THE BIODIVERSITY AND METABOLISM OF PEATLAND POOLS

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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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Abstract

Knowledge of the ecology and ecosystem functioning of pools created by the peatland restoration method of drain-blocking is limited. This thesis provides the most comprehensive study of these peatland pool ecosystems to date. Data were collected to investigate the spatial and temporal distribution of macroinvertebrate communities in both drain-blocked and naturally-occurring pools on areas of blanket bog in northern England. Corresponding environmental data were analysed to identify any mechanisms underpinning biodiversity metrics. The metabolism (i.e. rates of photosynthesis and respiration) of drain-blocked pools was estimated using the diel dissolved oxygen (DO) method.

Drain-blocked pools were found to house macroinvertebrate communities similar to those in natural pools, including taxa characteristic of acid-mire pool habitats, thus providing suitable habitat for peatland aquatic taxa. There was some evidence that pools in reprofiled drains were more biodiverse than L-shaped pools. New pools were colonised quickly with taxon richness peaking in pools aged five to eight years, and pools aged 15 years housing some fauna not found in younger pools. Results suggested that gamma diversity would be best encouraged by creating a range of pool sizes with diverse vegetation composition.

Drain-blocked pools were found to be strongly heterotrophic, with high rates of respiration driven by elevated levels of dissolved organic carbon and the relatively large sediment-water interface. Water temperature and DO profiles obtained from pools in England, Scotland and Sweden revealed severe diurnal stratification regimes, with implications for sampling methodologies, gas fluxes and carbon cycling. This research will help to inform future drain-blocking schemes and also has relevance for studies analysing the biogeochemistry and biota of other shallow waterbodies.

List of Abbreviations

DO	dissolved oxygen
DOC	dissolved organic carbon
EC	electrical conductivity
GPP	gross primary production
MOB	methane oxidising bacteria
NEP	net ecosystem production
POC	particulate organic carbon
R	respiration
TDS	total dissolved solids

Glossary

Alpha diversity

The diversity of a single site (local species pool).

Autotrophic

A system which fixes more carbon via photosynthesis than it respires. An organism capable of photosynthesis.

Beta diversity

The difference in species composition between sites.

Dystrophic

Having brown acidic water that is low in oxygen and supports little life, owing to high levels of dissolved humus.

Eutrophic

Rich in nutrients and so supporting a dense plant population, the decomposition of which may be harmful to biota by depriving it of oxygen.

Gamma biodiversity

Diversity measured at a landscape scale (the regional species pool).

Heterotrophic

A system which releases more carbon via respiration that it fixes via photosynthesis.

An organism which cannot fix carbon for itself and relies on external sources.

Humic substances

A major component of the DOC in peatland aquatic systems; an organic compound of decaying organic matter made up of humic and fulvic acids.

Minerotrophic

Fed by water which has flowed over or through rocks or other minerals, often acquiring dissolved chemicals which raise the nutrient levels and reduce the acidity.

Oligotrophic

Relatively poor in plant nutrients but often containing abundant oxygen in the deeper parts.

Ombrotrophic

Fed exclusively by precipitation

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Chapter 1: Introduction

1.1 Research context

Peatlands are an important global resource of carbon, water and biodiversity. They cover approximately 3% of the Earth's terrestrial surface, but northern temperate and high latitude peatlands alone store between 15–30% of the world's soil carbon (Limpens et al., 2008). In the UK, peatlands cover an estimated 18058 km^2 (Baird et al., 2009) and provide valuable ecosystem services such as water provision, the regulation of greenhouse gases by the sequestration of carbon (C), recreation, agriculture and the provision of renewable energy via wind farms (Ramchunder et al., 2009). Blanket peat, which forms over gently rolling terrain in cool, wet hyperoceanic regions where there is an excess of rainfall over evapotranspiration, accounts for 87% of UK peatland coverage (around 10-15% of the global distribution) making the UK an internationally recognised 'type location' for this habitat (Holden et al., 2004, Baird et al., 2009, Lindsay, 2010). However, common management practises such as rotational heather-burning, over-grazing and the installation of drainage ditches have resulted in widespread peatland degradation (Holden et al., 2007b, Ramchunder et al., 2009).

Historical peatland drainage, implemented on a wide scale in the UK after World War II in an attempt to improve the landscape for forestry and farming, generally failed to meet its objectives (Stewart and Lance, 1983). Furthermore, drainage has been shown to be detrimental; it alters hydrological processes (Holden et al., 2004), increases carbon emissions (Hooijer et al., 2010), affects the terrestrial and stream ecology (Carroll et al., 2011, Ramchunder et al., 2012b) and increases sediment loads and discoloration in upland streams (Mitchell and McDonald, 1995, Holden et al., 2007a, Armstrong et al., 2010). In response to these issues, and also to UK and

European legislation which requires peatland habitats to be maintained in a favourable condition, a program of peatland rewetting schemes (mainly drain-blocking) has been implemented widely across the UK over the last two decades (Holden et al., 2007b, Armstrong et al., 2009, Parry et al., 2014). Drain-blocking methods vary between projects but typically involve the installation of dams, usually made from peat turves, spaced at regular intervals down the length of the drainage ditch (Armstrong et al., 2009). Water quickly collects behind the dams, and so drain-blocking has created of hundreds of thousands (possibly millions) of small pools across the UK peatland landscape. To date, research into the potential consequences of drain-blocking has concentrated mainly on hydrological aspects with a legal and / or financial implication for landowners / water companies, such as levels of dissolved organic carbon (DOC) and water discoloration in peatlands streams (Wallage et al., 2006, Armstrong et al., 2010). However, despite the fact that drain-blocking is a rare case of freshwater habitat creation, comparatively little is known about the ecology of pools themselves.

