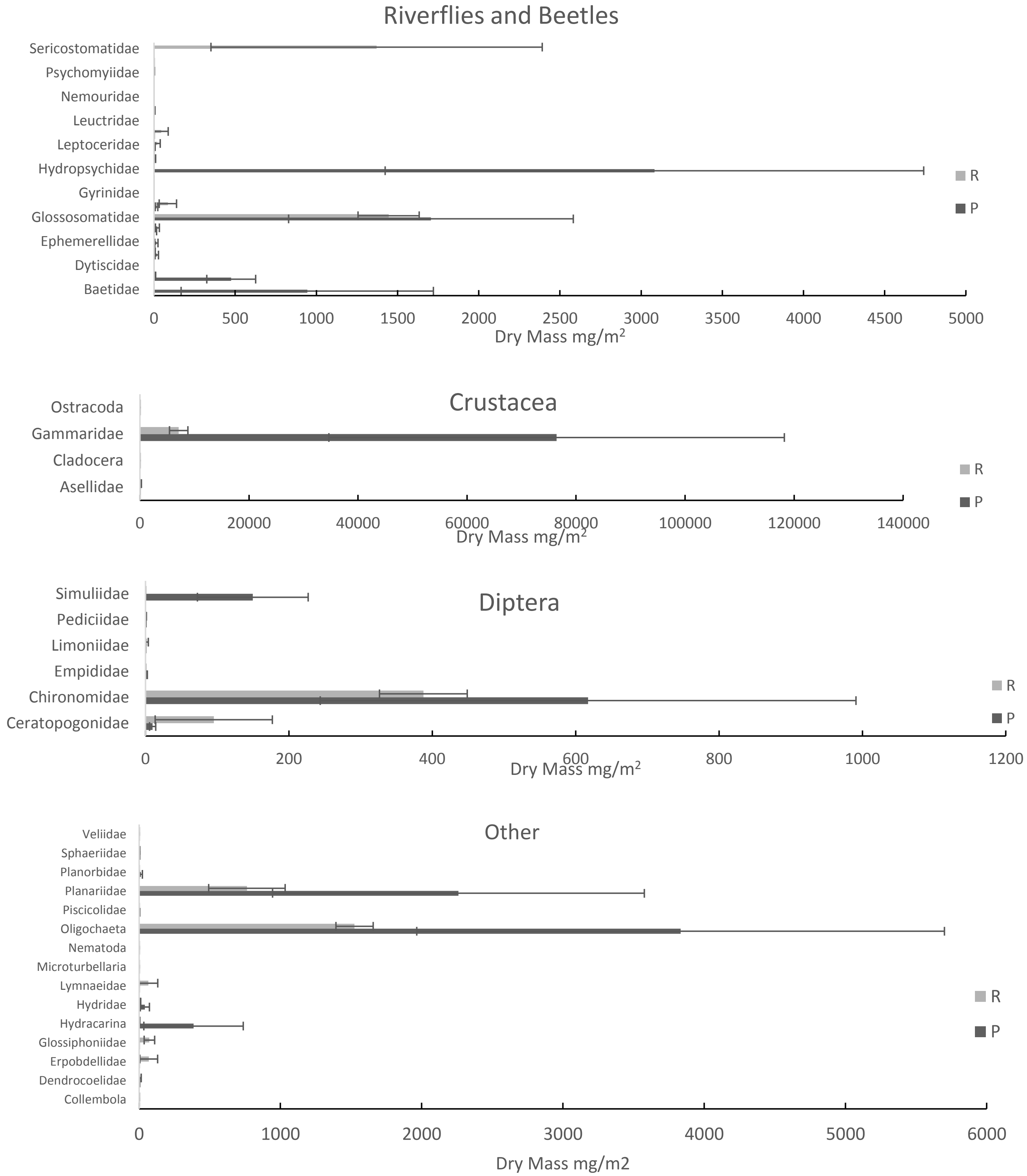


Figure 4.20. The River Winterbourne October. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

The River Kennet had a similar pattern as the Lambourn. The families containing the most biomass in June differed between perennial and rewetted sites (Figure 4.21). In the rewetted site Oligochaeta was the family with greatest mass, followed by Chironomidae and Ephemerellidae compared with Gammaridae, Ephemerellidae and Oligochaeta in the perennial site. Families which were present in the perennial site but missing in the rewetted site in June included: Rhyacophilidae, Leptoceridae, Polycentropodidae, Lepidostomatidae and Caenidae. The only families which were unique to the rewetted site were Asellidae and Empididae. In July and August the taxonomic composition was more similar between the sites (Figures 4.22 and 4.23), Chironomidae were present in a higher mass in the rewetted site still and there were more Oligochaeta, Pedicidae and Planadiidae. Rhyacophilidae was present in the rewetted site which was not present in June but the other families missing in June were still missing in July. Riverfly and beetle species do not reach a high biomass by October, however Gammaridae, Oligochaeta, Chironomidae and other Diptera species reach similar or larger biomass by September and October.

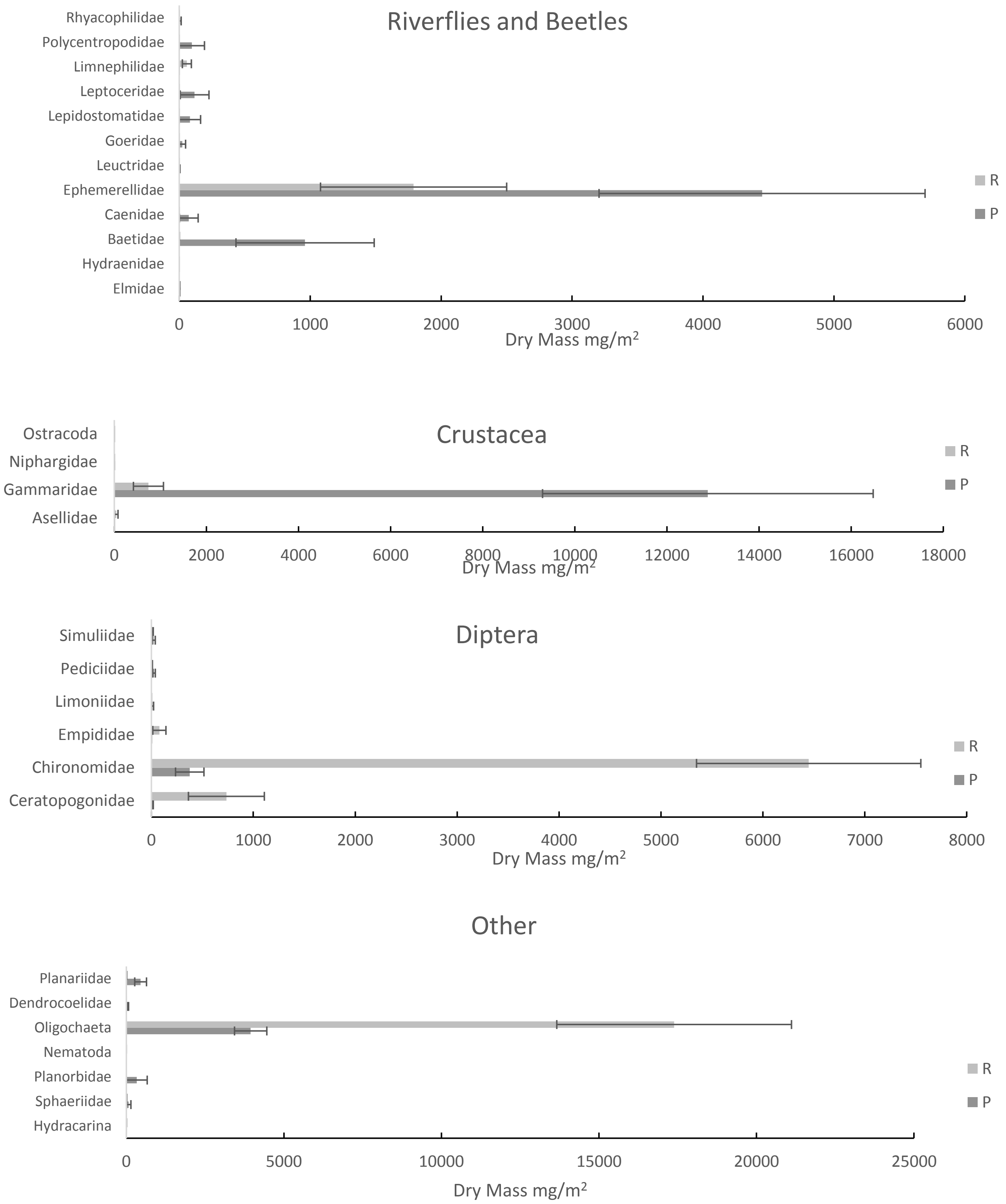


Figure 4.21. The River Kennet June. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

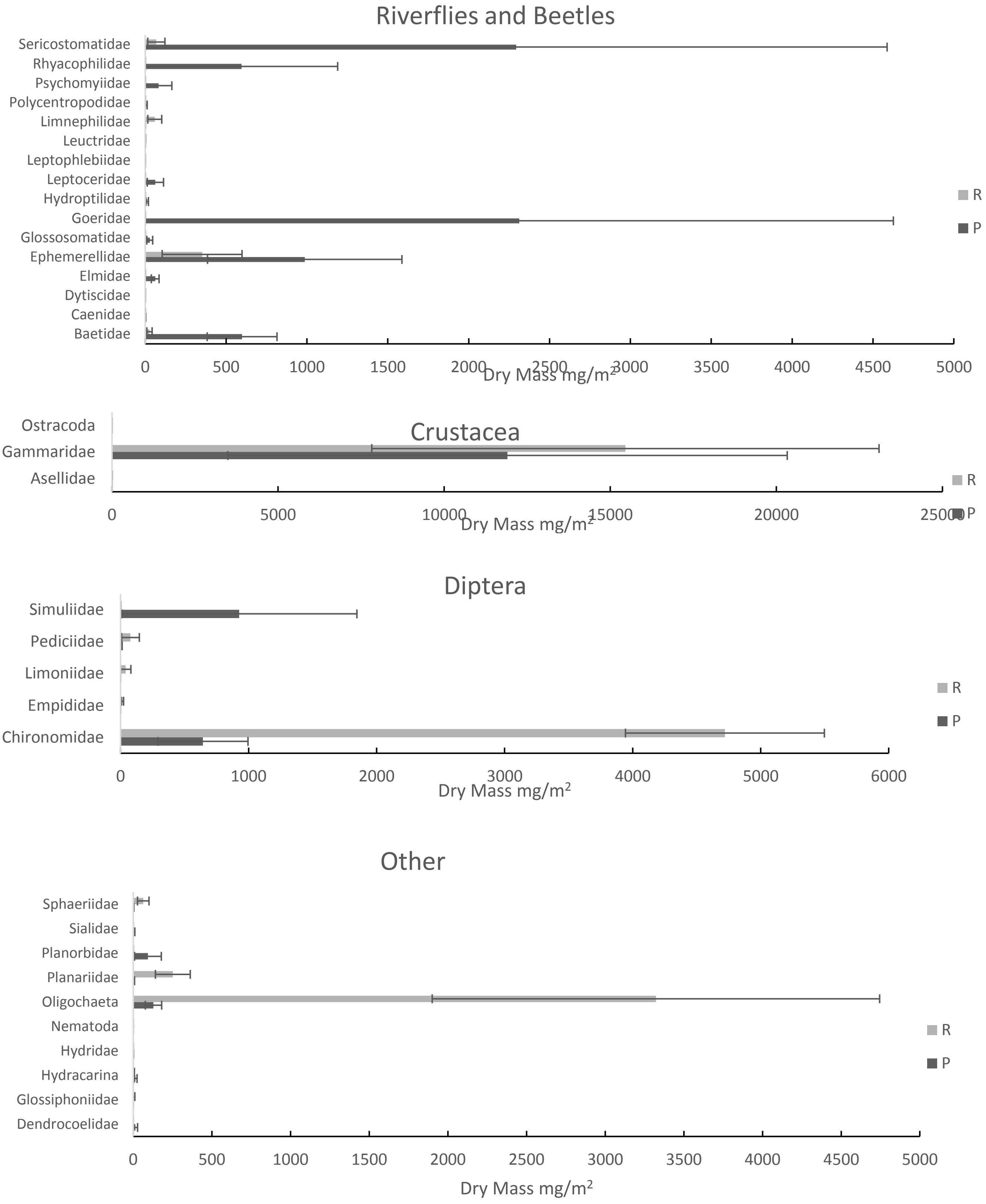


Figure 4.22. The River Kennet July. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

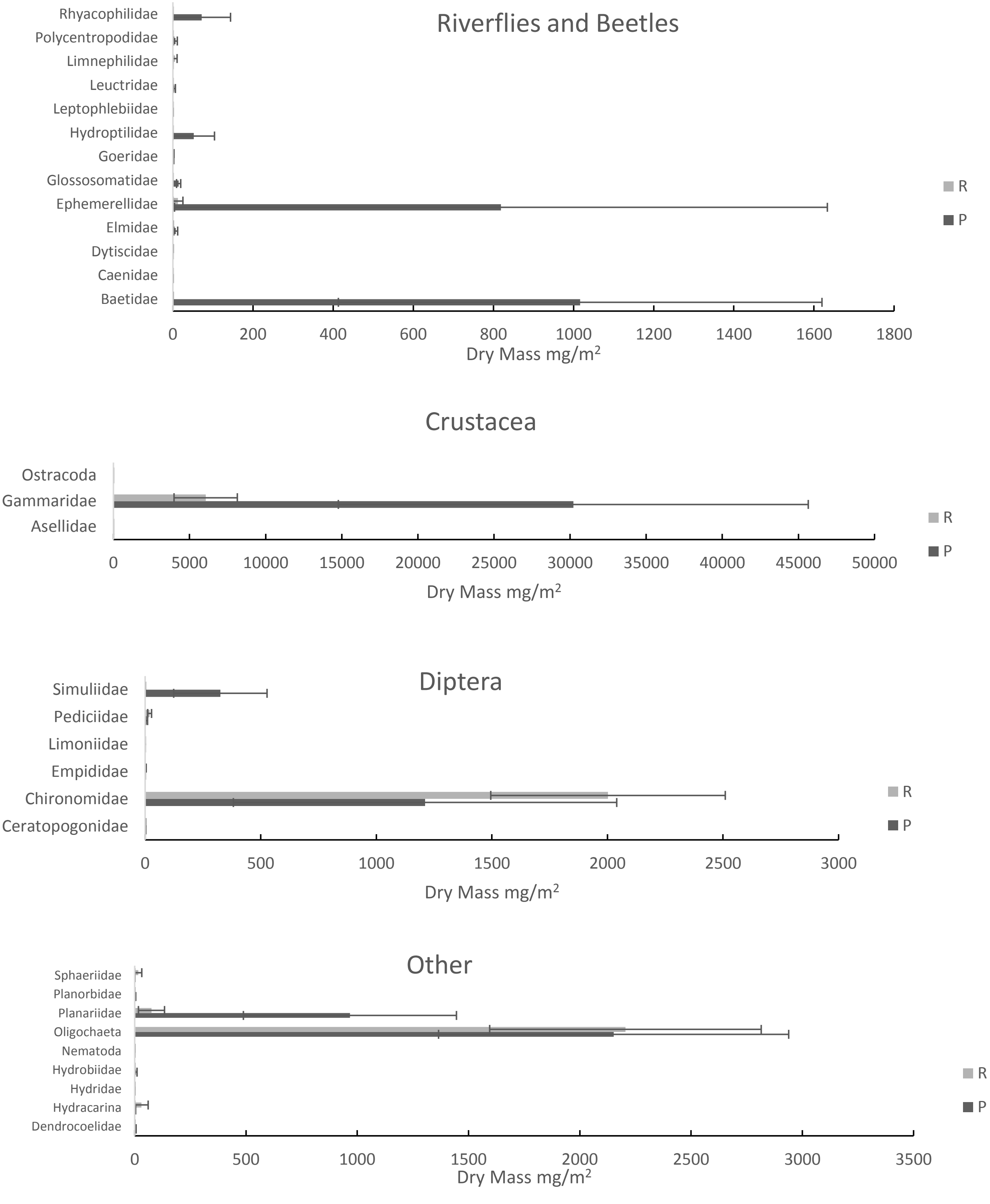


Figure 4.23. The River Kennet August. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

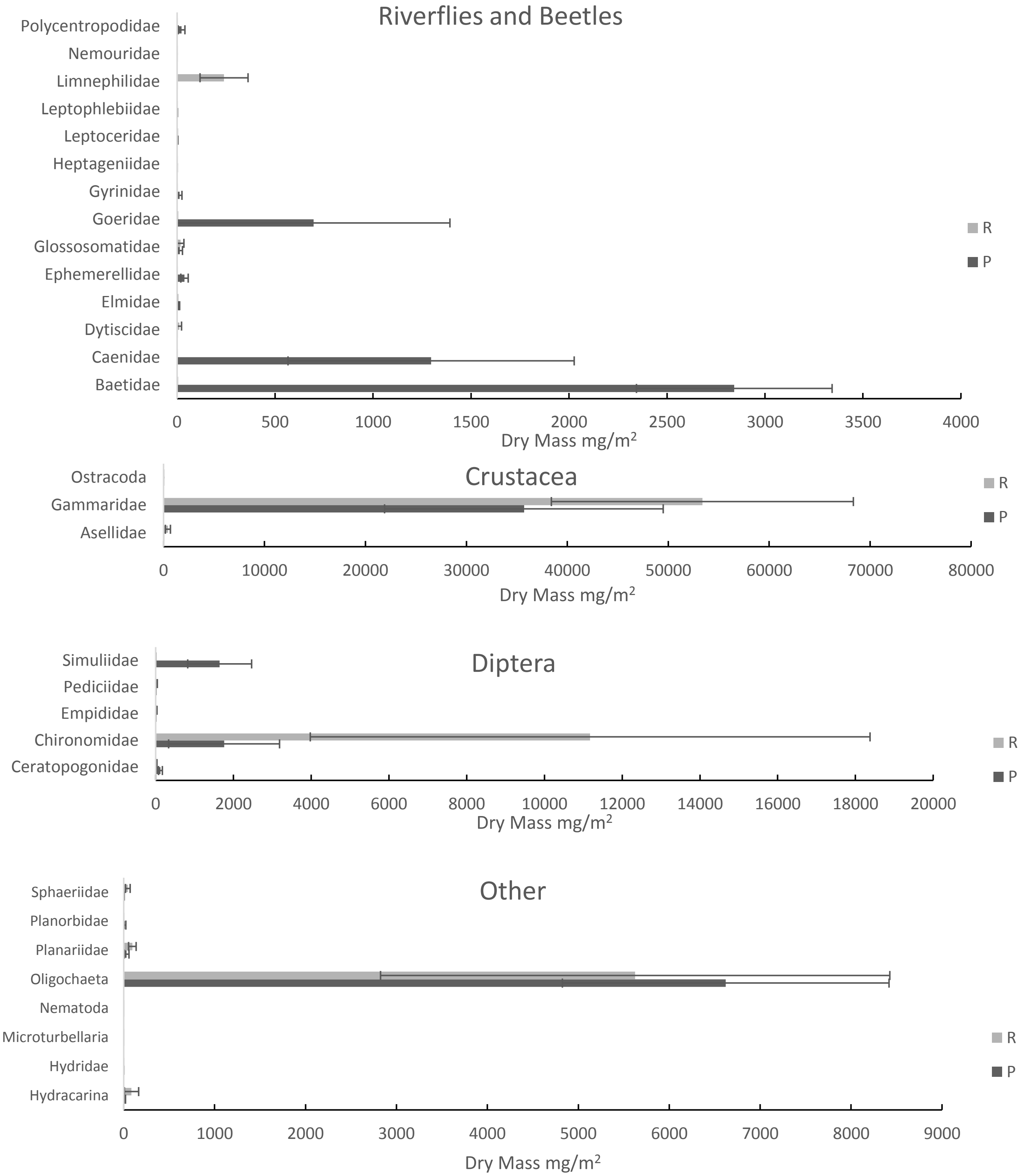


Figure 4.24. The River Kennet September. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

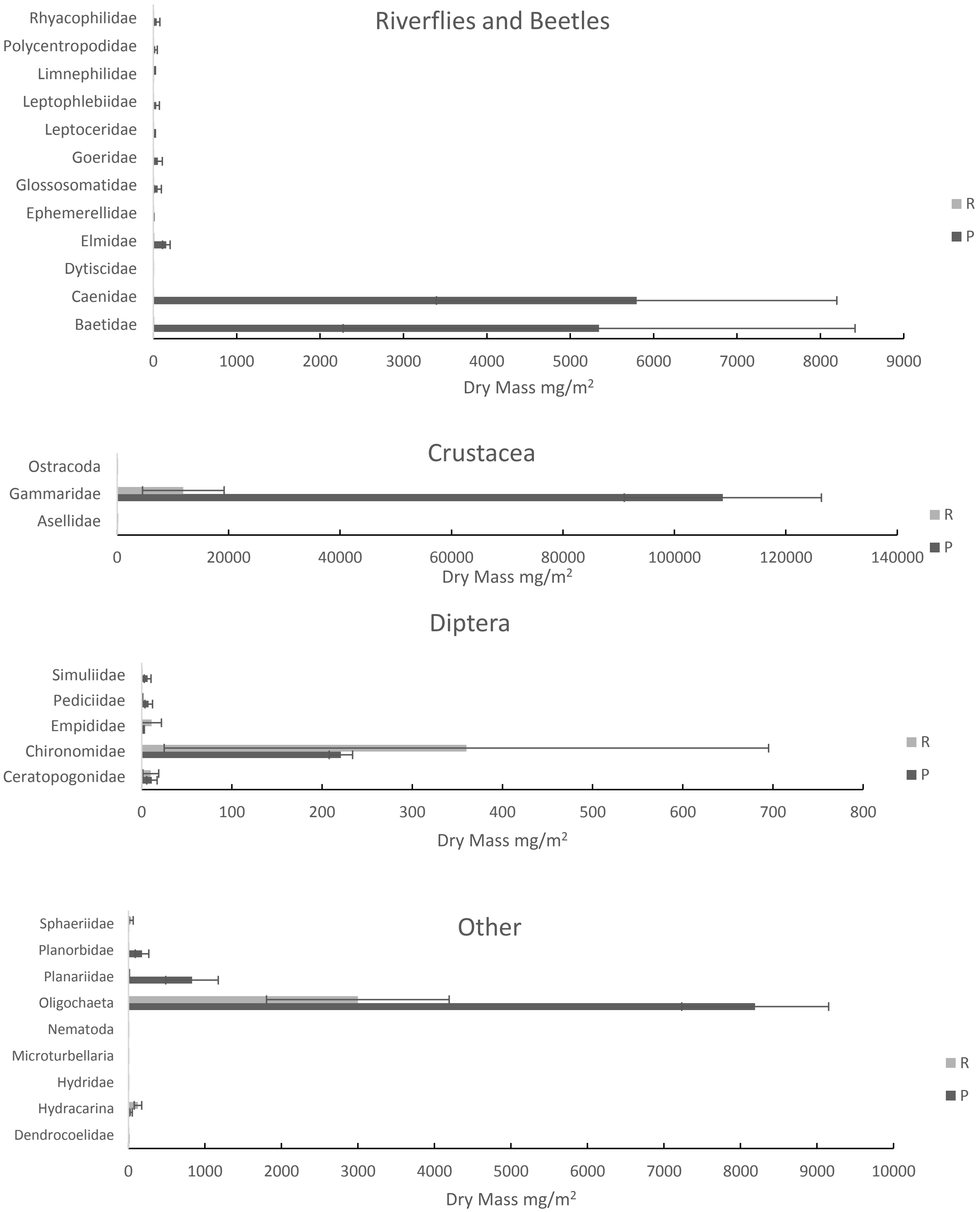


Figure 4.25. The River Kennet October. Biomass mg-m^2 ± 1 SE of the families of macroinvertebrates in perennial and dewatering sites grouped by taxonomic group. Taxonomic groups are as follows: graph 1: riverflies (Trichoptera, Plecoptera and Ephemeroptera) and Coleoptera; graph 2: Diptera graph 3: Crustacea and graph 4: Others including Gastropoda, Bivalvia, Oligochaeta, Tricladia and Hirudinea. Note change in scale on axes between graphs

4.3.5 Velocity Measurements

In the River Lambourn benthic current velocity was consistently higher in the rewetted site than the perennial site (Figure 4.26) but at 0.4 depth values were more similar. The Winterbourne and Kennet showed little pattern, but flow in the rewetted site was not different to the perennial site for either the bed or 0.4 in the Kennet or benthic in the Winterbourne (Figures 4.27 & 4.28).