The importance of studying the ecology of drain-blocked pools is underpinned by the fact that small, lentic water bodies are known to make a vital contribution to biodiversity, particularly at a landscape level, by sustaining a high number of rare and uncommon macroinvertebrate species (Williams et al., 2003, Biggs et al., 2005). The high level of gamma biodiversity seen in ponds and ditches is facilitated by their isolated nature, small catchment areas and heterogeneous physico-chemical attributes, which enable individual ponds to support diverse floral and faunal communities. Indeed, naturally-occurring peatland pools are known to house rare and endangered macroinvertebrate taxa (Maitland, 1999, Verberk et al., 2001, Verberk et al., 2006b). Even pools that do not house rare or endangered species are likely to host taxa that rely, to varying degrees, on acid-mire habitat and are therefore important for their persistence (Boyce, 2004).

While some areas of UK blanket peat already have extensive natural pool complexes, most notably the Flow Country in northern Scotland (Belyea and Lancaster, 2002), others, like the Pennines in northern England, are mainly terrestrial landscapes, with aquatic features limited to streams and isolated sink holes and tarns. It is in these areas that drain-blocking has the potential to be especially beneficial to aquatic biodiversity, by extending the aquatic landscape to new frontiers. Not only will this benefit the taxa which live in the pools, but also the fauna higher up the food chain which feed on them, mainly moorland birds such as Black Grouse (*Tetrao tetrix*), Dunlin (*Calidris alpina*), Golden Plover (*Pluvialis apricaria*), Greenshank (*Tringa nebularia*), Curlew (*Numenius arquata*) and Redshank (*Tringa totanus*), most of which are categorised as red or amber on the UK Birds of Conservation Concern list, and also the economically important Red Grouse (*Lagopus lagopus scoticus*) (Downie et al., 1998b, Buchanan et al., 2006). Furthermore, the configuration of pools in blocked drainage systems (i.e. a cluster of pools regularly spaced over a given area) should act to facilitate the existence of metacommunities, allowing aquatic species to persist in the wider landscape when stochastic disturbances make one or more pools in the cluster temporarily uninhabitable (Leibold et al., 2004). This clustered pool configuration may also attract more moorland birds, as Dunlin abundance in the Flow Country was found to increase along with proximity of a patch of moorland to a pool system (Lavers and Haines-Young, 1996). Furthermore, pools created by drain-blocking may provide future refuge for species forced to migrate upwards and northwards in the face of climate change (Walther et al., 2002, Rosset and Oertli, 2011).

The many potential benefits to peatland biodiversity created by drain-blocking will, however, need to be weighed against any increase in carbon emissions. For example, terrestrial carbon inputs to lentic waterbodies were reported to be, on average, eight times more likely to be mineralised and emitted to the atmosphere than to be buried in sediment (Algesten et al., 2004). Peatland pools are already regarded as hotspots for methane (CH_4) release (Baird et al., 2009, Holden, 2009) and, although less is known about fluxes of carbon dioxide (CO_2), it is now widely accepted that most freshwater systems act as carbon sources rather than carbon sinks (Hoellein et al., 2013). Indeed, the small size of drain-blocked pools might serve to increase their potential as bioreactors compared to larger lakes, due to the proportionately larger water-sediment interface compared to larger lakes, which facilitates the input of organic matter and nutrients to the system and also provides a home for the bacterial communities which process them. Therefore, the role that peatland pools play in the carbon cycle needs further clarification, especially as one of the reasons given to justify the large amounts of money spent drain-blocking is a reduction of carbon emissions from peatlands (Baird et al., 2009, Holden et al., in press).

1.2 Research aims

The overall aim of this thesis is to increase understanding of the environmental characteristics, macroinvertebrate communities and metabolism of drain-blocked pools located on blanket bog in the UK, and to compare them to naturally-occurring pools. Specifically, it aims to answer the following questions:

1) What are the environmental characteristics and macroinvertebrate communities of drain-blocked pools, will they act as suitable ecological surrogates for natural peatland pools, and does the drain-blocking methodology impact on pool biodiversity?
2) How do the environmental characteristics and macroinvertebrate communities of drain-blocked pools change over time and what are the main drivers underpinning any changes?
3) How do rates of photosynthesis and respiration vary in space and time in peatland pools, and are these systems acting as biological sources or sinks of carbon?

By answering these questions, this thesis aims to enhance our understanding of the ecological consequences of drain-blocking, with a view to informing land management policy in the British Isles and beyond and helping land managers when undertaking new drain-blocking schemes and/or managing already restored catchments.