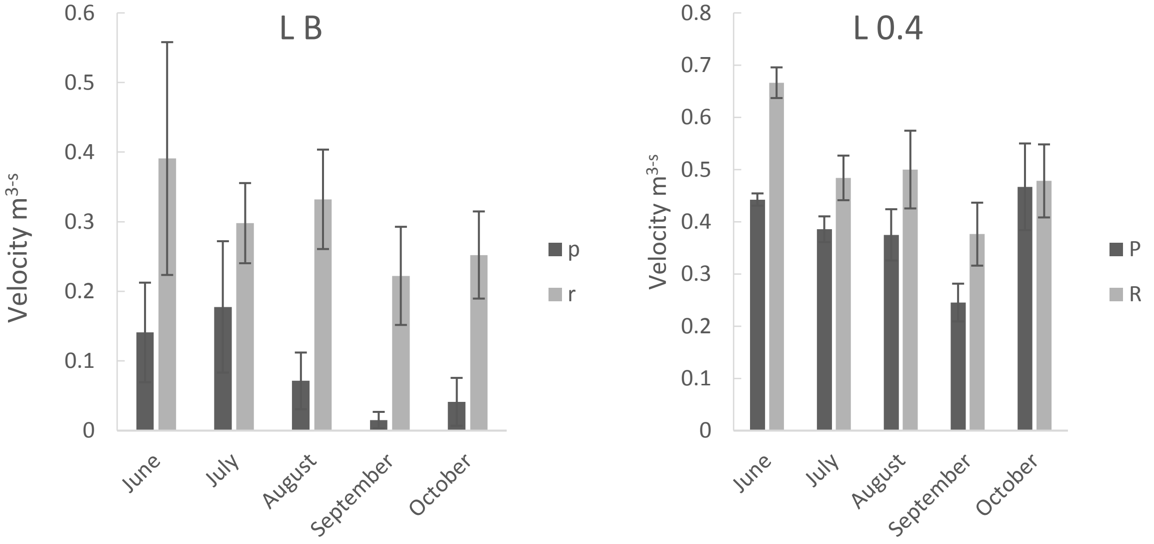


Figure 4.26. The River Lambourn. Mean velocity at 0.4 (40%) depth in the channel, and benthic depth (2.5 cm above benthos) of both perennial and rewetting sites ± 1 SE.

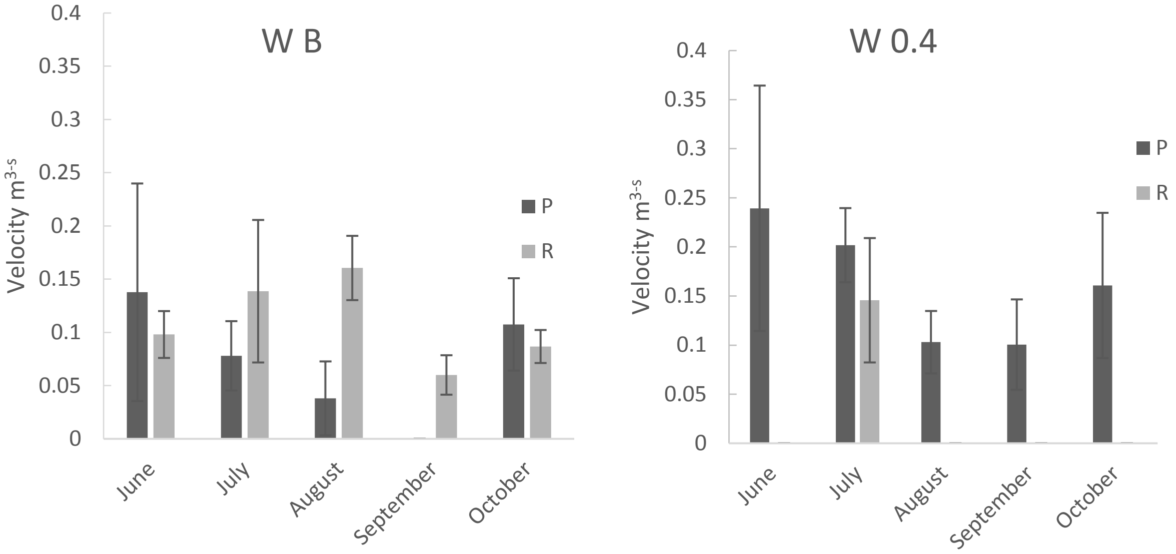


Figure 4.27. The Winterbourne Stream. Mean velocity at 0.4 (40%) depth in the channel, and benthic depth (2.5 cm above benthos) of both perennial and rewetting sites ± 1 SE. The rewetted site was only deep enough for a 0.4 measurement in July, the other months it was too shallow.

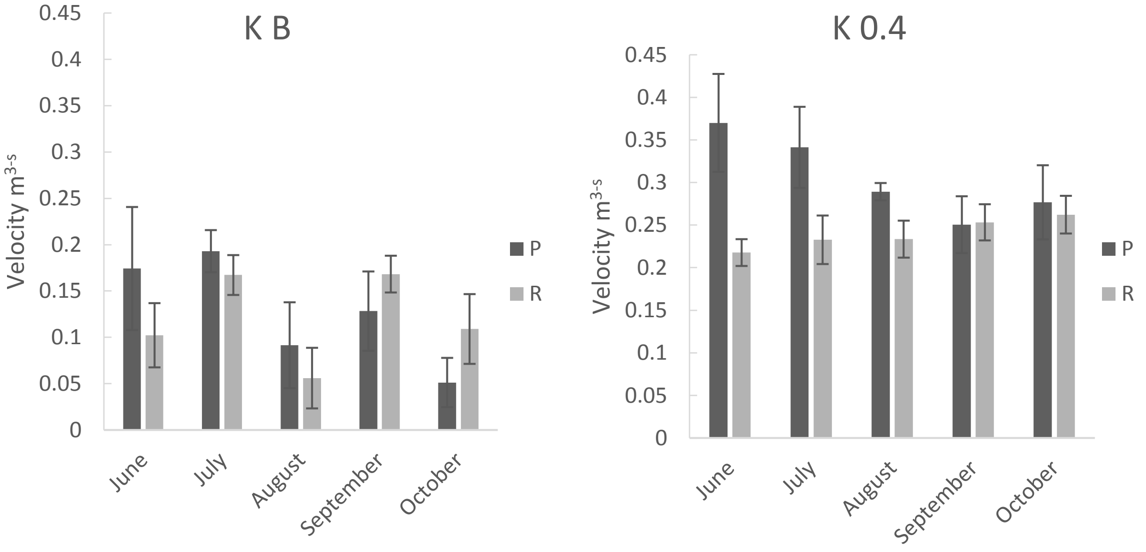


Figure 4.28. The River Kennet. Mean velocity at 0.4 (40%) depth in the channel, and benthic depth (2.5 cm above benthos) of both perennial and rewetting sites ± 1 SE.

4.3.6 Algal Biomass Results

The chlorophyll *a* results from the Lambourn show that there is algae present in the rewetted site from June (Figure 4.29). There appears to be more chlorophyll *a* in the dewatered site in September and October, however differences between status of perennial and rewetted sites were not significant ($p>0.05$) there was also no significant different in chlorophyll *a* between months ($p>0.05$) or any interaction between month and status (F=2.59, DF=3, $p=0.421$). The ash free dry mass results (Figure 4.30) show there were differences across months in mass (ANOVA, F=2.90, DF=3, $p=0.050$), Tukey post-hoc tests show that September had the highest mass and July had the lowest mass, the other months were somewhere in-between. There was no significant in masses across status ($p>0.05$) and there was no interaction between status and month ($p>0.05$). Autotrophic index for the Lambourn (Figure 4.31) was not significant for status (ANOVA, F=0.28, DF=1, $p=0.601$), month ($p>0.05$) or interaction ($p>0.05$).

The Winterbourne stream has much less chlorophyll *a* than the Lambourn or Kennet, however it showed similar patterns (Figure 4.29), with no significant differences between perennial and rewetted sites (status) (ANOVA) perennial and rewetted streams, $p>0.05$ there was also no significant differences between chlorophyll *a* over month ($p>0.05$) and no interaction between month and status ($p>0.05$). Ash free dry mass results (Figure 4.30) showed that there was a significant difference between status (F=25.20, DF=1, $p<0.001$) and no significant difference between months ($p>0.05$). However there was a significant interaction between month and status (F=4.79, DF=3, $p<0.01$). Tukey post-hoc tests showed the in October there was a significantly higher mass in the rewetted site. Autotrophic index (Figure 4.31) was not significantly different for status (ANOVA, p>0.05), there was a significant difference between month (ANOVA, F=4.86, DF=3, p<0.01), Tukey post-hoc tests showed this difference was due to a lower AI in September compared to the other months, and was no interaction between status and month (ANOVA, p>0.05).

The River Kennet showed higher Chlorophyll *a* levels (Figure 4.29) in the perennial sites and this is significant (ANOVA of differences between perennial and rewetted sites F=13.15, DF=1, p=0.001), and there was no difference in Chlorophyll *a* between month (ANOVA, p>0.05) and no interaction between status and month (ANOVA p>0.05). Tukey post-hoc tests showed the difference in status was due to an overall higher Chlorophyll *a* level in the perennial site. Ash free dry mass results show that there is a significantly different mass between status (ANOVA, F=6.16, DF=1, p<0.05), and a barely insignificant difference between month (ANOVA, F=2.83, DF=3, p=0.054). There is no significant interaction between month and status (p>0.05). Tukey post-hoc tests show that July has the highest mass and October has the lowest mass. Autotrophic index (Figure 4.30) was significantly different between status (ANOVA, F=16.80, DF=1, p<0.01), month (ANOVA, F=5.64, DF=3, p<0.01) and a barely insignificant difference in the interaction between status and month (ANOVA, F=2.81, DF=3, p=0.055). Tukey post-hoc tests show that October has a higher autotrophic index than the other months, rewetted sites have a higher autotrophic index than perennial sites and October has a difference between autotrophic index in perennial and rewetted sites.

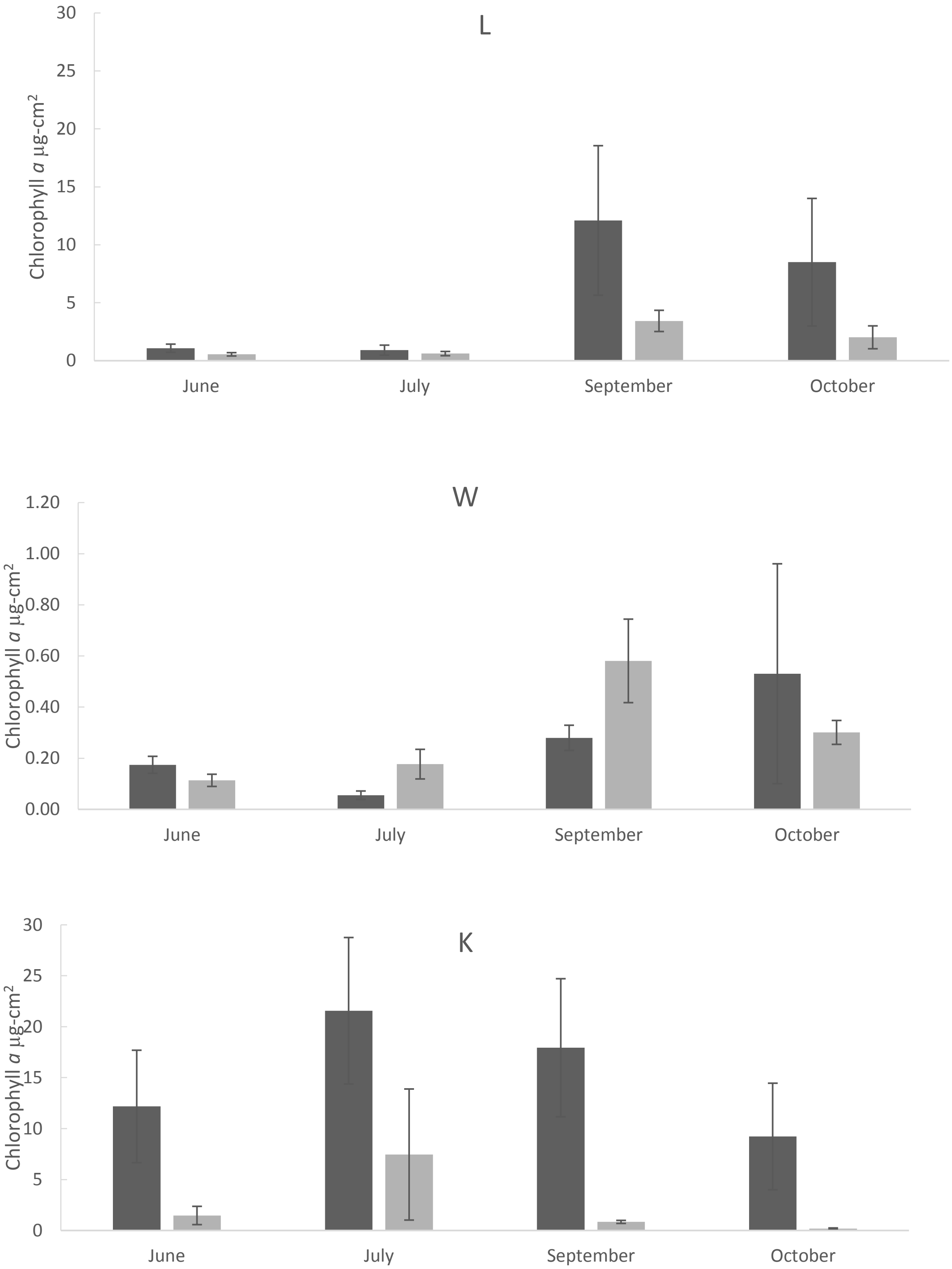


Figure 4.29. Chlorophyll *a* results of perennial and rewetted sites on the Lambourn (L), Winterbourne (W) and the Kennet (K) ± 1 SE. Please note that the Winterbourne scale differs to the other two streams.

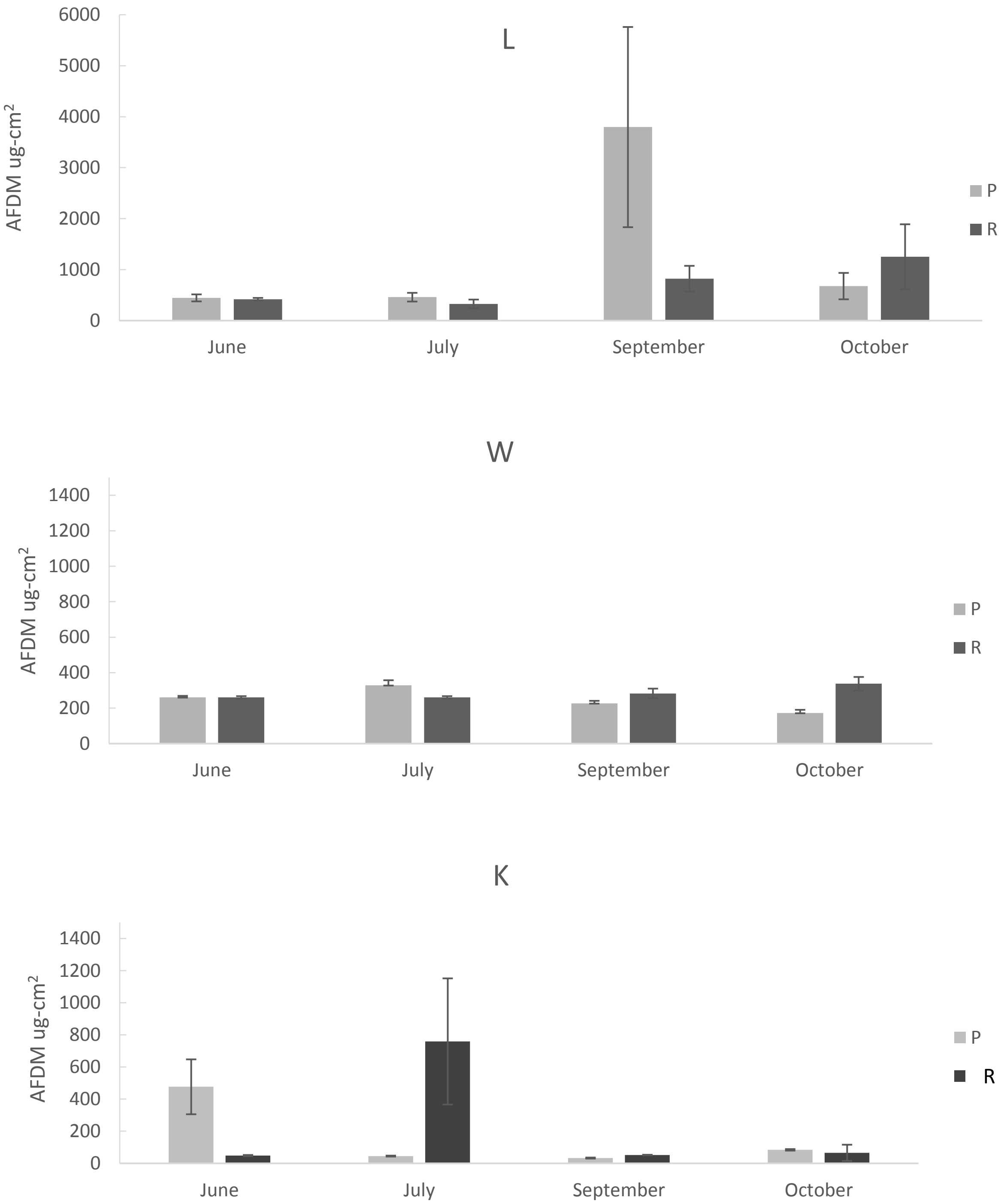


Figure 4.30. Ash Free Dry Mass (AFDM) of perennial and rewetted sites on the Lambourn (L), Winterbourne (W) and Kennet (K) ± 1 SE note that the River Lambourn is on a separate scale.

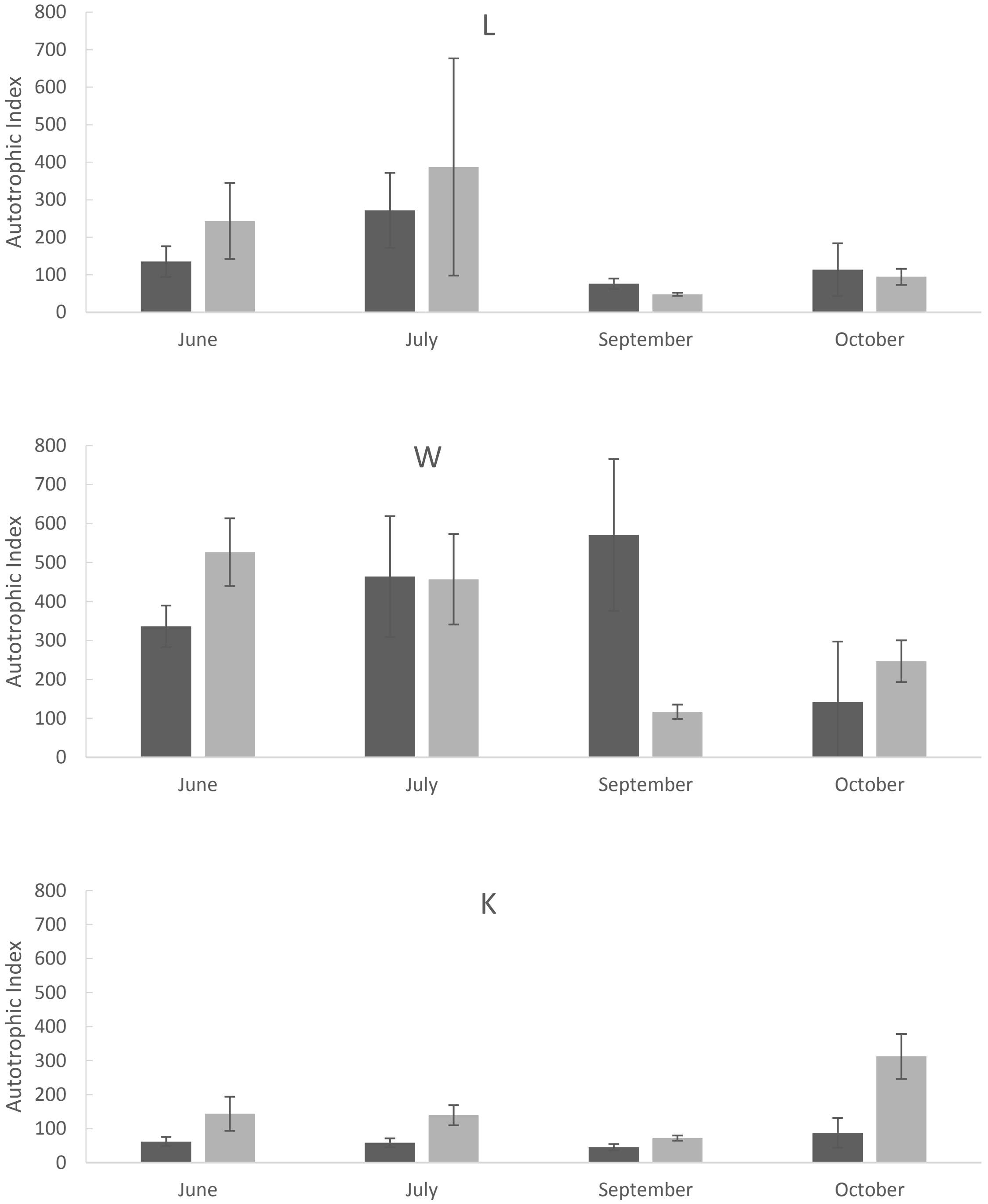


Figure 4.31. Autotrophic Index of perennial and rewetted sites of the Lambourn (L), Winterbourne (W) and Kennet (K) streams ± 1 SE.

4.4 Discussion

The taxonomic composition of the rewetted sites in the first month differed significantly from the perennial sites in all three streams (H_1). Although becoming more similar in the following months communities generally stayed distinct (H_2). The total biomass and densities of macroinvertebrates in June were variable in the rewetted sites and so we cannot accept H_3 in this case there wasn't consistent high biomass in the first month. Functional feeding groups present in June in the rewetted site varied greatly from that of the dewatered site and so we can accept H_4 as the differences were greatest in this month between perennial and rewetted site.