1.3 Thesis structure

The thesis structure is summarised in Figure 1.1. An in-depth review of the global literature review concerning historical drainage, rewetting measures and the ecology of natural peatland pools and those created by rewetting measures is provided in Chapter 2. Chapter 3 investigates the environmental characteristics and macroinvertebrate communities of a set of natural and drain-blocked pools in the Pennines, and also compares drain-blocked pools created by two different blocking methods. Chapter 4 is concerned with how the macroinvertebrate communities and environmental characteristics of drain-blocked pools change over time and uses both a chronosequence (space-for-time) and continuous monitoring approach. The metabolism of a set of drain-blocked pools is analysed in Chapter 5, and Chapter 6 goes on to investigate the diurnal thermal stratification of small, peatland pools and to discuss its impact on biogeochemistry. Finally, Chapter 7 synthesises the main research findings and summarises how they might be incorporated into drain-blocking schemes.

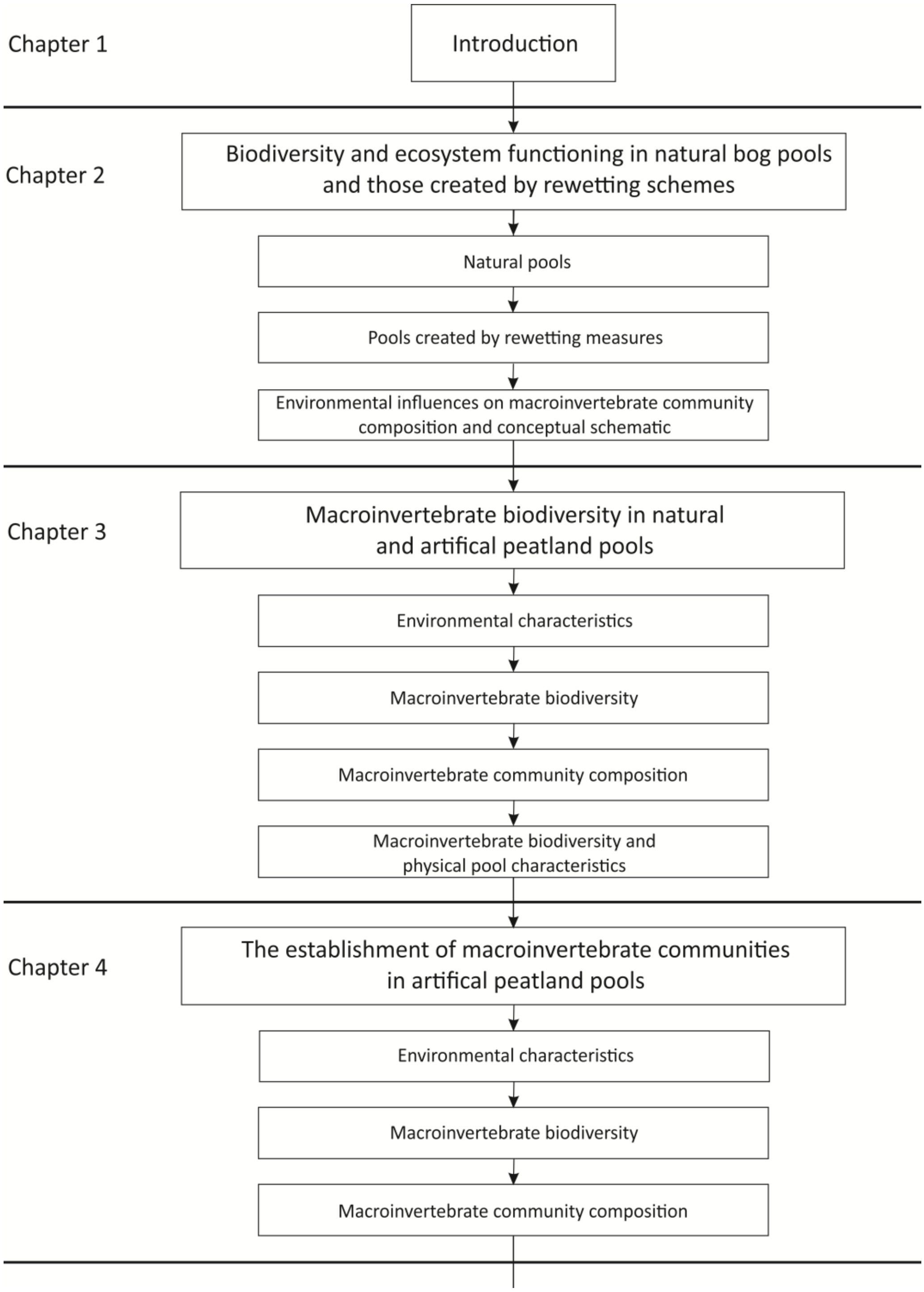

Figure 1.1. Flow diagram outlining thesis structure

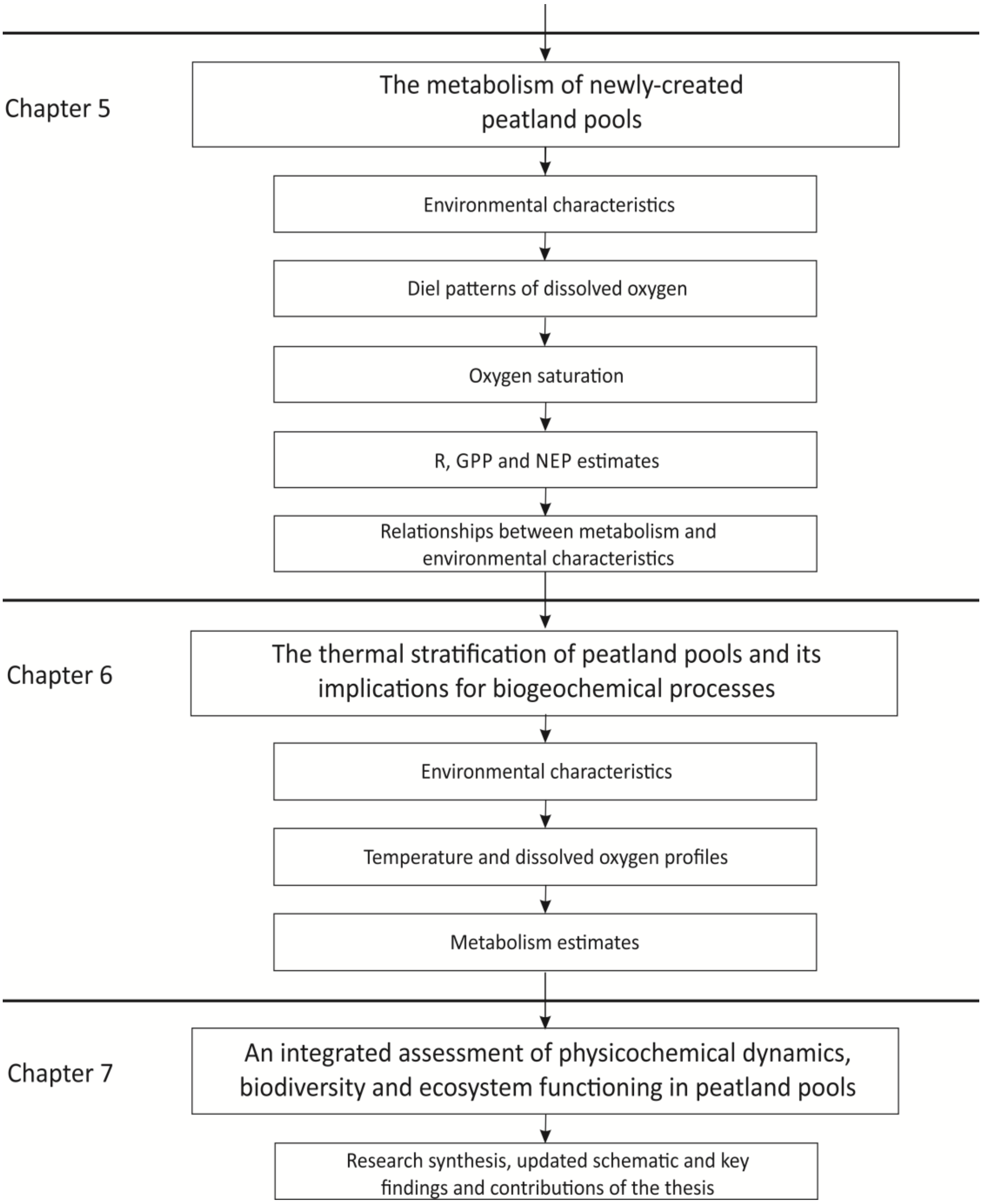

Figure 1.1. continued

Chapter 2: Biodiversity and ecosystem functioning in natural bog pools and those created by rewetting schemes

2.1 Introduction

Peat is an organic soil which consists of the slowly decaying remains of plant material (often *Sphagnum* spp.) which has developed in waterlogged conditions (Bragg and Tallis, 2001). Peatlands which actively accumulate peat are referred to as mires (Lindsay, 2010) and are important carbon sinks which store approximately one third of the world's soil carbon (Yu et al., 2010), although they have the potential to rapidly release it when they become degraded (Holden, 2005, Baird et al., 2009). Peatlands are sub-divided into bogs, which are ombrotrophic (exclusively rain-fed), and fens, which are minerotrophic (influenced by groundwater). However, a peatland landscape may contain areas of both fen and bog. For example, whilst raised bogs massifs (dome-like structures of peat) are indeed exclusively ombrotrophic (Lindsay, 2010) they can be found within a wider landscape which reflects a trophic gradient, including minerotrophic sources and transitional (lagg) zones (van Duinen, 2013). Blanket mires (in which peat cloaks the landscape in a layer that reflects the underlying topography) are mainly ombrotrophic (blanket bog) but may also contain areas of minerotrophic fen (Lindsay, 2010). Blanket mire is a globally scarce habitat which is especially well-represented in the UK and Ireland (Lindsay, 2010). This review concentrates mainly on pools that form on areas of ombrotrophic bog, but takes into account trophic gradients when studies have looked at the wider peatland landscape (e.g. van Duinen, 2013, Verberk et al., 2010a).