Functional feeding groups (FFG) were predicted to differ most in the rewetting month and this was realised (H_4), each stream had a dissimilar macroinvertebrate community in the rewetted and perennial sites in June. The rewetted sites in each stream had a unique composition of functional feeding groups, this signifies unpredictable functioning of the river in the rewetting month as each site had a unique FFG composition. By July the rewetted sites generally matched the perennial sites in the dominant FFG indicating functional recovery. Although no other studies have examined functional feeding groups in macroinvertebrate recovery in the UK, studies in other countries such as Spain found changes in traits such as body size in rewetted areas (Griswold et al., 2008) and similar results have been found in Australia (Chessman, 2015) more traits could be looked at in future droughts to determine the functioning of the overall habitat.

The rewetted sites in this study were assumed to have less refuges, unfortunately the sites were not thoroughly investigated prior to rewetting to determine the exact status of residual pools. The presence in the first few weeks at the River Lambourn of *Ancylus fluviatilis* which has the ability to respire outside of the water (Davis, 1971) and several leech species which are both taxa associated with slow flows (Dunbar et al., 2010) suggest pools may have been present. In addition most individuals were adults, suggesting resistance to drought through survival in pools. No examples of resistance to drought were found in the other two streams. Species which survive the drought through resistance have been observed to characterise the rewetting macroinvertebrate community (Chester and Robson, 2011), however resistance to drought is rare outside of arid streams (Boersma et al., 2014) and studies have found resilience to be the most important characteristic in determining post-disturbance communities (Fritz and Dodds, 2004; Beche et al., 2009). Chessman (2015) found that the first month after rewetting had a shift in macroinvertebrate assemblage which was not similar to during-drought assemblages, meaning it was a unique community which had recolonised showing that rewetting is a unique disturbance. Resilience was important for the initial rewetting period with many of the returning taxa such as Chironomidae and Oligochaeta being characteristic of pioneer taxa, this is similar to Griswold et al. (2008) who found small short-lived species were the first to recolonise, taxa such as Simuliidae, Chironomidae, Oligocheata and Ostracoda were prevalent in the first month after rewetting, this is similar to the disturbance taxa found during the drought (Section 3.3).

It is noted that there are drawbacks to the statistical analysis of the FFG and family data. Firstly, time was not accounted for. This was due to data having a high number of zero values which skewed the data heavily and data transformation attempts were unsuccessful.

Available methods to analyse time data only worked for parametric data and hence could not be used on this occasion. The drawbacks to this are that the BACI design of the data was unable to be analysed fully and differences between sites through time therefore cannot be assessed for statistical significance, however visual analysis of figures does show differences to an extent. Secondly replicates of site and river can be argued to be psuedoreplicates due to the connected nature of the river system (as seen in chapter 2) it is understood that this adds a source of covariation to the design of the experiments and this was dealt with as much as possible by nesting site into river in statistical analysis.

The macroinvertebrate community at the rewetted site becoming more distinct from the perennial site in October at the River Lambourn may be due to the sites still being at an early stage in the recovery cycle with few long-lived species present. In the Winterbourne Stream and River Kennet the perennial site is the one seen differing in September and October and the families which were driving these differences include many disturbance intolerant examples such as Caenidae, Baetidae, Goeridae and Glossosomatidae which were all also families which indicate a clean stream. Other studies have shown recovery of less resistant species can take two years (Wood and Petts, 1999; Wood and Armitage, 2004; Lake, 2011) and so perhaps the rewetted sites recovered enough species to be similar in the summer months, but not the autumn fauna such as returning riverflies (stoneflies, caddisflies and mayflies) which lay eggs in late spring or summer when the rewetted sites may have been dry or in initial stages of recovery (Wright, 1992). It is noted that these disparities could be due to site differences and it is not expected that perennial and rewetted sites will ever have identical communities. Patterns of family biomass were distinct across all months, however there were fewer differences from August onwards, showing the macroinvertebrate community was stabilising. The higher biomass of pioneer taxa, such as Oligochaeta and Chironomidae at the rewetted sites in June, indicates rapid colonization at these sites. By July biomass of these families was similar to the perennial site indicating successional processes. However families not associated with disturbance such as Leuctridae, Goeridae and Leptophlebiidae were still absent from rewetted sites for many months, similarly, Boulton (2003) found that free-living caddis and stoneflies had a delayed return after drought in Australian streams.

The dewatering sites studied during drought disturbance (Chapter 3) indicated more numerous pioneer taxa during the drought than this chapter has found during recovery. Recovery of biomass of macroinvertebrates was very rapid after drought suggesting that the community had resilient traits. Complete drying removes most macroinvertebrate species from the stream and is a major disturbance, however after rewetting further disturbance is not a major feature as species recovery is rapid and contains less stress-tolerant taxa than low-flowing areas during drought.

In most cases the highest biomass families matched with the highest biomass functional feeding group (FG), for example in the Lambourn in July and August the family with the highest biomass is Gammaridae which is a shredder and shredder is the FFG with highest biomass, however in June in the rewetted site the most numerous family is Chironomidae which are a mixture of predators and scrapers, however the highest biomass in the FFG is scraper. As the Chironomidae are several FFG's, this meant that the second most numerous family Gammaridae characterised the function rather than the Chironomidae. Similarly in July in the River Kennet the rewetted site has the family Oligochaeta in the highest biomass which is a deposit feeder, but filter feeders are the FFG with the highest biomass. In this case it must be a combination of families such as Ostracoda and Simuliidae which add up to become a higher biomass than the Oligochaeta which is the only deposit feeder found in that site that month. This showed why looking at FFG's can help determine the functioning of a recovering stream, if it had been assumed that the most numerous families determined the function we may have missed some vital information.

The rapid recovery of algal biomass with biomass equal or exceeding that of the perennial sites shown in both chlorophyll *a* and ash free dry mass measurements would provide food sources for grazing invertebrates and fish in the rewetted streams and all sites supported scrapers present in June. The River Lambourn and Winterbourne stream show no difference between perennial and rewetted sites in either chlorophyll *a* or ash free dry mass from June onwards indicating algal recovery. The River Kennet had a mixed response with the perennial site having a higher biomass of algae (both chlorophyll *a* and ash free dry mass) in June and the rewetted site having a peak in July. After this both sites have similar biomass of algae which is lower than the biomass seen in June and July. Scrapers were found in all sites in June, therefore the algal recovery allowed the recovery of the scraper functional feeding group.

The rewetted and dewatering sites had little differences in velocities in any month, so differences in macroinvertebrates and algae between these sites is unlikely to be caused by differences in flow. There were limitations to this study including a lack of algal taxonomic data which may have characterised the recovery. Filamentous algae dominated the benthos in the rewetting site in the river Kennet (Chapter 2), filamentous algae is often associated with slow flowing areas (Hart et al., 2013; Power et al., 2008) and as the rewetted site on the Kennet had the least discharge of the study these factors were likely linked.

4.4.1 Conclusions

Recovery was rapid following complete drying in the three chalk streams investigated. Algal and macroinvertebrate biomass reached similar levels as the perennial site within the same month as rewetting. The community of macroinvertebrates appeared different between rewetted and perennial sites in the rewetted month, rewetted sites being characterised by pioneer species. By July, one month after rewetting, biomass of macroinvertebrate communities and functional feeding groups were comparable to perennial sites. There was a disparity as the autumn months appear where perennial sites have a change in macroinvertebrate community, characterised by families of mayflies, caddisflies and beetles which are longer-lived species. Therefore the initial recolonisation occurred rapidly, but may take two years for longer-lived species to recolonise and communities to recover completely.

4.5 References

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CHAPTER 5

DROUGHT AND GRAZING: AN IN-SITU EXPERIMENT DURING A SUPRA-SEASONAL DROUGHT.

5.1 Introduction

Changing hydrology during drought will have ecological effects (Lake, 2003; Poff and Zimmerman, 2010, Watts et al., 2015). The ecological impacts of past droughts on UK river systems have been previously studied (Wright et al., 1982; Wright and Symes, 1999; Wood et al., 2000). These studies are typically opportunistic commencing when drought has already become established with no control for comparison. The south east of England has a warmer climate and lower mean rainfall than other regions of the UK (Perry and Hollis, 2005) as well as the highest population (Office for National Statistics, 2011), this increases the pressure on water resources and availability aggravating natural drought (IPCC, 2007).

Ecosystem functioning describes ecosystem processes such as respiration, nutrient uptake and resource consumption (Reiss et al., 2009). Ecosystem functioning is tightly linked to species diversity (Hooper et al., 2005; Ives and Carpenter, 2007; Hector and Bagchi, 2007). Unless there is functional redundancy in the biotic community at a site, local extinctions due to drought will affect ecosystem functioning (Walker, 1992). Hence individual species' resistance to drought will determine the continued functioning of the ecosystem in the early stages of drought. In dewatered areas, species resilience will shape the invertebrate community following cessation of the drought (Acuna et al., 2005).

Without functional redundancy, species loss can influence ecosystem functioning by altering the food web.   For example, in Panamanian tropical streams, the year following the loss of amphibians from the food web due to disease, algal consumption by insect grazers increased from 81% to 94% of total consumption (Colon-Gaud et al., 2010), indicating some degree of redundancy in grazing function, as when the tadpoles were lost, insects consumed more. A subsequent longer term study from 2006 until 2014 found large fluctuations in invertebrate species richness demonstrating that the food-web had not stabilised and that it was still in flux (Rantala et al., 2015). Invertebrate species richness decreased over the 6 year study period and algal biomass increased showing long-term effects of the loss of grazing species. If some species are more resilient than others and recover more quickly after drought, they will shape community structure, and these early pioneers may affect the functioning of the ecosystem. Most studies of recovery after drought indicate a high abundance of pioneer species, such as Chironomidae and Ceratopogoniidae larvae (Extence, 1981; Acuna et al., 2005), but our understanding of the functioning of the ecosystems during the recovery phase is limited.

5.1.1 Algae

The role of periphyton in the food webs of river systems is complex. Algae have a higher nutritional value than other plant derived material, such as detritus (Lamberti, 1996), which makes it a valuable food source. Some grazing invertebrates feed almost exclusively on algal resources (Feminella and Hawkins, 1995), but these can vary in their quality (Honeyfield and Maloney, 2015). Changes in algal communities during and after drought (Ledger et al., 2008) has consequences for the invertebrate grazers by altering the food quantity and quality available to grazers and influences their survival, growth and reproduction.

In addition to grazing rates, nutrients, flow, water temperature and light levels in the environment can greatly affect the biomass and taxonomy of algal biofilms (Denicola, 1996; Borchardt, 1996; Hill, 1996; Bowes et al., 2012). Rosemond et al. (1993) found the most grazed algal species can respond more quickly to increased nutrients, a trade-off between vulnerability to grazing and growth rates. The relationship between algae and nutrients can vary, as an increase in phosphorus levels can lead to an increase in filamentous green algae (Oberholster et al., 2013) although this is not always the case (Welch et al., 1988; Nelson et al., 2013). This may result from other limitations e.g. nitrogen or light (Bowes et al., 2012). Townsend et al. (2012) found higher flows lead to higher uptake of nutrients, although in slower flows there will be less sloughing of algae and thus algal biomass may remain relatively unchanged. The algal quality however may differ, with less sloughing more dead material and mineral contents may accumulate which may be of little nutritional value to invertebrates. Therefore it is likely that biofilms in fast flowing areas have a higher nutritional content.

The nutrient input during drought is discontinuous depending on precipitation levels. In general streams receive less organic carbon due to lower stream metabolism in low flow conditions, and less nitrogen, favouring nitrogen fixing organisms such as cyanobacteria (Dahm et al., 2003). Changes in flow levels can have a strong effect on how algae grow and absorb nutrients. Biggs (2000) found that the number of days of accrual drove algal biomass, and high flows scoured the rocks which stopped accrual. Ledger and Hildrew (2001) found that algae could survive drying for at least nine weeks on rocks during drought and then recolonise the area once water returned, however if the rocks were scoured by high flows the surviving algae were removed. Poff et al. (1990) found in in-situ mesocosms in Colorado River, USA that a filamentous green algae *Ulothrix zonata* was the first species of algae to colonise after drying and remained dominant for two weeks in all tested flow velocities, the diversity of algae then increased with diatoms becoming dominant a month after the experiment started. This could imply that filamentous green algae are acting as pioneer species with a mixture of diatoms being the climax community. In New Zealand, Suren et al. (2003) looked at two rivers one of which was oligotrophic and the other eutrophic. In the eutrophic river low flows resulted in dominance by the filamentous algae *Cladophora* whereas in the oligotrophic river low flows resulted in little change to the diatom dominated algal community. This suggests that the algal community in rivers with high nutrient availability will change and become dominated by filamentous algae during drought. Wellnitz and Rader (2003) also found changes in algal communities in scoured and non-scoured tiles in an experimental set up, the scoured tiles were dominated by cyanobacteria and chrysophytes (yellow/brown algae) where non-scoured tiles were dominated by diatoms. Although filamentous algae were absent from the system, the change in communities was similar to that in Suren et al. (2003) in that non-scoured communities tend to be dominated by diatoms.

The link between numbers of grazing macroinvertebrates and filamentous algae has also been shown by Power et al. (2008). In this study a long term data set was used to study algae, macroinvertebrates and fish communities during floods and droughts, with additional grazing experiments. In years where there were high spates in winter, which led to the scouring of the rocks, the following summer showed high growth of *Cladophora* algae, whereas in low flow winters the following summer had lower levels of *Cladophora*. The only anomalies were years where high numbers of steelhead trout consumed a high proportion of the algal grazers post-flood. Coupled with reductions in abundance by the flood, low abundance of grazers allowed prolific growth of algae. Therefore the relationship between filamentous algae and flow can be at least partly mediated by the abundance and diversity of macroinvertebrate grazers. Often droughts are followed by high flows (Lake, 2003; Parry et al., 2013), thus scouring is likely, and it is probable that the algal community has to recolonise from other sources such as other streams after drought. Increased nutrient input and low invertebrate abundance post-drought could select for an algal community dominated by filamentous algae.

If drought affects the structure of the algal assemblage then this will cause a bottom-up effect in the food web, in addition to the potential top-down effects caused by changes in macroinvertebrate community (Dahm et al., 2003; Ledger et al., 2013). Grazers would be directly affected by food availability and this would then affect all trophic levels (Osenberg and Mittelbach, 1996). Robson et al. (2008) found that the recovery of algal species in seasonally flowing streams in Australia is mediated by the use of refuges such as perennial pools during the drought. Robson et al.'s study was carried out in streams which suffer drought regularly and therefore the species living there are resistant to drought. The chalk streams in the UK are usually winterbourne, this means there is scope for algae to be adapted to a seasonal environment, however it is unknown if more frequent or a-seasonal droughts will entail the loss of the less resistant species. Ledger et al. (2008) found that frequent drought disturbance caused the community structure of algae to change from a dominance of crust-forming green algae to mat-forming diatoms. If rivers in the UK are predicted to become more prone to droughts and floods they may become more similar to rivers found in a

Mediterranean climate where these extremes in hydrology are typical (Acuna et al., 2005; Gaudes et al., 2010; Chester and Robson, 2011).

5.1.2 Grazers

Grazing is one of the main controls on algal biomass, it can lead to selection for certain types or species of algae due to grazing preferences and grazer density. Most studies report that if grazing levels are high, edible algal biomass will decrease and resistant algal biomass will increase (Hill and Knight, 1987; Lowe and Hunter, 1988; Kjeldsen, 1996), however the process of grazing can increase the growth rates of some algae (Agrawal, 1998). Aberle et al. (2009) used isotope labelling as well as cell counts in a grazing experiment with two invertebrate species, the aim was to determine strategies and selective resource use by grazers which could lead to co-existence. The assimilation of the algae by the two species was similar in single species treatments, but when together, one species assimilated algae more efficiently indicating that competition can not only affect grazing rates, but also the mechanisms by which animals digest food. If competition can alter physiological processes, such as digestion, the fitness of one species may rely on its coexistence with other species. Therefore there may be no such thing as functional redundancy as species may need to co-occur to deliver the ecosystem functioning to its fullest.

There have been studies of grazing function under experimental conditions, but there has not yet been a study of grazing function during an actual drought in the UK. An in-situ experiment was conducted using grazed and ungrazed tiles examining the levels of algal grazing in three streams during and following drought conditions. Within each stream three conditions were identified; (1) dry during drought and rewetted (2) in the dewatering phase and (3) perennial as a control site uninfluenced by drying. The aim of this study was to determine if grazing function can recover following a drought and the temporal scale of recovery. Two hypotheses were tested (H_1) grazing function will return to pre-drought levels when macroinvertebrate biomass recovers and (H_2) the quality and quantity of algae will be high post drought due to increased nutrients.

5.2 Methods

5.2.1 Study Site

A total of nine sites were selected within three chalk streams to represent differences in flow permanence in April 2012 (Table 5.1 & Chapter 2 Figure 2.1) perennial with no risk of drying, 2) dewatering i.e. in the process of drying out and 3) dry at the beginning of the study and rewetted once drought broke (Table 5..1).

Table 5.1. Site names and dewatering status.

Site Type	River Lambourn	River Kennet	Winterbourne Stream
Perennial	Boxford	Axford	Bagnor
Dewatering	East Shefford	Marlborough College	Honeybottom
Rewetted	U/S Great Shefford	Clatford	Shepherds Copse

5.2.2 Algae Rock Scrapes

Rock scrapes were collected monthly from April 2012 to October 2012 except August to compare tile algal growth to that on natural rocks. Method described in 3:2.5 which were also used to show algal biomass in chapter and chapter 4.

5.2.3 Tile Sampling

An in-situ experiment was undertaken three times in 2012 (May, July and September). Two 94 mm x 94 mm tiles were secured onto an engineering brick as an experimental grazing platform. The edges of one of the tiles of the pair were covered in Vaseline to deter grazing macroinvertebrates (McAuliffe, 1984). Five of these experimental grazing platforms were placed at each site, a minimum of 0.5 m apart at random points across the stream width, secured with a metal pole inserted into the substrate. After four weeks the bricks were recovered from the river and algal growth on the tiles was scraped into separate sterile bottles using toothbrushes, water and a funnel and preserved as previously described in section 3.2.5.

Chlorophyll *a* Analysis and Ash Free Dry Mass (AFDM)

Algal samples were analysed to determine the amount of chlorophyll present (i.e. the amount of algae) and the AFDM of the sampled biofilm

Method described in Chapter 3:2:5 (American Public Health Association, 2005).

5.2.4 Autotrophic Index

The autotrophic index (AI), an indicator of biofilm quality (Collins and Weber, 1978; American Public Health Association, 2005), was calculated by dividing the total AFDM µg-cm^2 by Chlorophyll *a* µg-cm^2 full method described in 3:2:6. Numbers over 400 are considered to be poor quality and usually are from rivers with high nutrient load.

5.2.5 Chemistry Data

Water samples were taken weekly from Boxford on the River Lambourn (the perennial site in this study) and Woolhampton on the River Kennet downstream of the in-situ experimental sites. The following parameters were determined; soluble reactive phosphorus and nitrate (NO3) as bio-available forms of the nutrients, chlorophyll *a* as the amount of phytoplanktonic algae in the river and boron (B) as an indicator of sewage treatment effluent (Neal et al., 2000).

5.2.6 Statistical Analyses

Chlorophyll *a* data for grazed and ungrazed sites were tested for normality. Despite being small samples the data showed a mostly normal distribution. Equal variances are shown with the probability plots (figure 5.1), shapiro-wilk tests show P values of over 0.05 for all confirming likely normal distribution Boxplots showed two outliers one in the grazed data in the Lambourn rewetted site and one in ungrazed dewatering site in ungrazed data (figure 5.2). Analyses were completed with and without outliers and no difference was found in result so it was decided to keep the outliers in the data set for analyses. Histograms show a close to normal distribution of data (figure 5.3).

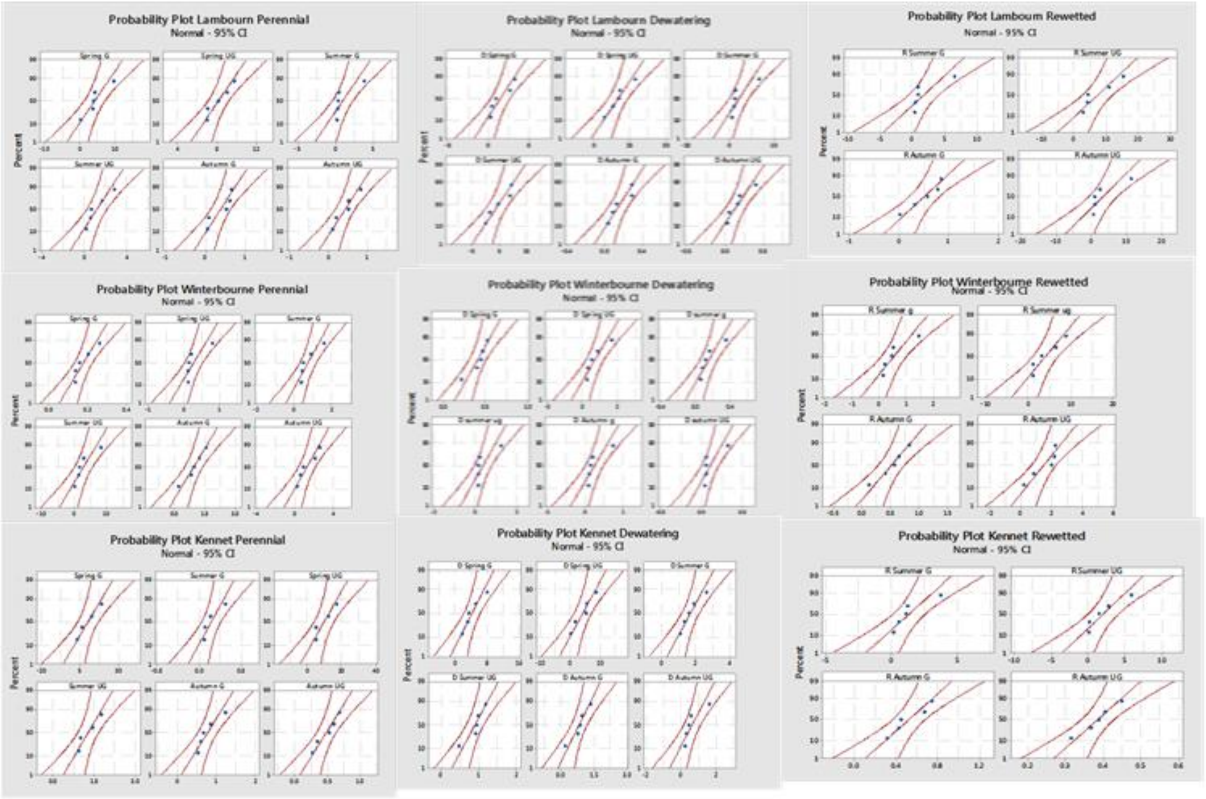

Figure 5.1. Probability plots of chlorophyll *a* data in the river Lambourn, Winterbourne stream and the River Kennet perennial (a), dewatering (b) and rewetted (c) sites. All sets of data had a p value of >0.05 in Shapiro-wilks test.