Permanent pools are common features on many northern bogs (Figure 2.1). They constitute one of a series of nanotopes (small-scale structural elements also known as microforms) (Lindsay, 2010) (Table 2.1) and there are many theories about how they form (cf.Belyea and Lancaster, 2002). Pools situated entirely within a rain-fed peat profile are characterised by low pH, low levels of primary production and nutrients but high levels of dissolved organic matter which stain the water brown, making the pools dystrophic rather than oligotrophic. However, pools which have any sort of minerotrophic input (e.g. those which are exposed to a mineral substrate) may differ from this pattern and have, for example, higher levels of pH. In general terms, ponds make a vital contribution to biodiversity, particularly at a landscape level, by sustaining a high richness (including rare) of macroinvertebrate species compared with other waterbodies (Williams et al., 2003). In the 2007 UK species and habitat review ponds were therefore added as a new priority habitat, along with dystrophic lakes (JNCC, 2007). However, dystrophic bog pools, which are known to house rare taxa including Red Data Book species and those with nationally notable status, remain relatively understudied (Maitland, 1999, Towers, 2004, Drinan et al., 2013).

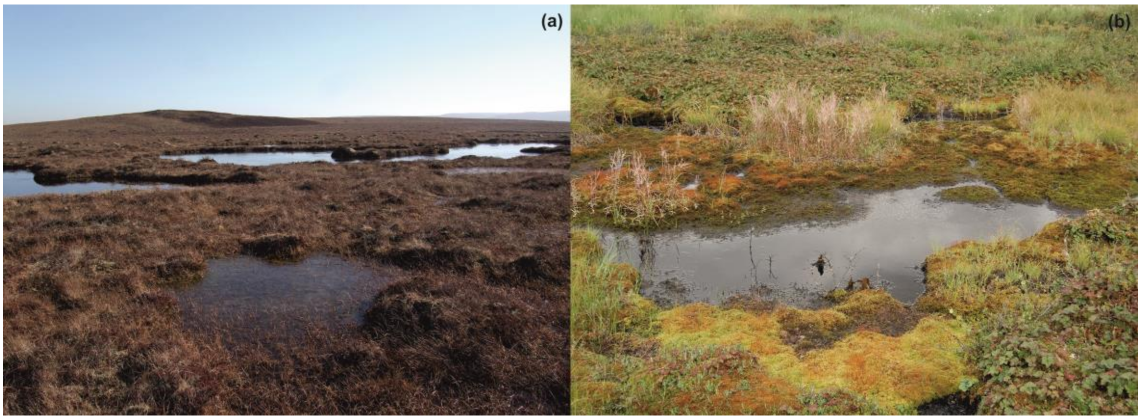

Figure 2.1. Photographs of natural pool systems (a) in the Flow Country, northern Scotland, and (b) on peatland near Abisko, Sweden

Degradation of blanket peat through drainage (an attempt to dry out and improve the land for forestry and farming) and cutting-over (harvesting for peat-based products) has resulted in global problems with increased carbon emissions (Silvola et al., 1996, Hooijer et al., 2010), loss of biodiversity and conservation issues (Littlewood et al., 2010, Carroll et al., 2011) (although see Chapman et al. (2003) for evidence that limited peat extraction may actually enhance biodiversity) and reduced water quality (Holden et al., 2004, Armstrong et al., 2010). However, peatlands have a high conservation value and are one of the habitats listed in the RAMSAR agreement (UN, 1971), '*Sphagnum* acid bogs' are listed under Annex 1 of the EU habitats directive (EU, 1992) and blanket bog is also a UK Biological Diversity Action Plan priority habitat (JNCC, 2007). In recent years emphasis has been placed on rewetting peatlands to try and restore them to a fully functioning, revegetated state (Holden et al., 2007b) and the benefits of rewetting for carbon sequestration has been recognised on an international scale by the Kyoto protocol (Joosten, 2012).

Table 2.1. Classification of nanotopes found on ombrotrophic bogs in Britain. Adapted from Lindsay (2010).

Terrestrial (T) microforms		
Code	**Name**	**Description**
T1	Low ridge	Occupies a vertical range of ~ 0 to 15cm above the average water table. Generally the most species rich zone.
T2	High ridge	Occupies the vertical zone of ~ 15 to 25 cm above the average water table. Forms the predominant nanotope for blanket bog where there is a distinct slope, and for bogs which have suffered some degree of human impact.
T3	Hummock	Occupies the vertical zone of ~ 25 to 1m above the average water table. Invariably formed by moss growth.
Aquatic (A) zones		
Code	**Name**	**Description**
A1	Sphagnum hollow	Occupies the vertical zone of ~ 0 to 10cm below the average water table. Dominated by a more-or-less continuous carpet of the aquatic Sphagnum cuspidatum.
A2	Mud bottom hollow	Shallow pools no more than 20cm deep. Has no dense, continuous mat of Sphagnum, merely scattered pockets of either S. subsecundum or S. cuspidatum.
A3	Drought sensitive pool	Occupies the vertical zone of ~ 20 to 40cm below the average water table. Has an evident expanse of open water, though there may also be loose floating mats of Sphagnum cuspidatum or S.Subsecundum.
A4	Permanent pool	Pools which may be 3 to 4m deep, extending almost to the mineral sub-base, with solid, vertical walls. Consists largely of an open water body in which some detritus and a range of aquatic invertebrates can be found.