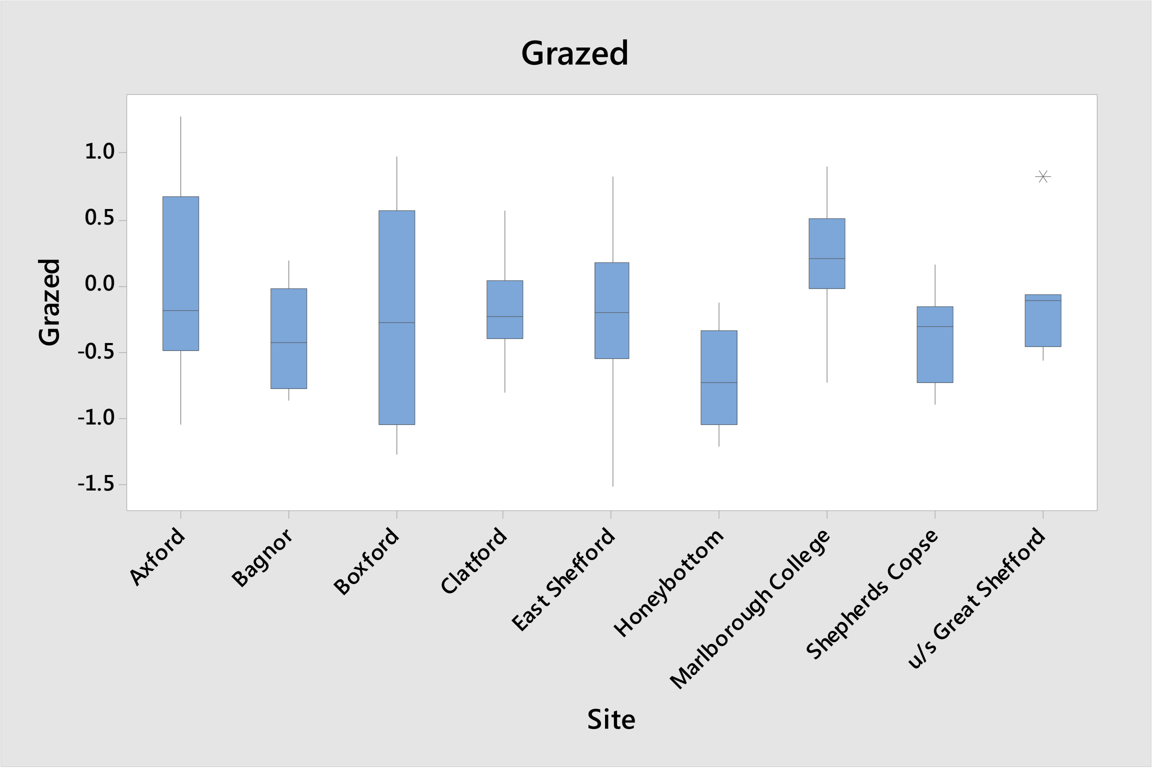

Figure 5.2. Boxplots of grazed and ungrazed data separated by site.

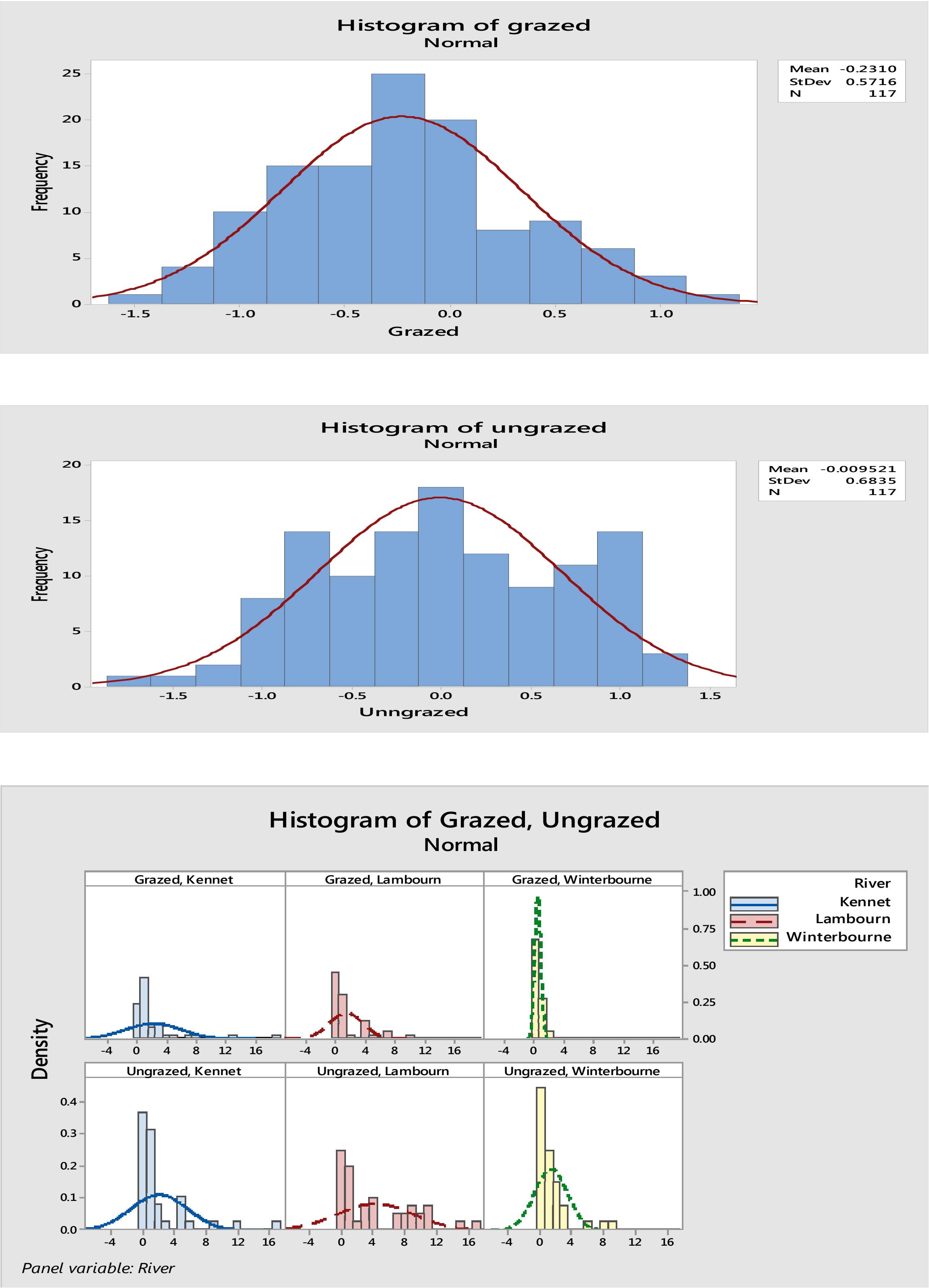

Figure 5.3. Histograms of grazed and ungrazed chlorophyll *a* data from all sites combined and each site and grazing status separately.

Paired T tests were chosen to use on the chlorophyll *a* and the AI data were used to compare the grazed vs ungrazed treatments because grazed and ungrazed tiles for each replicate were geographically paired. Kruskal-Wallis tests compared the stone scrapes and ungrazed tiles, to determine if one month of growth led to the natural level of algal biomass. Stonescrape data showed some non-normal characteristics due to some extreme values, therefore non-parametric tests were chosen for the analysis, three separate Kruskal-Wallis tests were carried out on stone scrape data, comparing chlorophyll *a* data between dates, river and site condition (Perennial control, Dewatering and Rewetted). Differences in Chlorophyll *a* concentration between grazed vs ungrazed tiles were tested using a Kruskal Wallis test with Chlorophyll *a* as the response and grazing status as the fixed factor, it was also tested for interactions between site and grazing status. Tests were carried out in Minitab 16® and R 2.3.0. All tests used the 95% confidence interval.

Grazing rates were determined by subtracting the chlorophyll *a* levels of the grazed tile from the ungrazed tile. This value was then divided by the number of degree days to determine daily grazing rate (McMaster and Wilhelm, 1997). If a negative result was found no grazing was assumed and the result changed to a zero.

5.3 Results

5.3.1 Grazing Rates

Tiles removed from the perennial site on the River Lambourn in the summer are shown in Figure 5.4, there was visibly more algae present on the ungrazed tiles and this algae was diatomous and not filamentous. A similar pattern was found at the Winterbourne dewatering site with clear visual differences between tiles (Figure 5.5). Figure 5.6 showed that at the Kennet rewetted site, the differences in algal biomass between tiles were harder to establish and filamentous algae were abundant.

Chlorophyll *a* levels were significantly different between grazed and ungrazed tiles in spring (ANOVA, $F = 4.97$, $DF = 1$, $p<0.05$) and summer (ANOVA, $F=11.97$, $DF=1$, $p<0.01$), and was not significant in autumn (ANOVA, $p>0.05$). Grazing rate significantly differed between sample dates and between rivers, but differences between sites statuses were not significant (Table 5.2). In all streams grazing occurred in the rewetted sites in summer (Figure 5.7) and in the Lambourn and Winterbourne this was also the case in the autumn (Figure 5.7). There was a grazing peak in spring and summer in the dewatering sites in Lambourn and Winterbourne reducing in the autumn, compared to the perennial site which peaked earlier in spring in the Lambourn and summer in the Winterbourne (Figure 5.7). The River Kennet did not follow these patterns, as the perennial site showed a slightly higher grazing rate in the summer than in spring and then no grazing in the autumn (Figure 5.7). The dewatering site had a slightly higher grazing rate than the perennial site in spring, and no grazing rate was detected in summer and very little in the autumn. Grazing rate in the dewatered site in the

River Kennet returned to pre-disturbance levels for this river, this was less than in the other two streams.

Figure 5.4. Two bricks removed from the Perennial Site Boxford on the River Lambourn in August 2012. The ungrazed tile is on the left.

Figure 5.5. Two bricks removed from the dewatering site Honeybottom on the Winterbourne Stream in August 2012. The ungrazed tile is on the left.

Figure 5.6. Two Bricks removed from the rewetted site on the River Kennet in August 2012. The ungrazed tile is on the left.

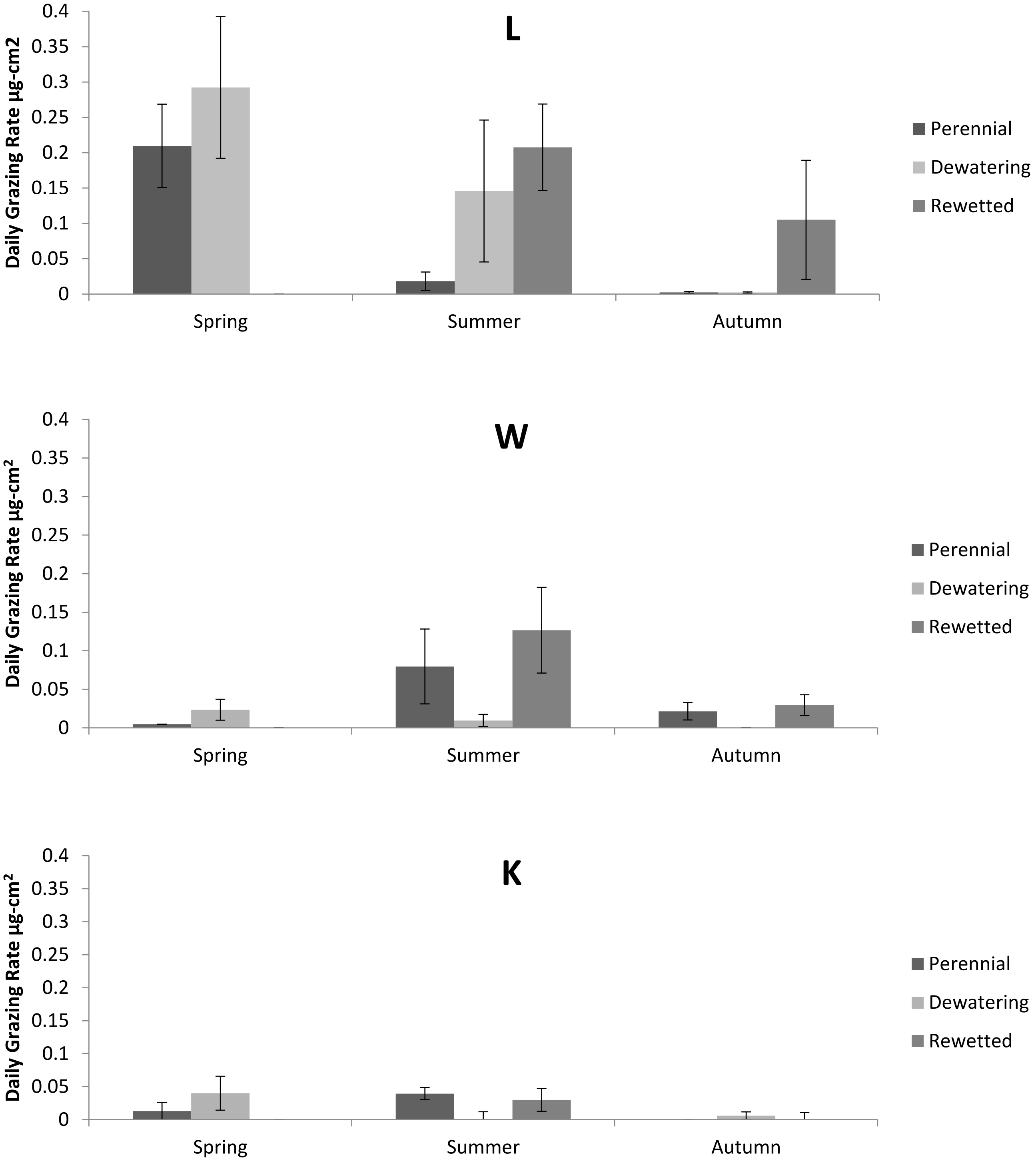

Figure 5.7. Daily Grazing Rates in the River Lambourn (L), Winterbourne Stream (W) and River Kennet (K) in perennial, dewatering and rewetted sites. No data for rewetted sites were available for spring.

Table 5.2. Kruskal Wallis tests of grazing rate (GR) or chlorophyll *a* (Chl A) data from experimental tiles tested for relationships with season, river and site status. Site type is a category of site including perennial sites, dewatering sites (during drought) and rewetted sites (sites which were dry during drought and concurrently rewetted). * = p < 0.05 and ** = p <0.01.

Test	P Value	H Value	DF
GR vs. Season	<0.01**	15.28	2
GR vs. River	<0.01**	15.77	2
GR vs. Site type	0.082	5.00	2
Chl A vs. Season	<0.01**	9.86	2
Chl A vs. River	<0.01**	16.88	2
Chl A vs. Site Type	0.931	0.14	2

5.3.2 Autotrophic Index (AI)

In the River Lambourn all sites displayed a slight or no increase in AI on the grazed tiles compared to the ungrazed tiles in spring and summer (Figure 5.8), but only spring was significant (Table 5.3). In the Winterbourne Stream (Figure 5.9), the dewatering site indicated a higher AI on the grazed tile in the summer but this was not significant, the other seasons did not follow a trend. The other sites on the Winterbourne exhibited little difference between grazed and ungrazed tiles. AI was lower in the River Kennet than the other streams (Figure 5.10), but results were not significant except in summer at Axford where grazed tiles have a higher AI.

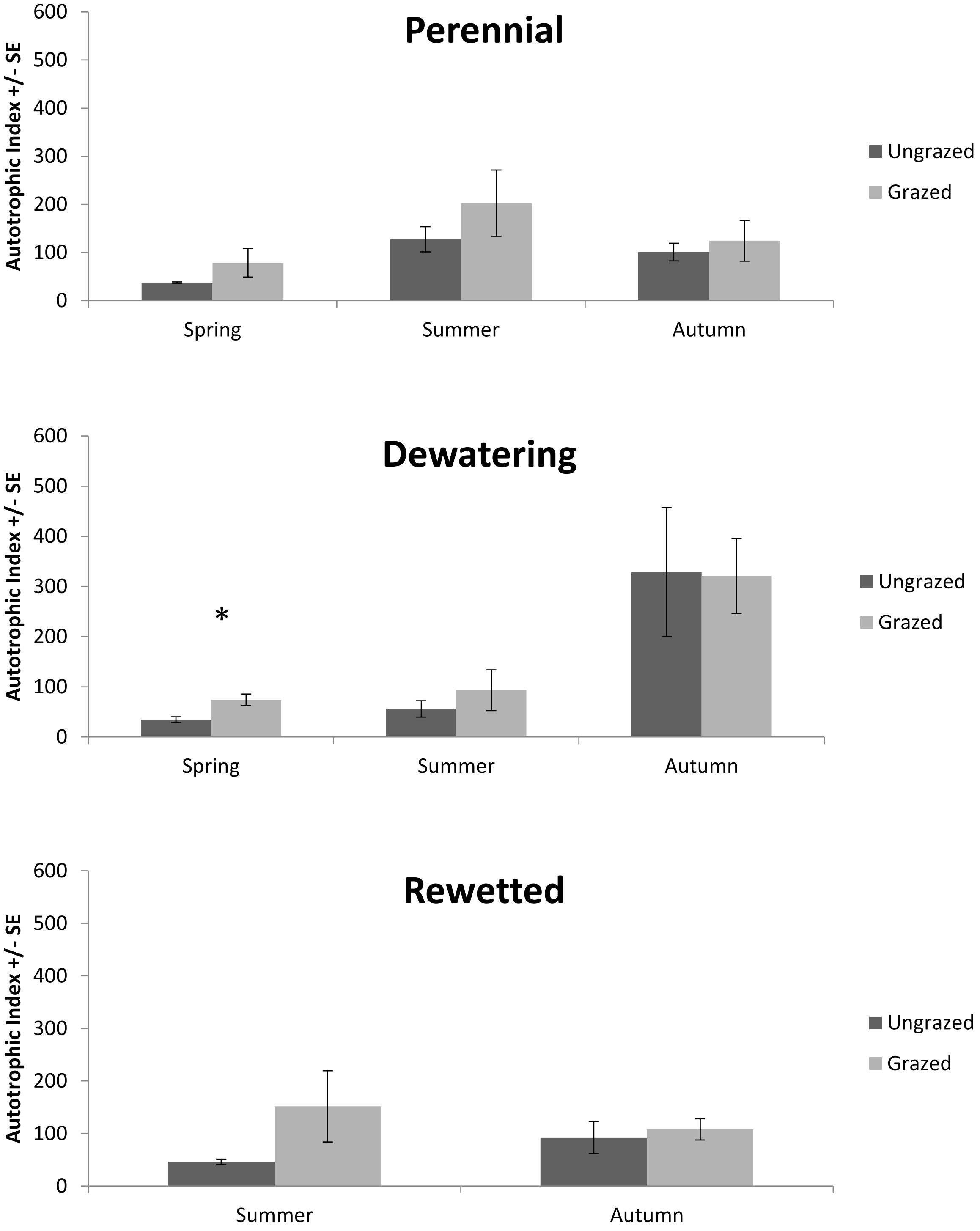

Figure 5.8. Autotrophic Index of ungrazed and grazed tiles at the three sites on the River Lambourn. Statistically significant results are marked with an asterisk (significant result of Kruskal Wallace test between AI of grazed and ungrazed River Lambourn at East Shefford in Spring T=-3.21, DF=4, p=0.033)

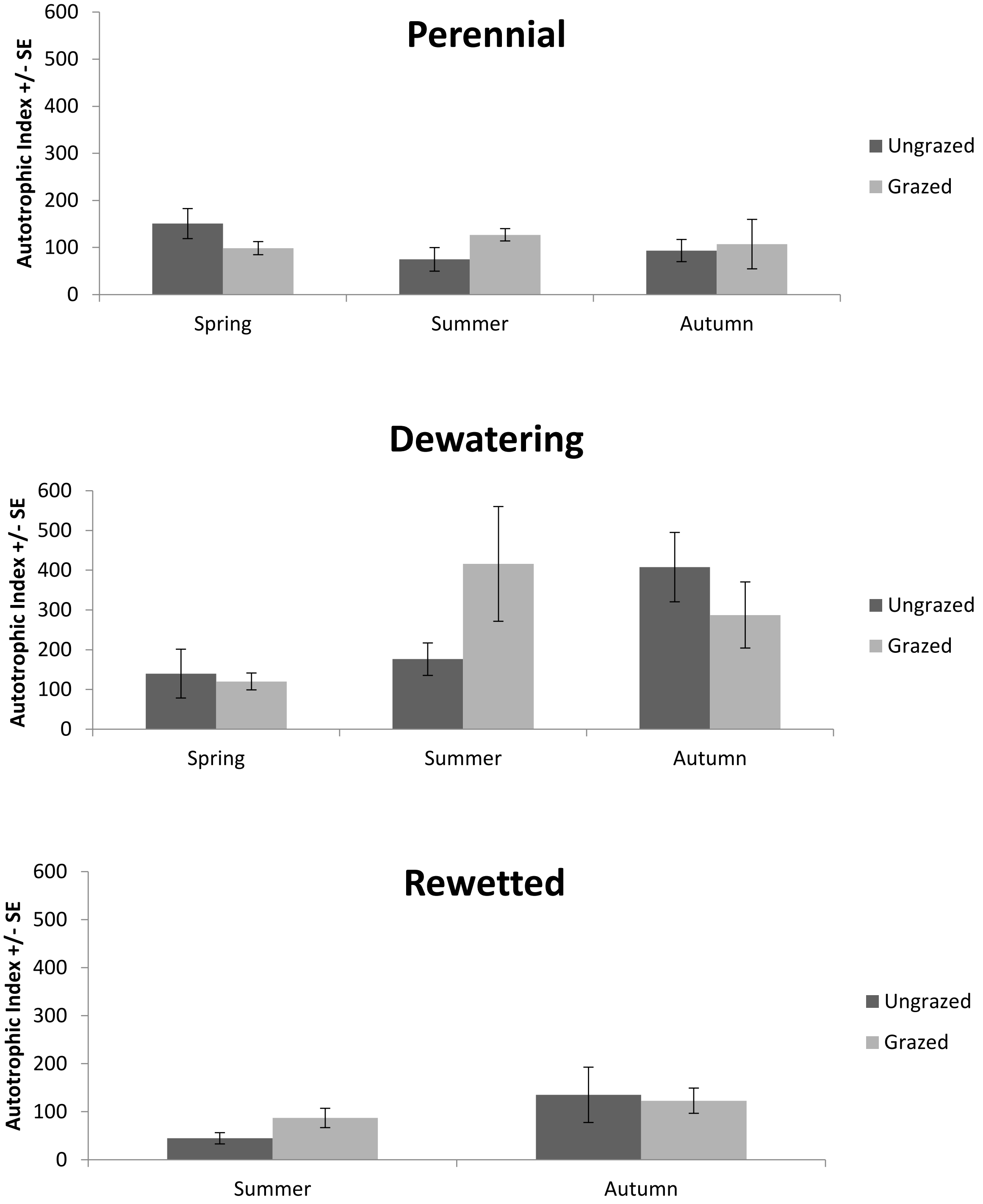

Figure 5.9. Autotrophic Index of the three sites on the Winterbourne Stream. Ungrazed and grazed tiles are shown. Statistically significant results are marked with an asterisk