By far the most common restoration method adopted in blanket peatlands around the world is to dam drainage ditches (Verberk et al., 2006a, Armstrong et al., 2009) creating pools of water behind each dam (Figure 2.2). The dams (and therefore the pools) are typically spaced evenly along the length of the drain and the pools, being constrained by the drain dimensions, are similar in size, unlike pools in natural systems which can vary substantially in area and depth (Belyea and Lancaster, 2002). In the British Isles many thousands of these artificial pools have been created to restore peatland hydrology (Ramchunder et al., 2012a). In many areas (e.g. much of the Pennines) pools in blocked drains form the only pool complexes within the peatland, thus extending the aquatic landscape to new frontiers and providing habitat for aquatic species as well as vital food and water sources for the many species of moorland birds that utilise blanket bog (Downie et al., 1998b, Buchanan et al., 2006). However, the ecological status of these artificially created pools is almost unknown with only two reports looking at their macroinvertebrate assemblages in the British Isles (Boyce, 2010, Ramchunder et al., 2012a). In the Netherlands, van Duinen et al. (2003) studied pools on areas of raised bog created by rewetting measures and in Canada, Mazerolle et al. (2006) studied pools that they had dug themselves on an area of restored peatland. Other studies have looked at the aquatic ecology of restored peatlands but concentrated on waterbodies which already existed prior to restoration. For example, Verberk et al. (2006a) sampled bog pools, ditches and puddles of different water types (e.g. minerotrophic / ombrotrophic) both before and after re-wetting measures on a heterogeneous bog remnant in the Netherlands.

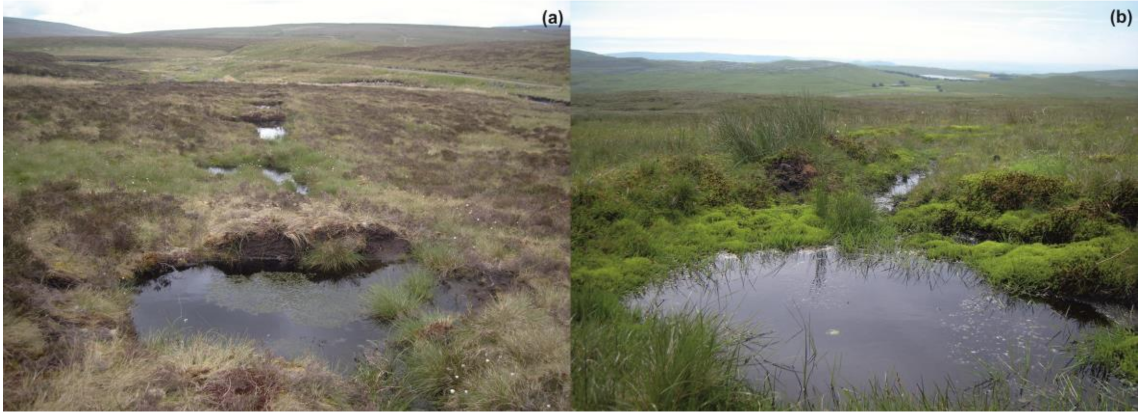

Figure 2.2 Photographs of pools in blocked drains (a) at Moor House National Nature Reserve (NNR), Cumbria, England, and (b) near Malham Tarn, England.

The aim of this review is to provide guidance for land managers involved in drain-blocking schemes on areas of bog who wish to maximise ecological benefits to the aquatic communities in the newly-created pools. We provide some contextual background to the formation of natural pools and the creation of those formed by rewetting measures, before reviewing the literature on the ecology (macroinvertebrates, amphibians and primary producers) of both pool types. We then focus on macroinvertebrates and assess the main factors driving community composition in bog pools to help underpin predictions about community assembly in drain-blocked pools on areas of ombrotrophic bog. Based on the evidence outlined in the following sections, Figure 2.3 provides a conceptual schematic of the potential ecological development of drain-blocked bog pools through time, with corresponding suggestions for research questions. This thesis intends to answer the questions highlighted in red.

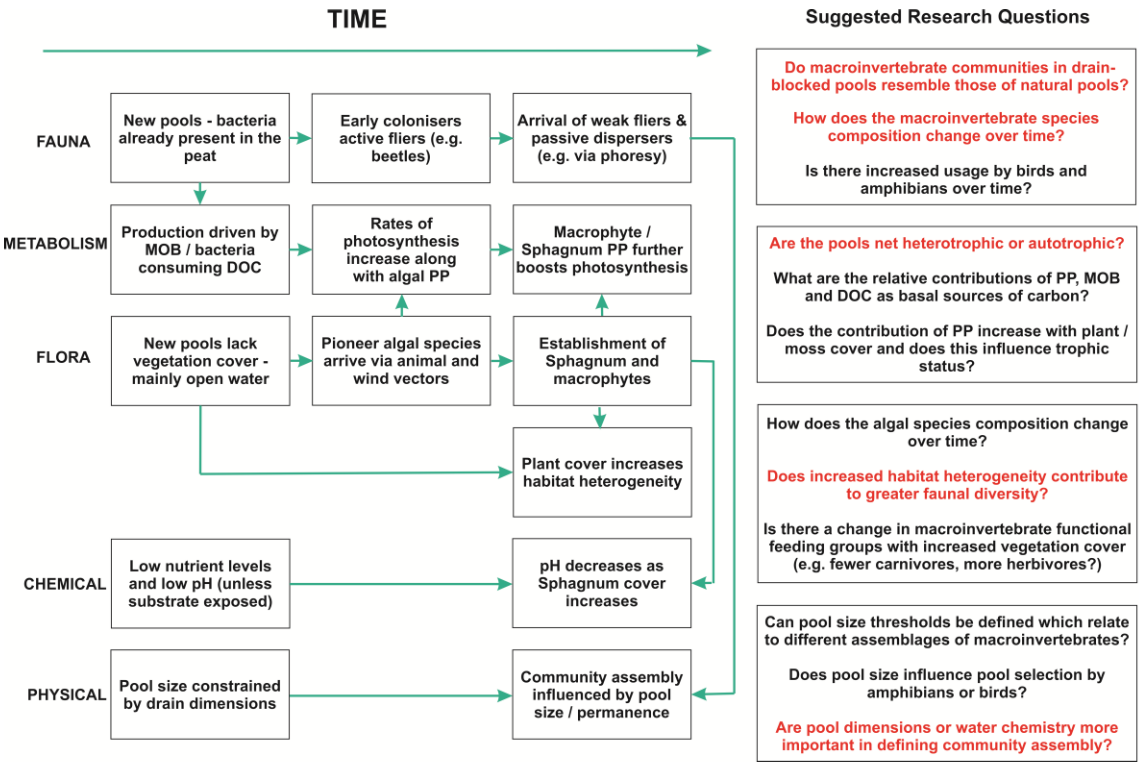

Figure 2.3. Conceptual schematic and associated research questions. How the different ecological elements of drain-blocked pools on areas of ombrotrophic bog might develop and interact over time from the moment of pool creation (i.e., since blocking).

2.2 Natural pools

2.2.1 Formation, distribution and morphology

Open water bog pools have been reported from every continent except Antarctica (Glaser, 1998) and form one of a series of nanotopes which contribute to the patterning characteristic of bogs (Table 2.1). Under the right conditions pool complexes can be extensive. For example, small, open water features (<1km^2) cover up to 77% of the surface area of minerotrophic peatlands in high boreal Quebec, Canada (Connolly et al., 2014). In the British Isles, the presence of permanent open water pools is generally restricted to the most northerly, oceanic areas, making them especially prevalent in areas of Scotland (Lindsay, 1995) where, in strongly patterned areas such as parts of the Flow Country, pools may cover up to half of the surface area (Bragg and Tallis, 2001).

The formation and development of bog pools is strongly related to the local hydrological regime and its interaction with the prevailing climate and topography (e.g. Glaser, 1998). These factors also interact with vegetation to determine the form and extent of the patterning (e.g. Eppinga et al., 2009). Many authors provide evidence for the role of differential rates of peat accumulation and the processes surrounding decay (e.g. Belyea and Lancaster, 2002). Recently, advances in technology such as Ground Penetrating Radar (GPR) have enabled potential links between the positioning of some pools and underlying geological features (e.g. esker crests formed by glacial retreat) to be posited (Comas et al., 2011).

Morphologically, the dimensions of natural pools on blanket bog are generally constrained by the depth of the peat profile; therefore they are typically shallow with a large surface-area to depth ratio. Fundamentally, this structure affects the ecology of the pools; vegetation is able to colonise further into the centre of the water body, although high levels of turbidity can constrain this process leading to mainly open-water pools. Shallow pools do not exhibit the seasonal thermal stratification seen in larger lakes and are more susceptible to reduced water levels in periods of drought.

2.2.2 Primary producers

Although some natural bog pools are heavily vegetated the macrophyte diversity is low. In the British Isles bog pool vegetation is limited to a few aquatic *Sphagnum* species such as *S. cuspidatum* and *S. auriculatum*, sundews such as *Drosera intermedia*, the sedges *Carex rostrata* and *Eriophorum angustifolium* and the bog bean; *Menyanthes trifoliata* (Lindsay, 1995). This pattern seems to be repeated globally. For example a study of natural bog pools in Canada found a similar community structure, dominated by *Sphagnum* mosses, other mosses and liverworts, with lower coverage of ericaceous shrubs, e.g. *Chamaedaphne calyculata* (leather leaf) and *Vaccinium oxycoccos* (bog cranberry), Carex grasses and sundews (e.g. *Drosera rotondifolia*) (Mazerolle et al., 2006).

Whilst *Sphagnum* is seen as the major vegetation component in bog pools, algal communities are also present (Mataloni and Tell, 1996, Nováková, 2002). Microalgae disperse between waterbodies via animal vectors (e.g. birds, water beetles) but there is also some evidence for airborne dispersal via the wind, especially for green algae (cf. Kristiansen, 1996). Although *Sphagnum* generally contributes much more than algae to primary production in wetland habitats (Sigee, 2005), there is evidence that algae forms an important constituent of the food webs in bog pools. A study by van Duinen et al. (2013) undertaken in pristine raised bogs in Estonia found algae to be an important basal component in the diets of consumers. Isotopic analysis suggested that periphtyon (of which green algae was the major component) sustained ~ ½ of the invertebrate population, but results also implied that different species of algae might be responsible for sustaining the entire invertebrate food web.