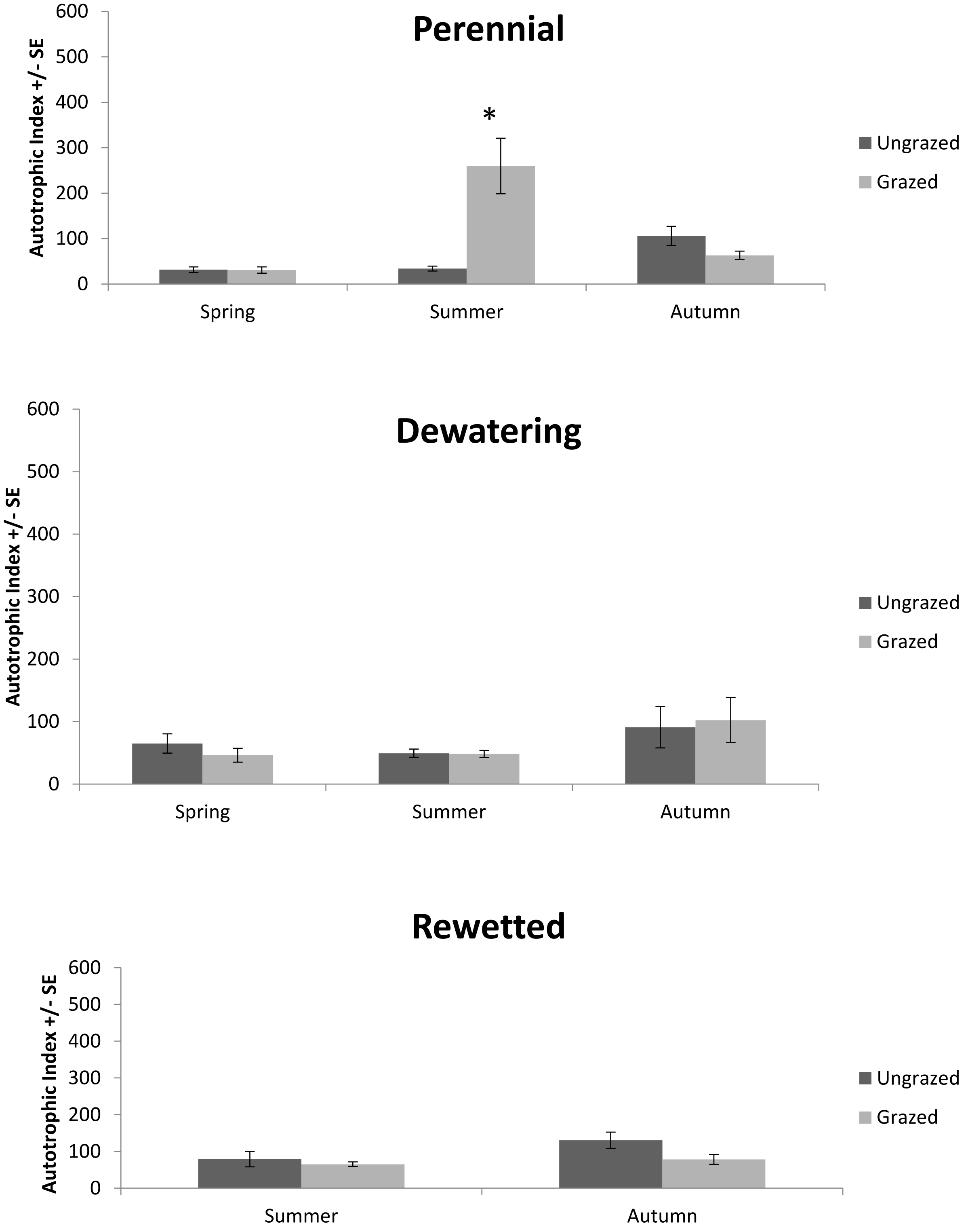

Figure 5.10. Autotrophic Index of the three sites on the River Kennet. Ungrazed and grazed tiles are shown. Statistically significant results are marked with an * (Significant result of Kruskal Wallace test between AI of grazed and ungrazed at Kennet at Axford in summer T=-3.46, DF=3 p=0.041)

5.3.3 Chlorophyll a from stone scrapes

Distinct patterns of chlorophyll *a* were evident in the three sites studied on the River Lambourn (Figure 5.11). The highest levels of chlorophyll *a* were found at the perennial site in April and May, falling in the months of June and July and rising again in September before decreasing again in October. The dewatering site showed an alternating pattern with the highest values of chlorophyll *a* found in June and July and levels falling in September. Chlorophyll *a* at the rewetted site (wet at the end of May) exhibited a slow increase from June until September with the levels falling again in October. The patterns were similar in the Winterbourne Stream (Figure 5.11) but with a much smaller mass of algae.

The River Kennet does not follow the same pattern as the River Lambourn and Winterbourne Stream (Figure 5.11). A peak of chlorophyll *a* concentration occurred in the summer at the perennial site, and at the dewatering site in the autumn. Chlorophyll *a* peaked at the rewetted site in the summer followed by a sharp decline. Values were higher than the River Lambourn, (Figure 5.11 & Table 5.3) and displayed different patterns. The site with the most permanent flow, Axford, showed a peak in chlorophyll *a* concentration in July with a slow reduction after this.

Table 5.3 Results from Kruskal-Wallis tests on Chlorophyll *a* results from the stone scrapes. Season was the season the sample was taken in, either spring, summer or autumn. River was either the River Kennet, the River Lambourn of the Winterbourne Stream. Site Type refers to whether the site was perennial such as Boxford, Axford and Bagnor, dewatering such as East Shefford, Marlborough College or Honeybottom or a site which rewetted in the summer such as U/S Great Shefford, Clatford or Shepherds Copse.

Test	P Value	H Value	DF
Season	<0.05	6.60	2
River	>0.01	96.9	2
Site Type	>0.01	14.21	2

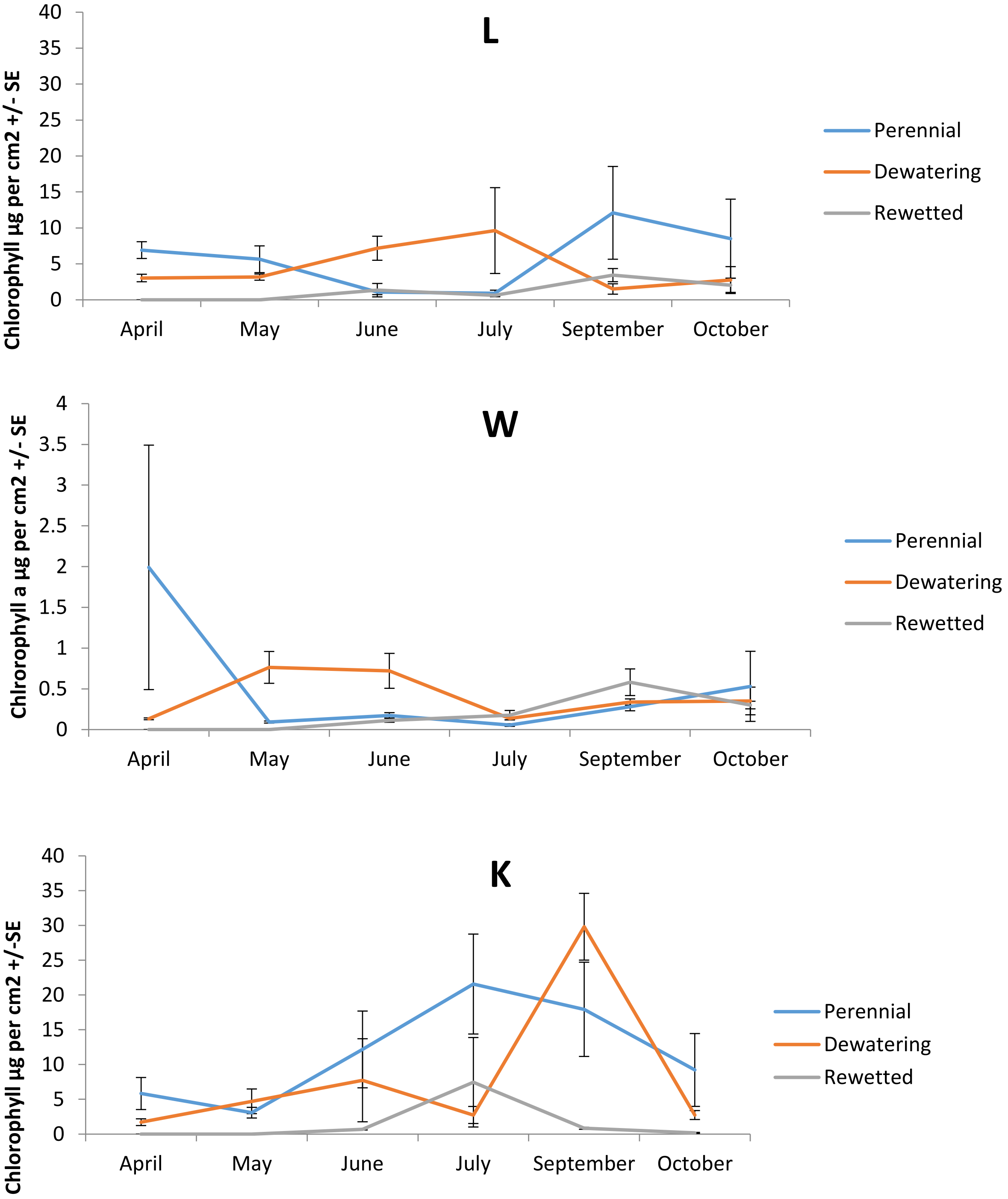

Figure 5.11. Mean chlorophyll *a* results from stone scrapes in River Lambourn (L), Winterbourne Stream (W) and River Kennet (K). Note Y axes differ.

5.3.4 Water Chemistry

Both sites in the Rivers Lambourn and Kennet showed similar patterns of chemical concentration with some notable differences (Figure 5.11 & 5.12). Boron levels remained relatively constant throughout the time period at both sites, however, the River Lambourn had levels at 13-16 µg l^{-1} while the Kennet was between 19-25 µg l^{-1}. NO3 levels also remained stable at both sites throughout, the river Lambourn between 28-35 mg l^{-1} -NO3 and the River Kennet at 18-25 m l^{-1} l-NO3. Both rivers showed a large peak in SRP in February 2012 that subsequently decreased. As boron was constant through this period, phosphorus is assumed to arise from agricultural run-off. Chlorophyll *a* showed more fluctuation in the River Kennet than in the River Lambourn, there is a delayed effect of high SRP on increasing chlorophyll *a* concentration seen most clearly in the River Kennet.

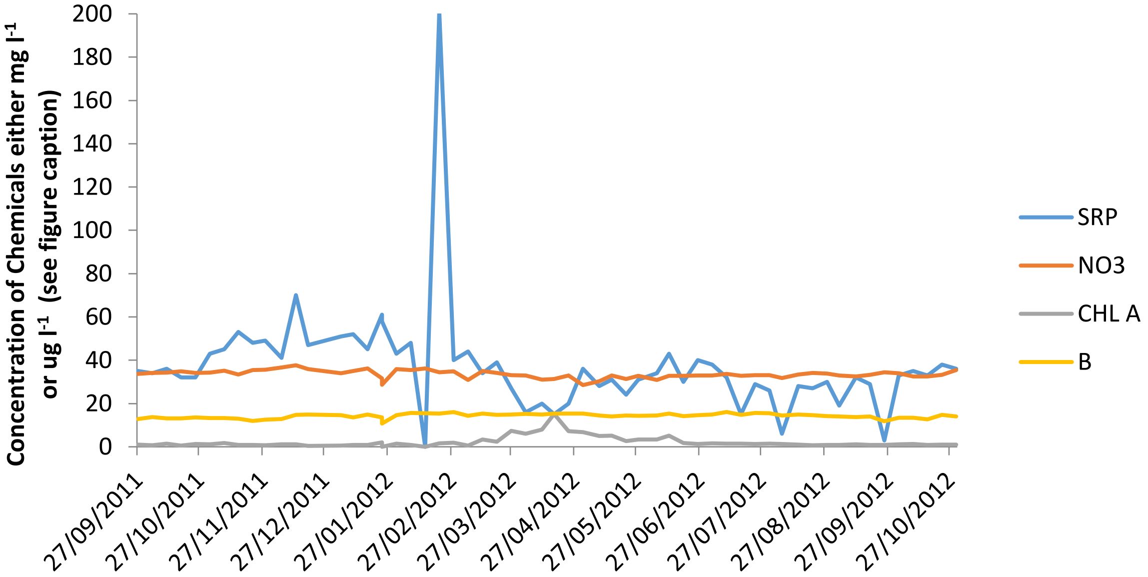

Figure 5.12. Water chemistry results of the River Lambourn at Boxford, the perennial site in this study. Chemicals shown are: bio-available soluble reactive phosphorus (SRP) in ug l^{-1} ; Nitrate (NO3) in mg/l; Chlorophyll *a* (CHL A) in ug l^{-1} and Boron (B) in ug/l. Boron is used as a tracer for sewage treatment effluent and so would show changes in inputs of nutrients from sewage treatment effluent.

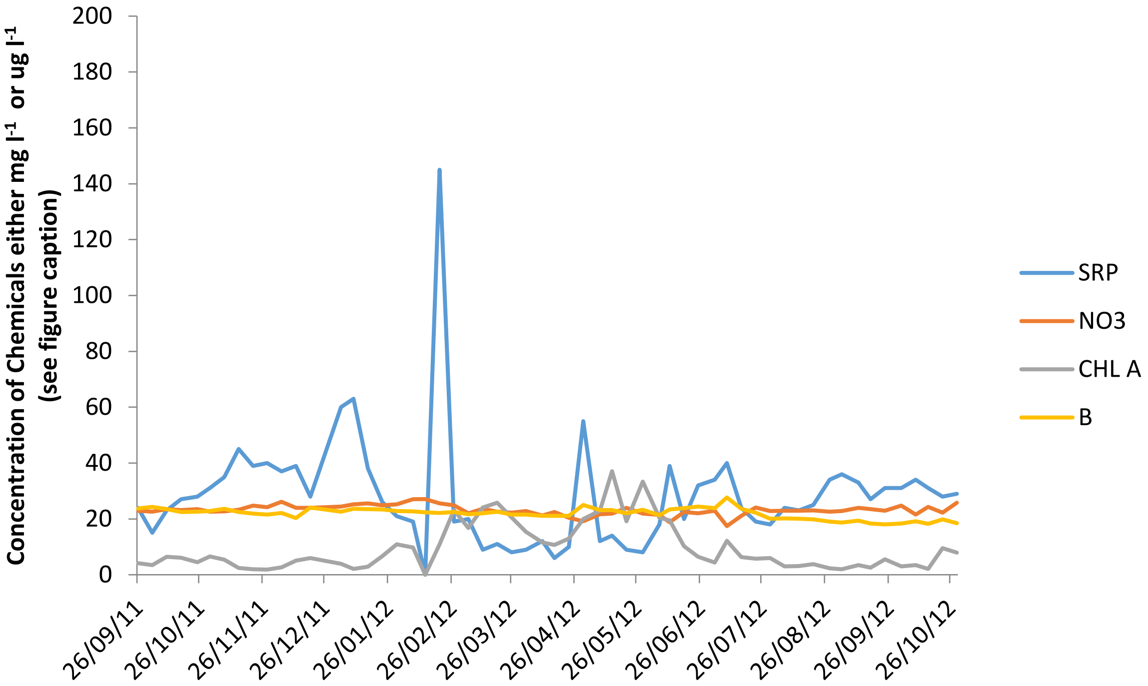

Figure 5.13. Water chemistry results of the River Kennet at Woolhampton, downstream of all sampling sites. Chemicals shown are: bio-available soluble reactive phosphorus (SRP) in µg l^{-1}; Nitrate (NO3) in mg/l; Chlorophyll *a* (CHL A) in µg l^{-1} and Boron (B) in µg l^{-1}. Boron is used as a tracer for sewage treatment effluent and so would show changes in inputs of nutrients from sewage treatment effluent.

5.4 Discussion

5.4.1 Drought recovery

Within a month of rewetting, periphyton were present at all the sites (H_2) with grazing rates equal to or exceeding those of perennial sites (H_1). This demonstrated that functional recovery was rapid, consistent with the high turnover rate of algae and the spike in nutrients documented in other studies following a drought (Ledger and Hildrew, 2001; Dahm et al., 2003).

SRP had a second peak in the River Kennet in April when heavy rain started to break the drought (the first peak likely to be a one off rainfall event). The return of grazing showed that the recovery of invertebrate abundance and biomass (Section 3.3) supported the functional recovery, despite the invertebrate community differing from the perennial sites. These findings indicate the recolonizing pioneer taxa such as Chironomidae can deliver the same level of ecosystem functioning that is driven by such groups as Ephemeridae, Ephemerellidae, Caenidae (which are all mayflies whose algal consumption is minor), Glossosomatidae and Goeridae at perennial sites. This rapid recovery of the algae and invertebrate communities ensures rapid functional recovery, at least for grazing. Other studies have found rapid invertebrate recovery (Wood and Petts, 1999; Wright and Symes, 1999; Wright et al., 2002)., however, such rapid recovery has not been observed where complete drying has occurred (Acuna et al. 2005). Boulton (2003) found that the effect of drought on invertebrates varies with the severity and longevity of the drought. Similar results are reported in Chapter 4, where invertebrate abundance returned rapidly yet invertebrate diversity and community structure took much longer to recover to pre-drought conditions. As the previous studies had not looked at function along with invertebrate identity it is not possible to know what the status of functional recovery was in these studies.

Grazing peaked in spring at perennial sites but was delayed at the dewatering and rewetted sites until the summer and autumn. The fastest colonizing invertebrates in the dewatering sites were pioneer r selected species with short life spans, fast growth rates and high fecundity. Grazing rates for pioneer species are relatively unknown, however if they do have high grazing rates it would account for the high level of grazing in the rewetted sites in summer when perennial sites had less grazing (Ely Rincon, 2010).

5.4.2 Filamentous algae in the River Kennet.

The high algal abundance, but limited grazing at the River Kennet differed to the other two streams, and can be accounted for by a number of mechanisms. The River Kennet is longer and has a larger catchment size which increased the diffuse inputs to this river (Section 2.3). Also the River Kennet is heavily abstracted (Limbrick et al., 2000), and thus lower environmental flows may exacerbate the effects of drought (Wilby et al., 2006). There are also numerous sewage treatment plants along the length of the Kennet with a large one in Marlborough (Neal et al., 2000) downstream of the rewetted and dewatering sites but upstream of the perennial site. The higher boron levels confirm that this stream has higher sewage effluent. These sewage works could be increasing nutrient levels in that part of the river, and therefore, during drought, the drop in the dilution factor may increase nutrient concentrations further. Nutrient data showed that phosphorus and nitrogen were not significantly different from the River Lambourn.

These physical and chemical changes will have an effect on the type of algae present, including potentially increasing the abundance of filamentous algae as they are known to increase in growth due to low flows and increased nutrients (Poff et al., 1990; Suren et al., 2003; Wellnitz and Rader, 2003; Power et al., 2008). Filamentous algae are more difficult for invertebrates to consume (Lamberti, 1996), and bricks from the River Kennet, supported filamentous algae on both grazed and ungrazed tiles in contrast to the Lambourn and Winterbourne. The presence of filamentous algae in the River Kennet could account for the high amount of chlorophyll *a* on the rocks scrapes, but low grazing rates (Figure 5.7). We do not have data from the rewetting period, however the end of the drought may have caused a spike in nutrients caused by rainfall washing nutrients and organic matter accumulated during the drought period into the river (Lake, 2011) encouraging the growth of filamentous algae (Oberholster et al., 2013), and delaying the recovery of invertebrate grazer species.

5.4.3 Conclusions

Overall, despite the differing results between streams there was a clear indication of recovery of ecosystem functioning. Grazing was detectable in all rewetted sites within weeks of rewetting. The speed of this recovery provides an indication that some functional was present in the stream systems as the invertebrate community differed from perennial controls (Section 3.3). This indicates that community resilience and sustainability of functional processes may offset the impacts of the predicted increase in drought severity and frequency. However, it is still unclear whether there are thresholds of drought magnitude, duration and frequency above which this functional redundancy and ecosystem resilience is lost. Pioneer species have evolved to take advantage of short-term niche vacancies, which will then be occupied by a succession of species. If there are more frequent droughts, multi-year droughts, a-seasonal droughts or droughts of increased magnitude, the natural succession process may be disrupted. This would lead to empty niche space and functional breakdown, which could compromise the integrity of the ecosystem. Further study is needed to determine the long-term consequences of this.

5.5 References

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CHAPTER 6

REDUCED FLOW AND DEWATERING EFFECTS ON MACROINVEREBRATE GRAZERS AND ALGAL BIOFILMS – AN INVESTIGATION USING MESOCOSMS

6.1 Introduction

Increasing likelihood of drought (IPCC, 2007, Environment Agency, 2011, IPCC, 2013, Watts et al., 2015) and an increasing population leads to mounting pressure on water resources through abstraction (Acreman et al., 2008), which in ground-water dependant areas could lead to reduced river flows (Haddeland et al., 2014; Hannaford, 2015). Supra-seasonal drought in streams, when caused by natural circumstances, is a ramp disturbance as it increases in severity over time (Lake, 2003; Lake, 2011). However, the ecological response to drought is characterised by distinct steps including reduction in water velocity.

The ecological effects of droughts will differ depending on its progression, the initial reduction in flow has only a minor effect on the ecology with few species losses (Bond et al., 2008), whereas complete drying has severe effects on the ecology with almost complete species loss (Boulton, 2003; Lake, 2003; Lake, 2011). The effects of initial pooling include increased macroinvertebrate densities as the habitat available to the organisms is reduced, but as the drought progresses, water quality and macroinvertebrate density decline (Acuna et al., 2005; Chester and Robson, 2011; Boersma et al., 2014). There have been numerous studies on the community structure of macroinvertebrates during drought which have found changes in macroinvertebrate taxonomic structure (Wood and Armitage, 2004; Wright et al., 2004; Griswold et al., 2008; Stubbington et al., 2011; Hille et al., 2014).

Studies investigating the functioning of an ecosystem during drought such as feeding rates or primary/secondary production are rarer (Poff and Zimmerman, 2010) but becoming more common (Ledger, et al., 2011). Functional changes during drought-induced low flows include reduced nutrient recycling and algal growth (Murdock et al., 2010; Timoner et al., 2012, Atkinson et al., 2014). In pooled areas, many species occur with drought-resistant traits and there is extensive functional redundancy (Acuna et al., 2005; Griswold et al., 2008; Boersma et al., 2014), however, these studies may not be directly applicable to UK Rivers due to geological and meteorological differences. Studies of real-time drought usually take place during extreme drought conditions and the functional changes in early stages of drought are unknown.

As the early stages of drought are not often studied, and supra-seasonal droughts in the UK are rare, we cannot rely solely on field studies to further understanding. Experimental approaches in mesocosms allow for a more controlled assessment of ecosystem functioning and some mesocosm environments have realistic similarities to the stream environment (Brown et al., 2011). There are strong limitations to mesocosm studies, as it is very difficult to bring the complexity of a stream system into a mesocosm, they are a simplified version of the real world. The mesocosm can be a simple petri dish in a lab to large-stream side channels (Stewart et al., 2013). The size and complexity of the mesocosm used for experimental studies depends upon the purpose, a microcosm experiment may be useful when looking at the behaviour of one macroinvertebrate under one changing condition, and large channels can be used to study macroinvertebrate communities or food-webs (Ledger et al., 2011). Microcosms and mesocosms are a simplified model of a real stream and experimental results should be treated with caution to ensure they are applicable to the natural world (Belanger, 1997). However, many things can be done in an experimental set-up that would be impossible in a real stream and hence they are necessary to investigate the important issues in freshwater ecology (Stewart et al., 2013). For drought research being able to control environmental variables helps to separate the stages of drought, allowing in-depth studies. In microcosms the macroinvertebrate community can be closely controlled, which enables the study of food-web and functional effects. The beginning of a drought can have various effects including habitat loss and low water velocities, disentangling these effects from each other is possible in experimental conditions where it may be impossible in the field.

Large mesocosms have been used to investigate macroinvertebrate responses to drought, key findings from these studies include a reduction of food-web linkage and a loss of larger-bodied species, particularly predators (Woodward et al., 2012; Ledger et al., 2013). Mortality from frequent drying has been found to be taxon specific with some taxa not changing in density, some reducing in density and some having density dependant effects (Lancaster and Ledger, 2015). With the loss of larger species including predators, and the selection of species which are resistant to drought the functioning of the ecosystem will be affected, such as secondary production. Ledger et al. (2011) found that functional feeding groups had different responses to drought with predators and shredders experiencing substantial declines while grazers were not affected. It is not yet understood whether functional redundancy can maintain ecosystem functioning during and after drought despite species losses (Walker, 1992; Young and Collier, 2009). There are few studies which look at function and we know little about individual species responses to slow flows and dewatering events.

Experiments in smaller mesocosms have found that the grazing activity of macroinvertebrates can either increase or decrease with flow reduction (Opsahl et al., 2003; Wellnitz and Poff, 2006; Townsend et al., 2012; Poff et al., 2003). Individual species have varying flow preferences, most species of mayfly which have been studied including examples from the Baetidae, Ephemerellidae and Heptageniidae families, increase grazing rates with increasing flow (Poff et al., 2003; Wellnitz and Poff, 2006; Wellnitz and Poff, 2012; Hintz and Wellnitz, 2013). Species of caddisfly from the Glossosomatidae family showed contrasting responses, in Wellnitz et al. (2001) *Agapetus boulderensis* chose slow flows of below 30cm s^{-1}, however in Wellnitz and Poff (2012) the categories of slow and fast changed with "slow" being (1-5 cm s(-1)), "medium" being (15-20 cm s(-1)), and "fast" (30-40 cm s(-1)) and in this study *Glossosoma spp.* preferred the higher flows. In the slow flows, filamentous algae grew much thicker, which trapped the individuals. The taxa that are adapted to slow flows, may increase their grazing activity due to lack of competition and an increase in resources. Poff et al. (2003) found species specific differences in grazing rate across three velocities, a representative from the Ephemerellidae family was unaffected by velocity, both *Glossosoma spp*, and *Baetis bicaudatus* (Baetidae) increased grazing activity with velocity. But *B. bicaudatus* outcompeted *Glossosoma spp.* at the highest velocity by consuming more algae. For many of the species in these studies, higher flow increased grazing activity however this is not always the case and a complex relationship between flow and species dominance can occur. Flow-grazing relationships have not been explored for some of the common herbivorous groups such as molluscs, and hence their response to low flows and dewatering are unknown.

The effect of drought on algal biomass and biofilm quality is also important. Slow flows can often lead to an overall increase in algal growth (Freeman et al., 1994; Dahm et al., 2003), the response is dependent upon the type of algae as it has been found that diatom growth decreases and filamentous algal increases (Hart et al., 2013). Algal cells can remain viable even after long periods of drying (Ledger and Hildrew, 2001; Robson et al., 2008) and frequent drying can change the algal communities to become more patchily distributed (Ledger et al., 2008). The quality of the algal biofilm is an important aspect for the functioning of the ecosystem, but little work has been done on the effect of slow flows or dewatering on the algal quality. Timoner et al. (2012) found that the chemistry of the algae changed when dewatering occurred with higher phosphorus and nitrogen to carbon ratios. It is unknown how this change in ratio would affect the nutritional content.

Chalk streams are less responsive than other rivers to extremes of precipitation because the aquifer mediates the stream flow response (Berrie, 1992). However, as many chalk streams are seasonally intermittent under normal conditions, a-seasonal droughts could mean large areas of the river bed may dry up or fail to re-wet at the correct season. Chalk streams have been studied during drought in the past, Berrie and Wright (1984) and Wright and Symes (1999), studied chalk streams in the severe droughts of 1976 showing macroinvertebrate community changes during and after drought. However the implications for ecosystem functioning are poorly understood.

Hydrological drought varies in intensity, so low flows and dewatering will have different impacts on the ecology of streams. We understand some invertebrate community effects but the knowledge about traits such as feeding behaviours or the mortality at low flows vs dewatering are less well understood. In this experimental study, the effect of drought on three species of grazing macroinvertebrates which are common herbivorous taxa in chalk streams: *Agapetus spp.* a caddisfly; *Serratella ignita* a mayfly and *Ancylus fluviatilis* a mollusc were investigated. Two different stages of drought were simulated, very slow velocities which represent a pooled environment, and dewatering which is a more advanced stage of drought, these were compared to a control which had constant intermediate flows throughout.

The aim of the study was to determine if grazing rate was reduced under slow flows and dewatered treatments, and to assess mortality rates. The hypotheses were: H_1: that mortality would increase in slow flows and dewatering treatments with dewatering having the highest mortality rate. H_2: Slow flows would cause a decrease in grazing as found in (Poff et al., 2003; Wellnitz et al., 2001). H_3: Dewatering would reduce grazing due to the higher mortality rate. The species of grazers with the highest level of mortality would be the species with the least resistance to drought, H_4: *A.* fluviatilis would have the least mortality because they could survive dewatering by respiring air. Grazing activity should reduce with slowing flow, and be further reduced with dewatering, however if *A. fluviatilis* survived dewatering, grazing could return with rewetting. H_5: The algae on the tiles are predicted to reduce in quantity and quality with decreasing flow, hence the control would have the most algae and the dewatered treatment would have the least with the slow flow treatment intermediate.

6.2 Methods

6.2.1 Experiment Logistics

The experiments were carried out over a four week period from 11/04/14 to 09/05/2014. Three water filled channels were used to host the experiments (Figure 6.2), located at the Centre for Ecology and Hydrology in Wallingford, Oxfordshire, UK (18.965°N, 46.168°E). These channels are 16m long x 0.4 m wide x 0.4 m deep, each with a maximum volume of 2.56m^3 and a slope of 1/1000. The flumes each have two independent pumps which re-circulate the water and a refrigeration unit which can regulate water temperature. A honeycomb plastic filter is placed at the top end of each flume to evenly distribute the water and to catch any debris which may fall into the channel. Each flume has an inlet storage tank with a volume of 1.0m^3 and an outlet storage tank with a volume of 2.8m^3, therefore each flume has an overall volume of 3.8m^3. The flumes were filled from a nearby borehole which is from a chalk aquifer. The discharge of the water was kept at 15 litres per second and the temperature was maintained between 8 and 15 degrees Celsius (Figure 6.1).

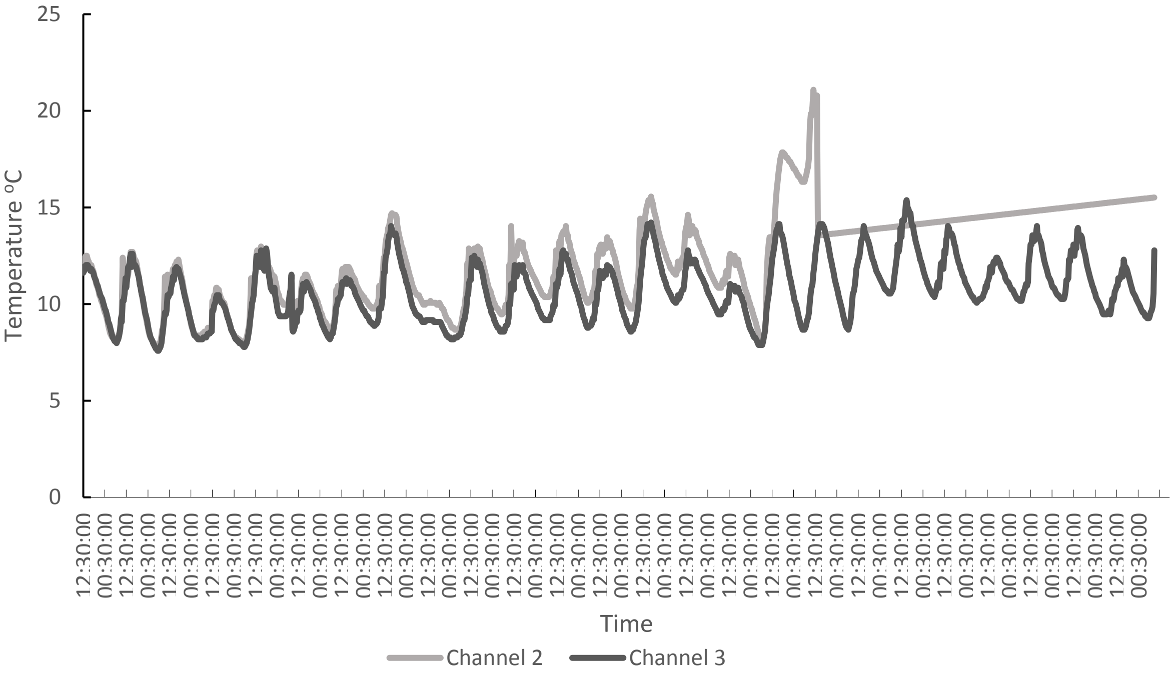

Figure 6.1. Temperature of two of the channels used in the experiments. Temperature was recorded every 30 minutes.

6.2.2 Microcosm design

Figure 6.2. Photograph of the three channels with microcosms in situ.

Microcosms were made from plastic containers without lids, measuring 21x15x10 cm, a 10 cm x 4 cm rectangle was cut from each narrow end, and either 0.5mm or 0.03 mm mesh was secured with adhesive (Figure 6.4). Each microcosm was filled with 3cm of gravel. The position of the microcosms in the channels was decided using a random number generator, mixing all treatments randomly across all three channels (Figure 6.2, Figure 6.3).

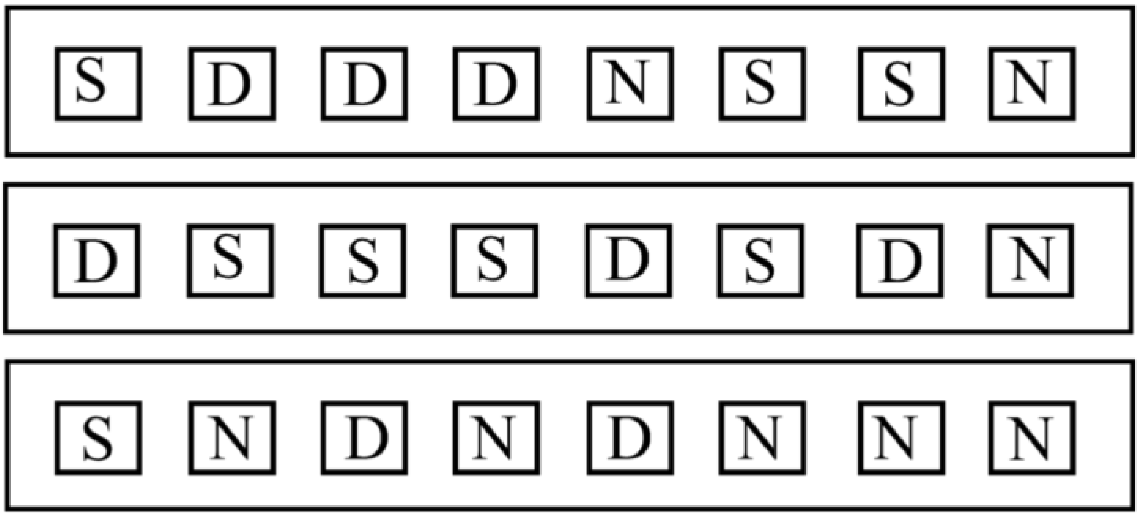

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Figure 6.3. Schematic diagram of channels with treatment order. N = normal control flow, S = slow flow and D = dewatered treatment. Order was picked using a random number generator.

Three treatments were used with eight replicates in each channel:

Control: microcosms had 0.5mm mesh. The flow rate was measured as 10.2 cm/s microcosms were submerged under 10cm of water.

Slow flow: microcosms had 0.03 mm mesh. This was used to represent a pooled environment and flow rate was measured as 3.6cm/s which is 35% of the control flow with 10cm water depth.

Dewatered: Microcosms with 0.5mm mesh were removed from the water completely 8 days into the experiment for two days by lifting the microcosms above the water line, by raising them onto bricks within the channel. This removed all the water from the microcosm which left the substrate to dry out. The microcosms were placed back into the channel after 48 hours. This was to represent a temporary drying environment.

Figure 6.4. Microcosm with tiles and gravel inserted

Two unglazed terracotta 50 mm x 50 mm tiles used as substrates for algal growth were secured to a 156 mm x 76 mm glazed tile (Figure 6.4). The tiles were incubated in the River Lambourn at East Shefford for four weeks to establish natural biofilms. Tiles were then transferred to the Centre for Ecology and Hydrology, Wallingford in containers of river water and placed into the channels 48 hours before the onset of the experiment. Twelve hours before the experiment Vaseline was placed around the edge of one of the paired tiles and one pair of tiles were then placed inside each of the microcosms.

6.2.3 Macroinvertebrate collection and processing

The experiment was carried out for four weeks in the spring (April 2014) as pilot studies which were carried out the previous year showed that mayflies and caddisflies were too small in the summer months (June-August), difficult to collect and keep alive. Macroinvertebrates were larger in the spring which made them easier to collect and handle. The macroinvertebrates were collected from the River Lambourn, both from Boxford (51.446° N, 1.383° W) and upstream of Great Shefford (51.476° N, 1.453° W) in March and April 2014. The three most abundant grazers at the time of sampling which are categorised as scrapers (Arens, 1989) were chosen and used in a density which was equivalent to the average density of the River Lambourn and the amount that could be collected from the field. This allowed a range of macroinvertebrate orders to be tested and for the range of species to accurately represent the River Lambourn, where the samples came from. In each microcosm there were 7 *Serratella ignita*, 2 *Ancylus fluviatilis* and 8 *Agapetus spp.* these numbers also took into account the larger biomass of *A. fluviatilis* when compared to the two other species. The species information is shown in table 6.1. To prevent damage to the macroinvertebrates they were handled with wide plastic pipettes or plastic spoons, when collecting and moving them into holding containers and mesocosms. Holding containers followed the same design as mesocosms with 0.5 mm mesh and contained gravel and rocks taken from the River Lambourn to ensure algae was present for macroinvertebrates to feed. Spare individuals of each of the macroinvertebrate species were kept in holding containers in the channels.

Table 6.1. Nomenclature, density and grazing type of macroinvertebrate species used in the experiment.

Species	Authority and Higher Nomenclature	Total number macroinvertebrates	Grazing Type
Serratella ignita	*(Poda, 1761,* Ephemeroptera, Ephemerellidae)*,*	7	Scraper
Ancylus fluviatilis	*O.F. Muller, 1774 (*Gastropoda, Planorbiidae*)*	2	Scraper
Agapetus spp.	*(Curtis 1834,* Trichoptera, Glossosomatidae*).*	8	Scraper

During the experiment the channels were checked twice a day. Any debris which had accumulated on the honeycomb or the mesh of each microcosm was removed. The temperature and flow were checked daily by looking at the built in flow meters and temperature logger and temperature was measured and stored using a HOBO® temperature logger which logged temperature every 30 minutes, however one of the loggers malfunctioned and so temperature data is only available for two of the channels.

6.2.4 End of the experiment

The experiment was ended after four weeks. One microcosm was removed at a time, the tiles were removed from the water, Vaseline wiped off and the algae from the grazed and ungrazed tiles were scraped into separate bottles using a toothbrush, funnel and water.

The macroinvertebrates were then removed and placed into vials containing 70% IDA solution with glycerol. Macroinvertebrates which were missing or pupating were noted. Macroinvertebrates from each mesocosm were counted and head widths or body lengths measured under a dissecting microscope with a graticule, for biomass estimation.

6.2.5 Algal Analysis

The algal samples were made up to 150ml and homogenised by inverting the bottle 30 times. Of the 150 ml, 50ml was then removed and preserved in formaldehyde in a bottle which was stored in a cold room for potential algal identification work in the future. The remaining 100 ml of the sample was frozen on the day of collection in a -20°c freezer. The samples were analysed in batches of between 12 and 30, these frozen samples were removed from the freezer and left to defrost overnight.

50ml of the sample was used for chlorophyll *a* analysis, see chapter 3.2.5 for full method. 50ml of the sample was used for AFDM analysis, see chapter 3.2.5 for method

Autotrophic index (AI) is used as an indicator of the quality of the biofilm. Higher values mean that the biofilm has a higher bacterial/fungal content vs algal. See chapter 3.2.6 for full method.

6.2.6 Data Analysis

Macroinvertebrate measurements taken at the end of the experiment, (which were head width for *Agapetus spp.* and *Serratella ignita* and longest dimension for *Ancylus fluviatilis*) were converted into biomass using calculations from previous studies (Meyer, 1989; Burgherr and Meyer, 1997). Data exploration showed that some data failed to meet assumption of ANOVA, individual species abundances and biomass showed deviation from normal distribution. Therefore it was decided Kruskal Wallis tests were the best choice. Kruskal Wallis tests were carried out to test total macroinvertebrate biomass differences and individual species biomass differences (responses) between the control, slow flow and dewatering treatments (treatments) (Minitab 16®). Kruskal Wallis tests were also carried out in the same way for macroinvertebrate abundances with total abundance and individual species a as responses and treatment as the factor.

For chlorophyll and AFDM data, the means with standard errors were calculated for each treatment. Data exploration showed that residuals were normal with no outliers (Figure 6.5), histogram showed deviation from normal distribution but it was determined that this did not break the assumptions of ANOVA analyses (Figure 6.5). Two-way analyses of variance (ANOVA) tested Chlorophyll *a*, AFDM and autotrophic index (responses) results for differences between the flow treatments: control; slow flow and dewatered, and testing for differences between the grazing treatment: grazed and ungrazed (flow and grazing treatments were fixed factors) and Tukey post-hoc tests were carried out to determine which means were different.

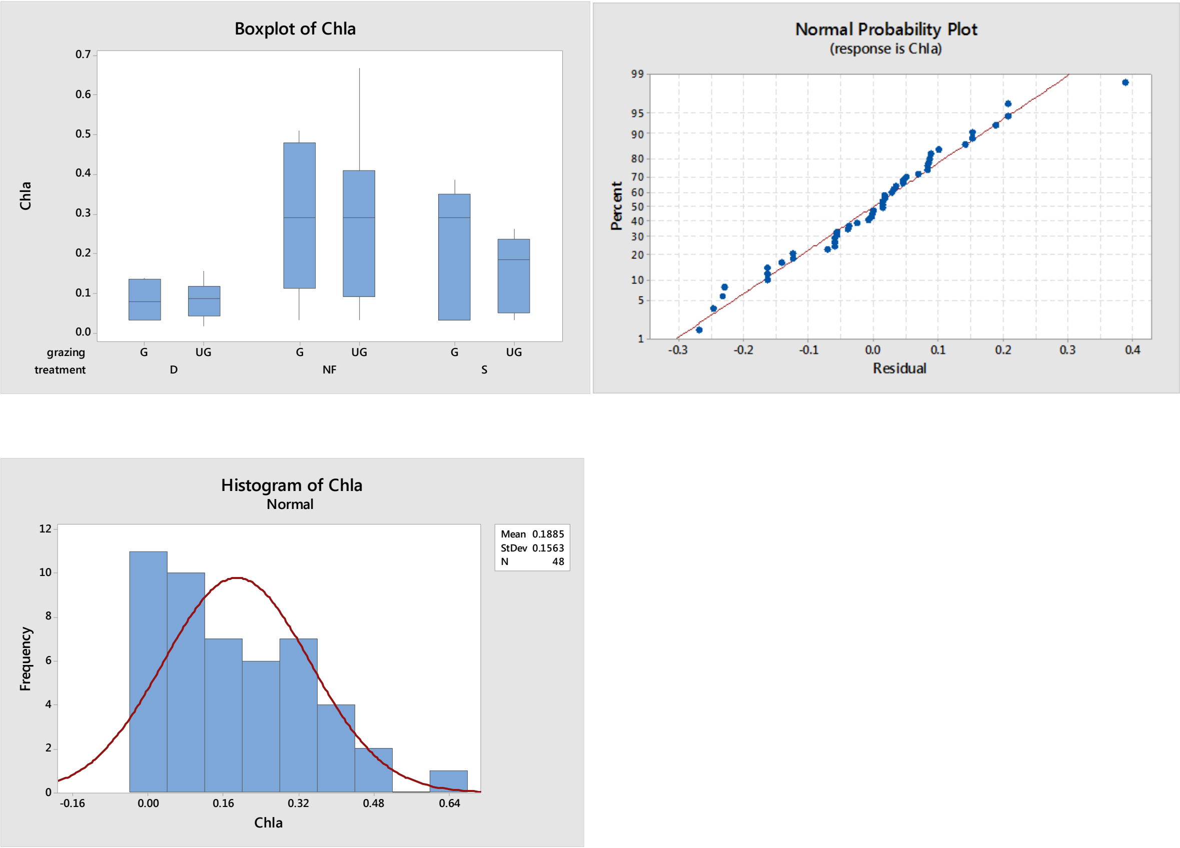

Figure 6.5. Data exploration graphs for Chlorophyll data, boxplots, QQ plots and histogram.

6.3 Results

6.3.1 Macroinvertebrate abundances and biomass

There was a main effect of flow treatment on total abundance of macroinvertebrates (Figure 6.5, $p<0.01$, Table 6.2) and post hoc tests revealed that abundances were greater in the slow flow treatment ($p<0.05$) (Figure 6.6). The control and the dewatered treatment had similar abundances. Total numbers masked contrasting responses at the species level, individual species abundance differences are shown in Figure 6.7, *Serratella ignita* and *Agapetus spp.* had significantly different abundances between treatments ($p<0.01$ and $p<0.01$ Table 6.2), Tukey post-hoc tests reveal this is due to higher abundances in the slow treatment ($p<0.05$).The abundance of *Ancylus fluviatilis* did not differ significantly between treatments ($p>0.05$).

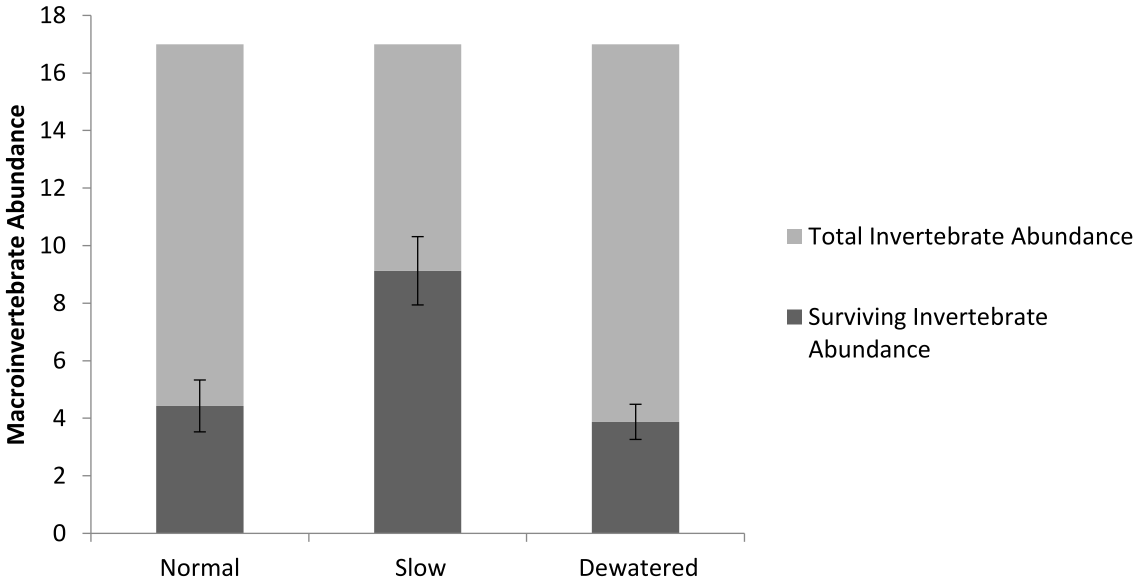

Figure 6.6. Mean surviving macroinvertebrate abundance per mesocosm as a proportion of total abundance per mesocosm ± 1 SE. Dark bar is density of macroinvertebrates surviving at the end of the experiment. Light bar signifies the mortality in each treatment, the initial total number of macroinvertebrates equalled seventeen individuals in all cases.

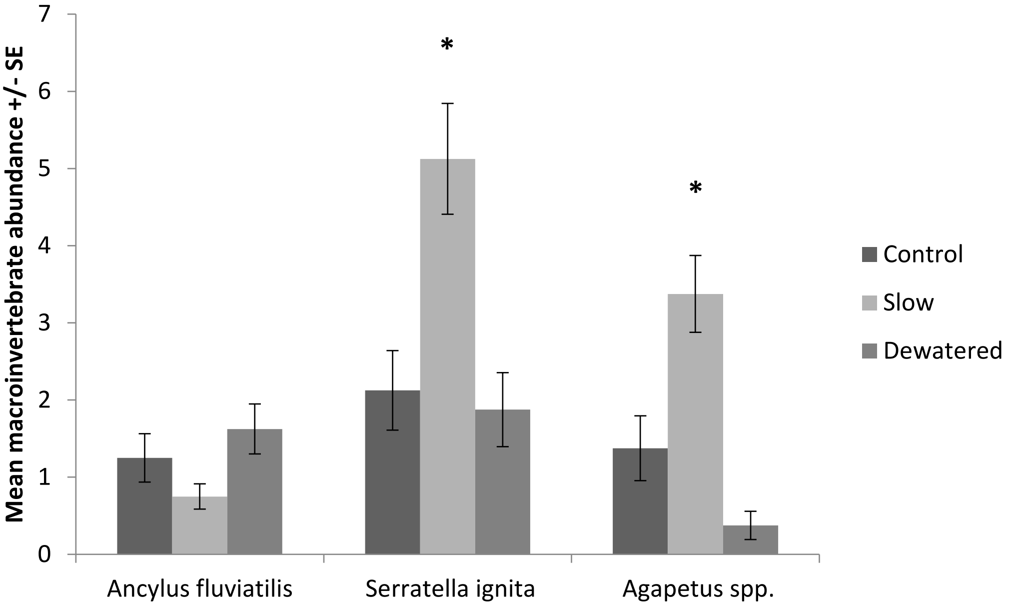

Figure 6.7. Mean abundances of the three macroinvertebrate species across the three flow treatments ± 1 SE. * indicates significant differences in one-way ANOVA and Tukey post-hoc tests.

Table 6.2. Kruskal Wallis results for Macroinvertebrate abundance and macroinvertebrate biomass between treatments taken from the end of the experiment. DF stands for Degrees of Freedom. P values were adjusted for multiple comparisons using the Bonferroni correction.

Method	H Values	P Values	DF
Total Abundance	**8.54**	**0.014**	2
***A. fluviatilis* Abundance**	5.57	0.062	2
***S. ignita* Abundance**	8.96	**0.011**	2
***Agapetus* spp. Abundance**	13.52	**0.001**	2
Total Biomass	1.64	0.442	3
***A. fluviatilis* Biomass**	4.60	0.100	2
***S. ignita* Biomass**	10.18	**0.006**	2
***Agapetus* spp. Biomass**	9.20	**0.010**	2

Total macroinvertebrate biomass (Figure 6.8) showed no significant differences between treatments (p>0.05, Table 6.2). However, this masked individual species differences, *S. ignita* (p<0.01) and *Agapetus spp.* (p<0.01) showed a significant increase in biomass in the slow flow treatment (Figure 6.9, Table 6.2), *Ancylus fluviatilis* did not show a significant difference between treatments (p>0.05).

The dewatered treatment had lower biomass of *Agapetus spp* showing that mortality was high in this species when exposed to dewatering. *S. ignita* and *A. fluviatilis* showed no difference in biomass between the control and dewatered treatments.

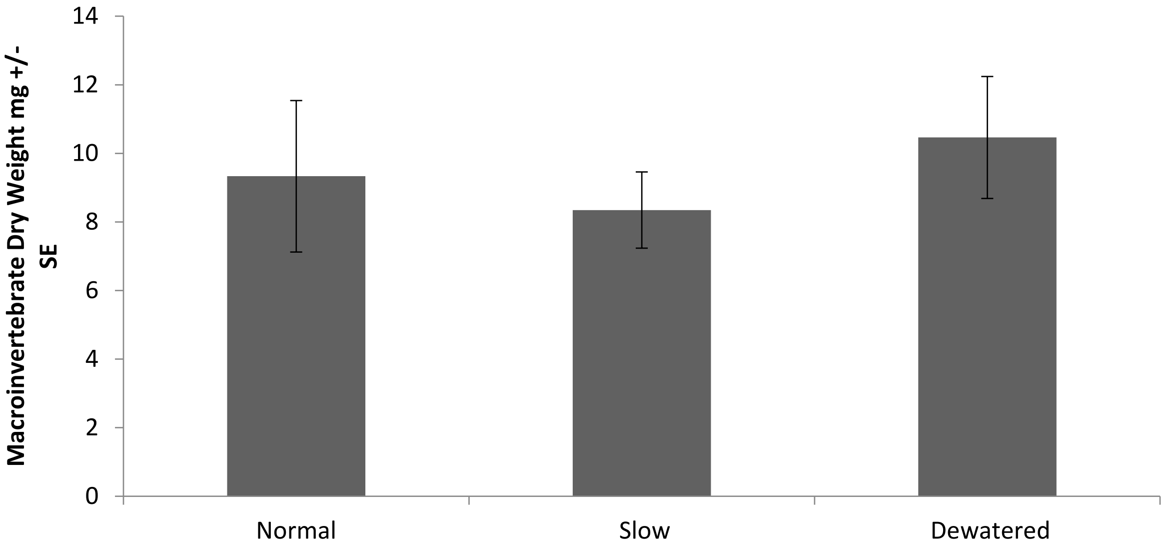

Figure 6.8. Mean surviving macroinvertebrate biomass in each microcosm across the three flow treatments ± 1 SE

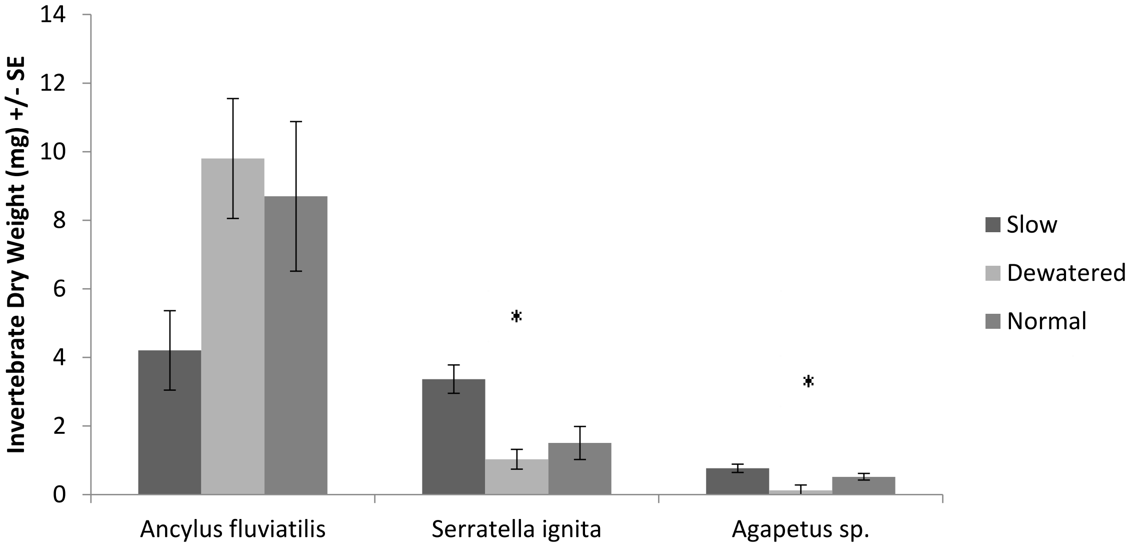

Figure 6.9. Mean biomass of surviving macroinvertebrate species per microcosm across the treatments ± 1 SE. * indicates significance in one-way ANOVA tests see Table 2.

6.3.2 Algal Results

There were significant differences in chlorophyll biomass between flow treatments (Table 6.3) and post-hoc tests showed that normal flow had significantly higher chlorophyll *a* mass than the dewatered treatment ($p<0.05$), the slow flow treatment was not significantly different to either controls or the dewatered treatment. There were no significant effects of grazing treatments (Table 6.3). There were no differences in chlorophyll *a* between grazed and ungrazed in all flow treatments (Figure 6.10). There were significant differences in AFDM between flow treatments but not grazing treatment (Table 6.3), there was less AFDM in the slow flow than the other two treatments (Figure 6.11). The autotrophic index of controls was significantly lower than in both the slow and dewatered treatments indicating a higher quality biofilm (Figure 6.12, Table 6.3), although the control treatment AI was approximately 400 which is still considered a high number.

Table 6.3. Values from ANOVA tests (Two-way ANOVA's for Chlorophyll *a*, AFDM and AI as the responses and Grazing and Flow Treatment as the factors) including p and F values, degrees of freedom (DF) and the interaction value which is the p value of the interaction between grazing and flow treatments.

Method	Grazing Treatment F Values	Grazing Treatment p values	DF	Flow Treatments F Values	Flow Treatments p Values	DF	Interaction p value
Chlorophyll *a*	0.31	0.574	1	9.14	**0.001***	2	0.738
AFDM	0.37	0.549	1	3.94	**0.027***	2	0.663
AI	0.17	0.681	1	4.63	**0.015***	2	0.649

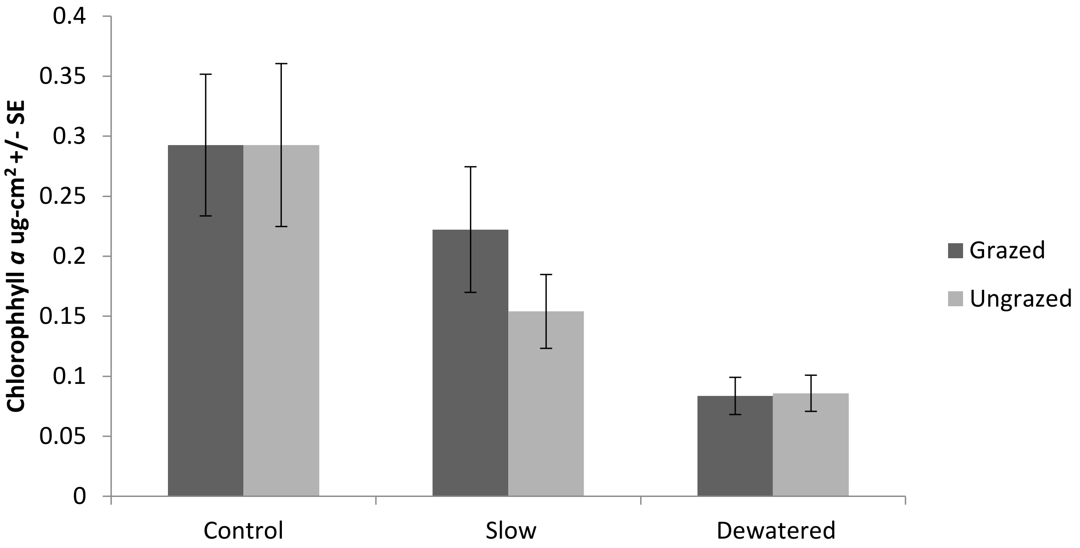

Figure 6.10. Mean Chlorophyll *a* ± 1 SE of biofilms from tiles in microcosms, comparing grazed and ungrazed tiles in across all three flow treatments.

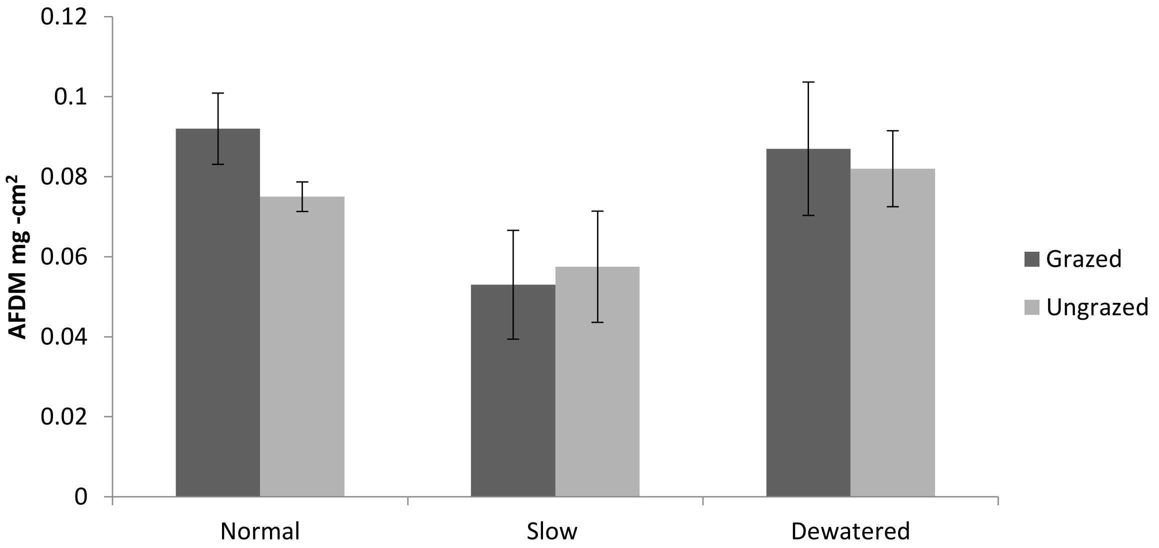

Figure 6.11. Mean Ash Free Dry Mass (AFDM) of biofilms from tiles in microcosms ± 1 SE. Comparing grazed and ungrazed tiles across all three flow treatments.

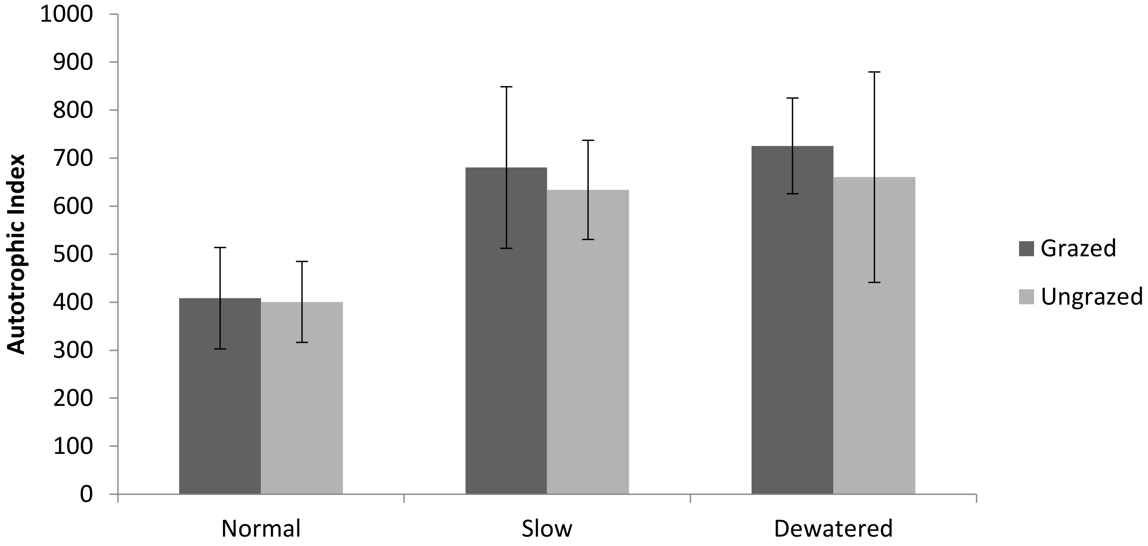

Figure 6.12. Autotrophic Index (AI) ± SE. A measure of biofilm quality, with lower numbers meaning the biofilm consists of more algae and less detritus or bacteria. Comparing grazed and ungrazed tiles across all three flow treatments.

6.4 Discussion

Drought brings changes to flow dynamics and also dewatering events (Lake, 2011). This experiment found that macroinvertebrates had species-specific responses to treatments imitating the stages of drought. The survival of the insects used in this study *Agapetus spp.* and *Serratella ignita* increased in slow flows and so we must partly reject H_1 as slow flow did not increase mortality, whereas the mollusc *Ancylus fluviatilis* showed no significant changes between any treatments (H_4), dewatering events did not significantly change survival in any of the species which rejects the other part of H_1. As the different stages of drought unfold we can expect differing ecological responses to the changing environment. However, in this experiment we found that grazing was not strongly affected by flow so we must accept the null hypothesis for H_2 and H_3. The biofilm on the tiles was sparse which may have masked grazing effects, however all the areas of the River Lambourn that were visited in the spring of 2014 did not have thick biofilms either

There are many studies which have found species specific flow relationships, for example Poff et al. (2003) found differences in grazing rates at different flows with three macroinvertebrates, two mayfly species *Baetis bicaudatus* and *Drunella grandis* and one caddisfly species *Glossosoma verdona. Drunella grandis* did not alter its grazing rate with flow, however the other two species increased grazing rate with increasing flow. Other studies have found species which prefer slow flows such as Wellnitz et al. (2001) who found that *Agapetus boulderensis* chose slow flows in an experiment, in contrast to *G. verdona* within the same family who in (Poff et al., 2003) chose fast flows. If species within a family differ in their flow preferences it may be hard to predict the effect of changes in flow of a macroinvertebrate community without first knowing each species' preferences.

Mortality in all three treatments in this experiment were high ranging from 40-60%. Normal flow, which was indented as the control treatment sustained higher mortality than slow flow. Ecotoxicology literature debates the expected mortality of no observed effect concentration (NOEC) chemical treatments of between ten and thirty percent, although there is no standard mortality rate as it differs between species and circumstance (Crane & Newman, 2000; Jager, Heugens, Kooijman, 2006). In addition, ecotoxicology studies are carried out on animals usually captive born and held in highly controlled situations (Crane & Newman, 2000). This study was carried out on wild-born macroinvertebrates in running water. Transporting the macroinvertebrates from the river to the controlled channels may have stressed the animals and increased mortality rates. The low density of algae on the tiles may also have had an effect on overall mortality, however the mortality rate of these animals I the wild is unknown so we cannot determine whether the mortality rates are anomalous or not4y.

The function of the ecosystem during and after drought will be determined by the species of macroinvertebrate which survive the different stages of drought. Slow flows in this experiment were characterised by having the highest macroinvertebrate biomass. Furthermore it was clear that flow had distinct effects on each species. Biomass did not differ between treatments, and yet density did. This could indicate that functional redundancy occurs with these three species as the overall biomass of grazers does not change this should mean the same biomass of producers is consumed. Regardless of changes in individual species abundances, the overall biomass of grazers stayed the same under slow flow and dewatering treatments, allowing the grazing function to persist through major disturbance. However, the biomass of the total community and production in the ecosystem is usually linked to species richness, (Duffy et al., 2007; Gruner et al., 2008), and thus although the function of grazing will continue if species are lost, the overall biomass of the food web may reduce as a result.

Each species grazing rate differences could be investigated further to determine the true functional redundancy. Poff and Ward (1992) and Wellnitz et al. (2001) found that the North American species *Agapetus boulderensis* Milne 1936, which could be have similar grazing rate as the species found in the UK, could tolerate a large range of velocities but preferred slow flows. In slow flows they showed the highest levels of movement and grazing activity which may be due to the relatively large stone case these animals live in. With regards to *S. ignita,* few studies have looked at grazing behaviour and the species is a generalist consumer which can also feed on detritus (López-Rodríguez et al., 2009), however Sagnes et al. (2008) found that this species preferred areas of rivers with slower velocities which validates the current study's findings. There are no contemporary studies which mention the habitat preferences of *A. fluviatilis*, but Davis (1971) suggested that this species was usually found in faster flowing areas of the river, which perhaps means they are better adapted to feeding in faster flows, and this may explain the low survival rate of this species in this study. Individual species' preferences mean that each stage of drought will exert different selective pressures upon the species. However if there was a long period of slow flow before dewatering *A. fluviatilis* could be outcompeted for resources during this period, and long periods of dewatering would remove less resistant species such as *Agapetus* spp. and *S. ignita* from the system. Consequently the surviving species in the aftermath of a drought will be directly influenced by the conditions before and during the drought.

The effects of dewatering on algal biomass is an important factor to consider in the recovery from drought as algae form the base of the food chain. A lower algal biomass was found in the dewatered treatment, this was also found in other studies which also found a fast recovery rate after the drought (Timoner et al., 2012; Ledger et al., 2008). This study was ended one week after dewatering which may have not been enough time for recovery to occur. This could mean that algae may take longer than a week to recover from complete drying after a short period of drought. Timoner et al. (2012) showed that intermittent streams in the Mediterranean can recover algal biomass almost instantly after three months of desiccation. One reason this may not have occurred in this study may be due to the algae being collected from a perennial field site and not an intermittent site meaning the species of algae were less resistant to drought. This is important to consider for cases of extreme drought where normally perennial areas dry, as recovery may be delayed.

This study did not show a strong effect of drought on grazing. Macroinvertebrate grazing did not show significant changes with flow rate, shallow water or dewatering. The overall biomass which grew on the tiles in the River Lambourn was low, it was noted that the biofilms in all sites visited that year in this river were much thinner than in previous years (personal observations). This thin biofilm may have masked changes due to grazing, as grazing can have a positive effect on algal growth especially in thin biofilms (Feminella and Hawkins, 1995; Saikia et al., 2011). Biofilm quality (measured by AI), was negatively affected by drought, the slow flow and dewatering treatments had less algae present in the biofilm. This could have an effect on the grazing macroinvertebrates as algae is often more easily digested than bacteria and fungi (Lear et al., 2012). The change in AI indicates that slow flows and dewatering caused a change in biofilm community structure. This could mean that grazing macroinvertebrates need to consume more biofilm in order to receive the same nutrition (Caramujo et al., 2008). Therefore drought can cause bottom-up changes in the food webs of river ecosystems.

6.4.1 Conclusions

The treatments had effects on macroinvertebrate mortality and algal quantity and quality. There were also clear differences between macroinvertebrate species' responses. The slow flow treatment representing pooling had less mortality of *Serratella ignita* and *Agapetus spp.* than the control treatment, indicating that these species may prefer slow flows over normal flows which is confirmed by the findings of Tachet *et al*. (2002) where both species were found to prefer slow and medium flows over fast flows. The dewatering treatment showed little change in mortality compared with the control treatment, showing the test species had high resistance to short-term drying. Overall biomass of macroinvertebrates did not show significant differences between treatments, indicating that the delivery of grazing function would remain throughout slow flows and temporary dewatering. However the reduction in biofilm quantity and quality in slow and dewatered treatments indicated there was less food available to grazers.

Changes in macroinvertebrate biomass signify interesting changes in macroinvertebrate mortality throughout the drought process which are important for survival of drought and recovery afterwards. To further test these hypotheses, a longer experiment with a higher starting mass of algae is suggested.

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CHAPTER 7

GENERAL DISCUSSION

7.1 Overall Summary

The results of this thesis show that drought acts as a disturbance on freshwater ecosystems, whether that be in reduced flows or complete drying. Low flow effects on macroinvertebrate diversity and richness were transient and the biomass of algae and macroinvertebrates recovered rapidly at all sites which rewetted following drought along with this we see a recovery of the function of grazing. The thesis is structured to investigate structural changes to macroinvertebrate communities as well as functional changes in perennial, dewatering and rewetted sites (Figure 7.1)

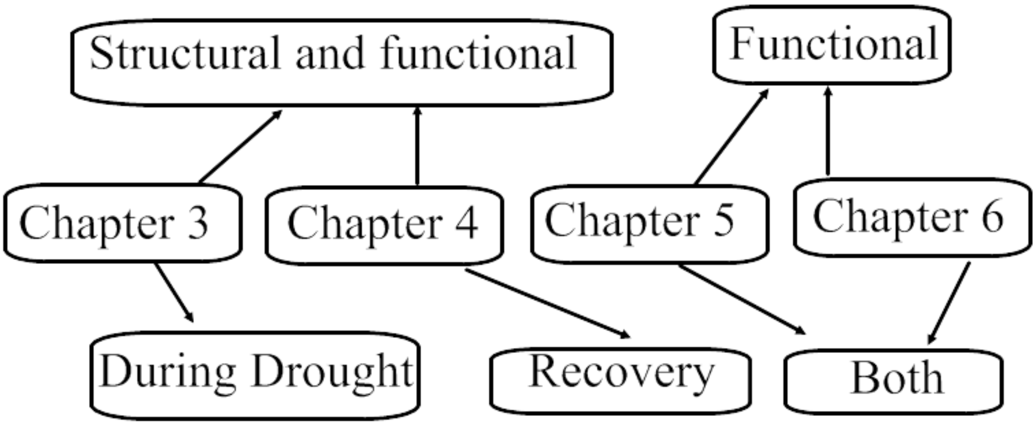

Figure 7.1. Conceptual model of structure of thesis. Chapters are linked to whether they focus on structure and function or purely functional ecology and whether they look at effects or drought, recovery or both combined.

7.2 Responses of algae and macroinvertebrates during drought (Chapter 3)

Low flows are characteristic of early stages of drought (Lake,2011) and droughts are often exacerbated by abstraction in ground-water areas (Acreman et al., 2008). Low flows due to droughts are likely to increase in frequency and duration (IPCC, 2007) therefore investigating the effects of low flows on the river ecosystem is pertinent. This thesis illustrated that low flows during drought in a chalk stream are a severe disturbance. There were clear shifts in macroinvertebrate communities towards a community consisting of pioneer species. Also there were some functional feeding group changes within the macroinvertebrate community, suggesting the ecosystem functioning of the stream changed.

However this chapter did have limitations, only one month of data was collected before the end of the drought.

7.3 Algal and macroinvertebrate recovery in the months following drought (Chapter 4)

The recovery of algal and macroinvertebrate biomass after drought was incredibly rapid, with few differences seen between perennial sites and rewetted sites one month after rewetting. Droughts of the magnitude which occurred in 2010-2012 are rare, the last drought of such magnitude occurred in 1976. However, if droughts become more frequent and intense as predicted, (IPCC, 2007; Watts et al., 2015) the algal and invertebrate communities have a degree of resilience and available species redundancy to allow quick recolonisation of dry riverbeds. Furthermore, the macroinvertebrate family and functional feeding group differences in the first month of rewetting were clear. These differences lessened over time apart from in the autumn which will be discussed in 7.6. The other studies of chalk stream recovery after drought also found rapid recovery of macroinvertebrate densities and species richness (Berrie and Wright, 1984; Wright et al., 2004; Wood et al., 2000; Wood and Armitage, 2004), however, this thesis was the first study to analyse community analyses and functional feeding groups in addition to densities. Functional feeding group biomass also showed a rapid recovery and by July the major functional feeding groups were similar in the rewetted and perennial sites. This showed that despite the community differences, the functioning of the streams in the rewetted sites is comparable to that of the perennial sites.

7.4 Functional responses during drought and recovery (Chapter 5)

The in-situ experiment ran both during the drought and recovery stages, allowing an investigation into the grazing function at these crucial stages in drought. During drought the function of grazing did not differ significantly between dewatering and perennial sites.

After drought the function of grazing in rewetted sites was equal to perennial sites within one month of rewetting, as macroinvertebrate and algae returned, the function of grazing returned simultaneously. This was a very important finding, we can determine that the food web was recovering as autotrophs and primary consumers are present. If grazing did not return quickly, food-web structure could not recover. Knowing one of the basic functions has rapid recovery could mean other functions dependent on macroinvertebrates (e.g. organic matter breakdown) and algae (e.g. nutrient cycling) also return rapidly.

7.5 Experimental Studies on Drought in mesocosms (Chapter 6)

The experiments in mesocosms showed interesting results regarding invertebrate mortality in dewatering or slow flow environments, the least mortality was found at slow flows, dewatering caused the most mortality and the control flow was in between. This showed that a species flow preferences are important in their responses to drought. However little change was seen in the grazing function although this may be due to the very thin biofilms which grew.

Having a controllable environment such as a mesocosm ensures the differences seen are due to the treatments. However, when investigating drought which had very complex responses it is important to tie in experimental studies to field surveys. This is difficult to undertake as droughts are not predictable, hence is it important not to assume experimental studies are a true representation of drought.

The mesocosm experiment carried out in this study had some limitations including a low level of algae growing in rivers in that season which meant a very thin biofilm grew on the tiles. Thin biofilms are known to respond to grazing with more vigorous growth (Liess and Hillebrand, 2004), explaining the positive grazing relationship. Perhaps algal biofilms grown within a laboratory could negate the need for biofilms to be grown in-situ in rivers in years with little algae in rivers.

7.6 Synthesis of results from all chapters

7.6.1 Recovery from drought (Chapters 4 & 5).

Chapter 4 demonstrated that algal biomass, macroinvertebrate biomass and to a certain extent macroinvertebrate communities recovered almost instantly after rewetting which is similar to finding in other studies of recovery after supra-seasonal drought (Morrison 1990; Wright & Symes 1999; Boulton 2003 and Churchel 2006);. In chapter 5 macroinvertebrate grazing, a key function in most stream food-webs, is shown to return to similar levels in rewetted and perennial streams within one month or rewetting. Therefore, the algae, the macroinvertebrate biomass and the grazing function have all returned to pre-drought levels all within 3-4 weeks of rewetting. This demonstrates the resilience of the stream ecosystem where disturbances are frequent and organisms have evolved to take advantage of this. This has rarely been shown in the literature after supra-seasonal drought although it has been shown for seasonal droughts (Stanley *et al* 1994; Brock *et al* 2003; Fritz & Dodds 2004; Beche 2009; Boersma *et al* 2014). However, macroinvertebrate communities were not the same in perennial and rewetted sites. The communities were still characterised by pioneer species in the two to three months after rewetting, and then the communities were very similar in August. Few studies in the literature focus on the taxonomic identity of macroinvertebrates many note a return of the number of families without specific mention of which families (Berrie & Wright 1984; Wright & Symes 1999; Wood & Armitage 2004; Wright *et al* 2004). Those studies which do mention taxonomic differences have similar results as shown in the thesis, Extence (1981) found an increase in Chironomidae and Oligocheata and a loss of riverflies, Cowx (1984) found similar results in Wales with less Plecoptera and Coleoptera but an increase in Oligochaeta, Chironomidae and Simuliidae. Wood & Petts (1999) found differing results with increases in Gammaridae and many Gastropoda during and after drought which was not found in this thesis. Perhaps showing that recovery to drought is not a wholly predictable occurrence and could be individual to the circumstances occurring within the river systems.

In later months we see a shift in community structure, the perennial sites had a shift in macroinvertebrate community composition in the months of September and October, as the autumnal riverfly species begin to appear. This shift in community structure was lacking in the rewetted sites where the communities stayed similar in the shift from summer to autumn. Although the biomass of macroinvertebrates had returned, and the function of grazing had returned, the full biodiversity had not, as the longer-lived, more drought-sensitive species had not yet returned five months following rewetting. This is similar to the findings of Boulton (2003) especially to their analysis of Australian streams where certain groups of macroinvertebrates did not recover swiftly after drought, two such families were riverflies, a stonefly and a free-living caddisfly which matches the findings of this thesis. The failure of certain macroinvertebrates to recover swiftly means that if there had been further droughts or other disturbances before full recovery this may have further delayed recovery. If frequent droughts increase the occurrence of dewatering, functional redundancy is likely to reduce along with species richness (Schmera et al.,2012), and if droughts are recurrent, long-term recovery may suffer as species which are longer-lived and sensitive to disturbance are lost from the ecosystem.

7.6.2 Resistance and resilience during and after drought (Chapters 6 & 7)

Findings from chapters 6 & 7 showed that drought and recovery had very little effect on grazing function. Grazing function has not been analysed independently in previous studies, and although it is noted it cannot be used as a proxy for all functions within an ecosystem, it shows other functions are likely to have recovered enough to enable a functioning ecosystem. Studies of functional recovery are mostly completed in Mediterranean or arid ecosystems, although they also show functional recovery, for example, Boersma *et al* (2014) found that trophic traits were similar in pre and post-drought communities despite taxonomic changes, although other studies find changes in traits in droughted and newly recovered ecosystems (Bonada 2007; Garcia-Rover *et al*, 2003 & Chessman 2015) and studies looking at larger, longer-lived taxa such as bivalves have found delayed recovery in functions such as water filtering (Villnäs *et al* 2012) and predatory species (Woodward *et al* 2012 & Ledger *et al* 2013). Hence, if longer-lived species carry out different functions to smaller species, drought will have a weighted effect on the ecosystem functioning as a whole.

7.7 Future Research Directions

With the data from the current study, macroinvertebrate trait analysis isrecommended as the next step both in the case of the dewatering site and rewetting site to determine the traits of the resistant and resilient taxa. It is also recommended that more species-specific analysis is carried out to determine the changes in invertebrate community at a finer level. Stored samples of algae are preserved and these could be analysed for diatom taxonomy to determine the resistance and resilience of diatom taxa.

If the opportunity arises once more to study a supra-seasonal drought, it would be recommended to repeat the same measurements of algal mass and macroinvertebrate community to have a means for comparison and determine if the patterns of change are similar. The pattern of macroinvertebrate recovery could also be followed, it is unlikely the exact order of species appearance after drought would be identical as it would depend on the macroinvertebrate seed bank, survival within refuges and time of year. Furthermore, additional ecosystem functions could be studied during drought, including using leaf packs to determine leaf litter breakdown and monitoring organic matter and sediment during and after drought. In order to study the full recovery of the communities, it would be recommended to sample the site for at least a year following rewetting which would allow an investigation into the recovery of longer-lived species.

7.9 Conclusions and final remarks

The processes observed in this thesis allow a deeper understanding of how drought acts as a disturbance in chalk streams and show that dewatering creates a stronger disturbance than previously assumed. This thesis identified that recovery from drought in chalk streams is rapid as had been seen in previous droughts. However, this study investigated community and functional recovery effects which had not been investigated previously in chalk stream droughts. The functional feeding group results show that macroinvertebrate functional recovery is also rapid, and yet, community analyses show that there wasn’t a full recovery five months following drought. This information improves understanding of the processes of freshwater ecosystems during droughts.

7.10 References

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Appendix I Supplementary materials from Chapter 4.

Data exploration graphs from chapter 4. Figure 1 shows boxplots of velocity data and figure 2 shows histograms of velocity data by month and site

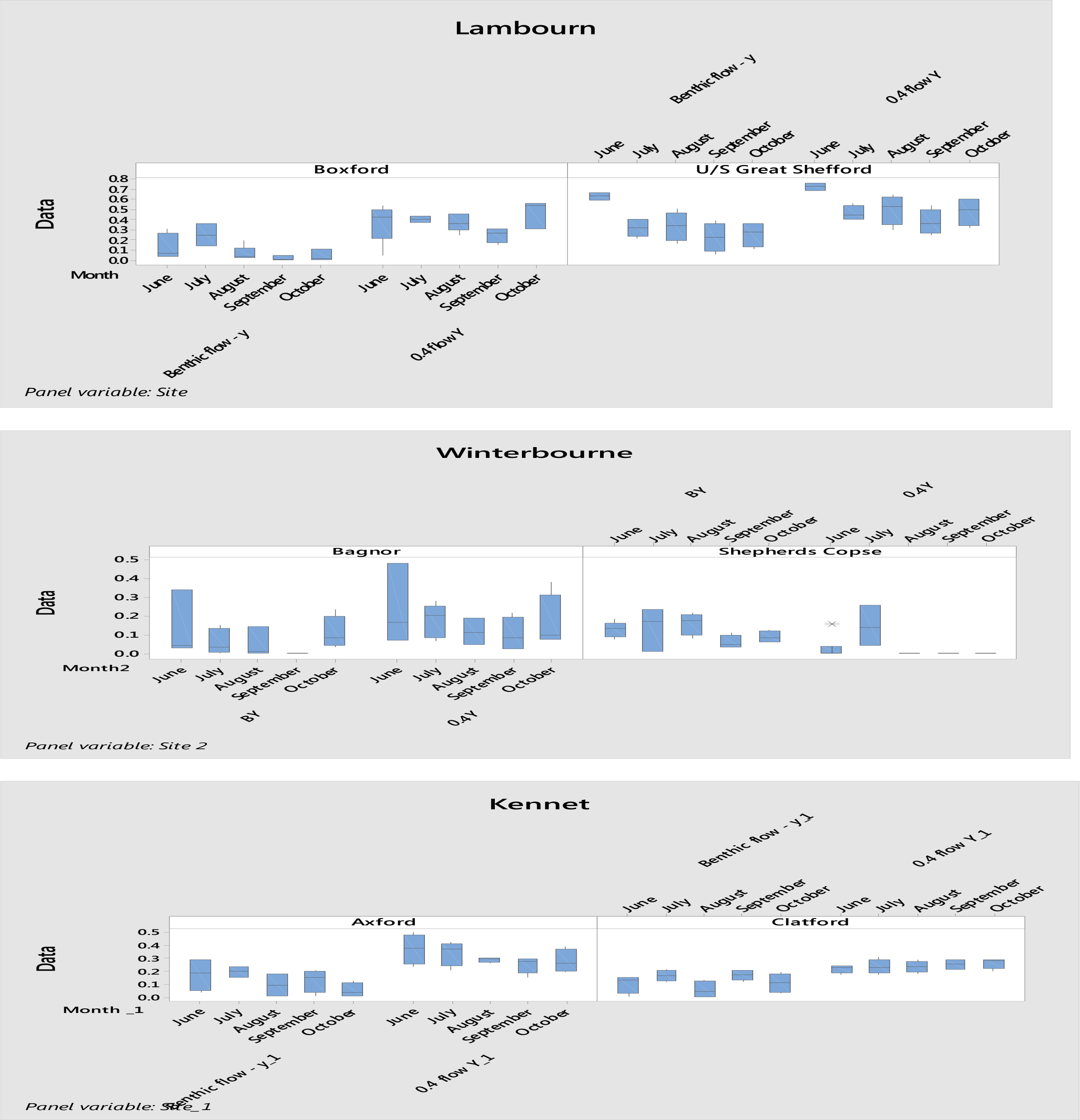


Figure 1: Boxplots of velocity data for chapter 4.

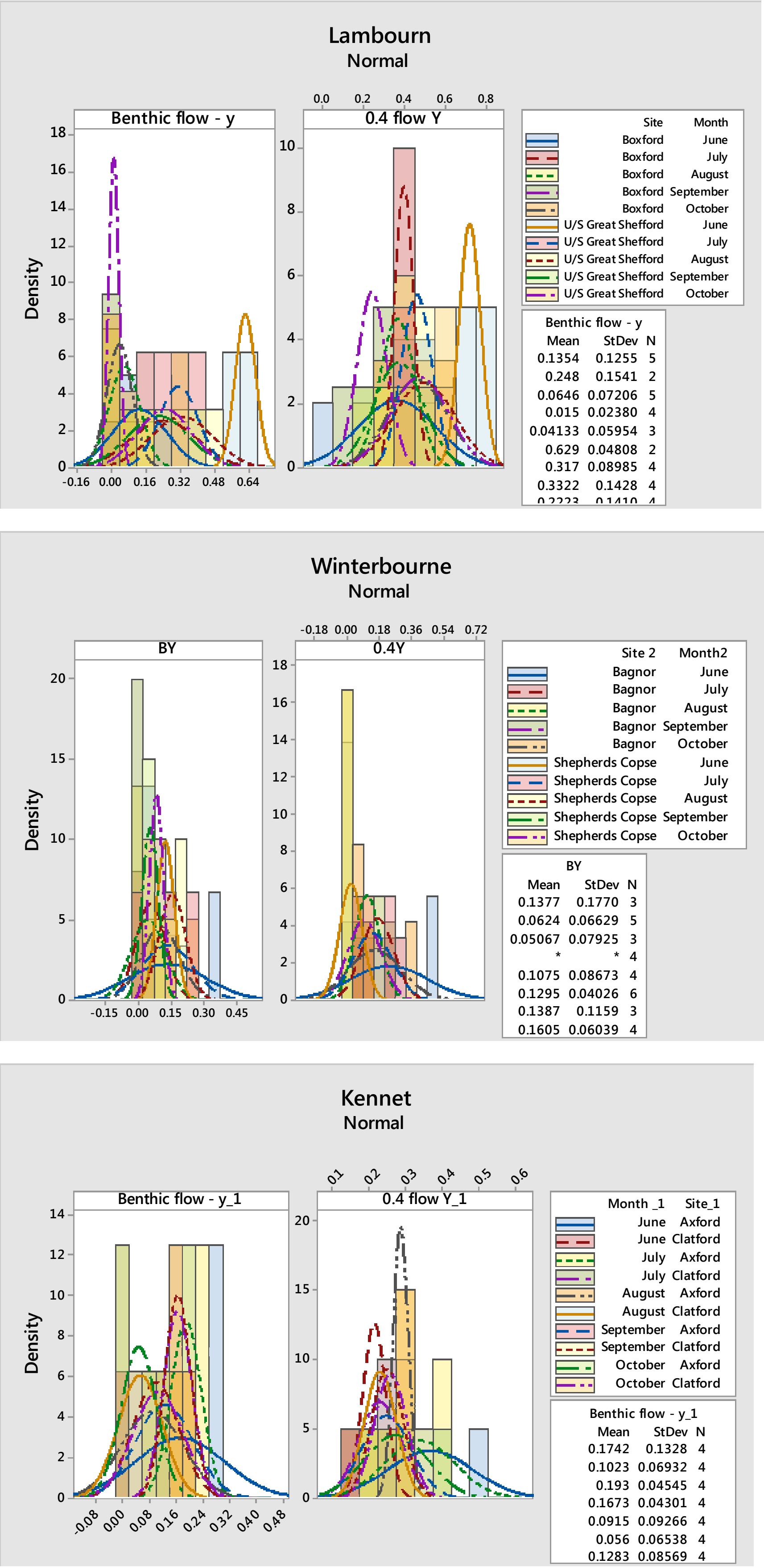
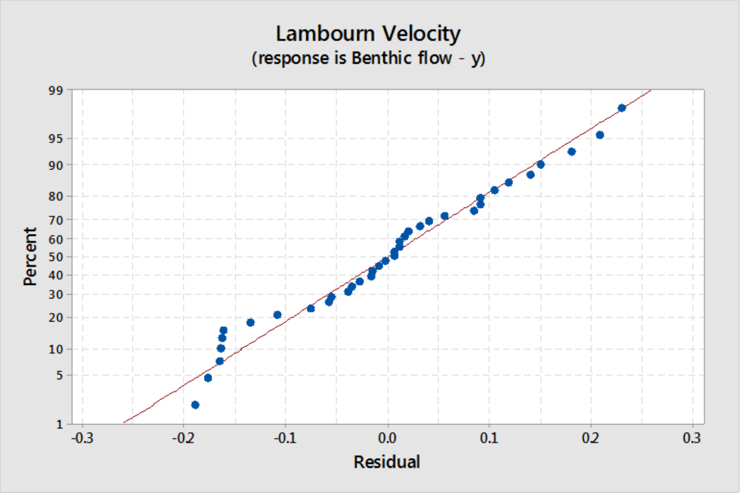
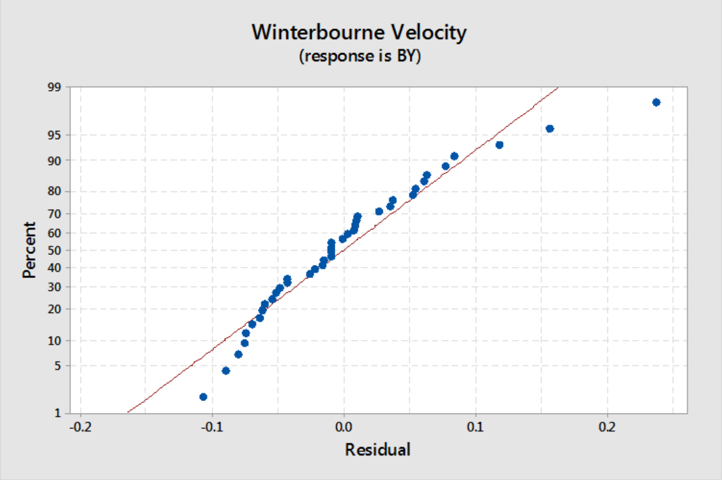


Figure 2: Histograms of velocity data for chapter 4.





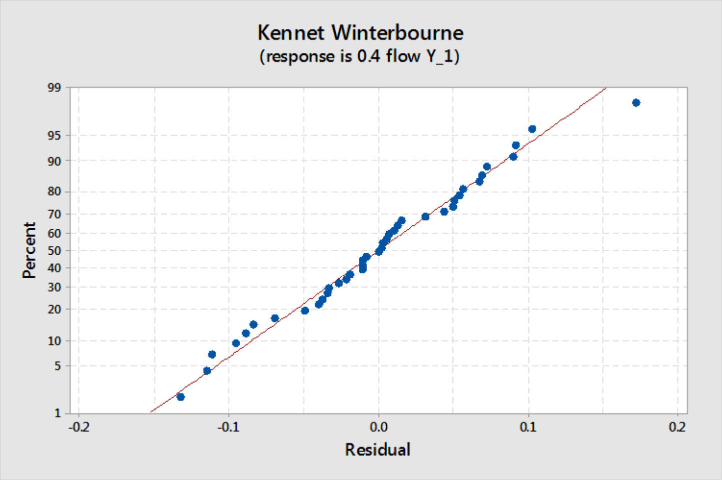


Figure 3: QQ plots of velocity data for chapter 4