A study of the phytoplankton communities of pools on raised bog in Tierro Del Fuego, Argentina, found distinct assemblages in different pools, which appeared to be driven mainly by physical variables (pool area and mean depth), with shallower pools displaying higher levels of algal density and species richness (Mataloni and Tell, 1996). Nováková found that algal communities in subalpine peat pools in the Czech Republic were dominated by diatoms and desmids with shallow, peaty pools displaying the highest levels of biodiversity (Nováková, 2002). In the British Isles recent scientific literature on bog pool algae is notably scarce, since Lund (1949) described several new and rare *Chrysophyceae* (golden algae) found in peat pools in the Lake District. However, a recent in-depth and systematic study of desmid communities found along the hummock-lawn-pool nanotope gradient in Scottish blanket mire systems has greatly enhanced our understanding of British peat pool algal communities, and also provided evidence for a new species of desmid, of the genus *Staurastrum* (Goodyer, 2014).

2.2.3 Macroinvertebrates

Table 2.2 lists papers which have studied macroinvertebrate communities in naturally-occurring water bodies on areas of bog along with the taxa identified. In the British Isles, much of this literature is based in the Flow Country of Caithness and Sutherland, Scotland, where study sites are readily available. This body of work is supplemented by studies from Ireland and England, although studies based in England are rare due to the relative paucity of naturally-occurring pools. The taxa identified most often in these studies are; Coleoptera (beetles), Diptera (true flies), Ephemeroptera (mayflies), Hemiptera (true bugs), Odonata (dragonflies and damselflies) and Trichoptera (caddisflies). Other taxa include; Araneae (spiders), small crustaceans such as amphipods, gastropods, copepods and cladocerans (water fleas), Hirudinea (leeches), Hydracarina (water mites), Hymenoptera (e.g. wasps, bees), Megaloptera (e.g. alderflies), Neuroptera (e.g. lacewings), Oligochaete (worms) and Tricladida (flatworms). Stoneflies (Plecoptera) were listed in only one study where the species *Nemoura cinerea* was present in the Korenburgerveen nature reserve in the Netherlands (Verberk et al., 2010a). The scarcity of stoneflies in peat pool studies can perhaps be explained by the fact that they are cold water stenotherms, rarely found in

Table 2.2. A selection of peatland pool macroinvertebrate studies by location along with taxa identified. Papers marked with * studied only the taxa indicated in the table. Ara =Araneae, Col = Coleoptera, Cru = Crustacea, Dip = Diptera, Eph = Ephemeroptera, Hem = Hemiptera, Hir = Hirudinea, Hyd = Hydracarina, Meg = Megaloptera, Neu = Neuroptera,Odo = Odonata, Oli = Oligochaete, Ort = Orthoptera, Ple = Plecoptera, Trich = Trichoptera, Tricl = Tricladida

Paper	Study Site	Water Body	Ara	Col	Cru	Dip	Eph	Hem	Hir	Hyd	Meg	Neu	Odo	Oli	Ort	Trich	Tricl
Caithness and Sutherland, Scotland																	
Foster (1995)*	Loch Fleet	Pools		✓				✓					✓				
Downie et al. (1998a)	Badanloch bog	Pools		✓		✓	✓	✓					✓			✓	
Standen et al. (1998) Standen (1999)	Loch nan Clar & Woodcock Hill	Pools		✓		✓		✓			✓		✓			✓	
Towers (2004)	Forsinard	Pools		✓	✓	✓	✓	✓		✓	✓		✓	✓		✓	
England & Ireland																	
Crisp and Heal (1998)*	Connemara (Ire) Moor House (Eng) South Pennines (Eng)	Lakes, tarns, pools & reservoirs			✓			✓									
Gibbons (1998)	Blake Mere, Staffordshire (Eng)	Mere		✓	✓	✓	✓	✓		✓	✓		✓	✓		✓	
Hannigan et al. (2011)	Kippure/Liffey (Ire) Head bog	Pools		✓	✓	✓	✓	✓					✓			✓	
Hannigan and Kelly-Quinn (2012)	Various - Ireland	pools >100 m^2, pools 10.1–100 m^2 Sphganum hollows		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	
Drinan et al. (2013)*	West of Ireland	Lakes and meres		✓				✓					✓				
International																	
Verberk et al. (2006a) Verberk et al. (2006b) Verberk et al. (2010a)	Korenburgerveen (Netherlands)	Pools, puddles & ditches	✓	✓	✓	✓		✓	✓				✓	✓		✓	✓
van Kleef et al. (2012)*	Estonia & the Netherlands	Various - raised bog landscape		✓									✓			✓	
Mazerolle et al. (2006)	New Brunswick (Canada)	Pools	✓	✓		✓	✓	✓							✓	✓	

water above 25°C, and are adapted to live almost exclusively in oxygenated, running waters (Brittain, 1990). Their presence in the still waters of bog pools is an interesting development and perhaps suggests the importance of such habitats as refuge for species not usually associated with them.

With regards to rare and vulnerable species, in the Flow Country, northern Scotland (blanket bog), Towers (2004) recorded three beetle species with Nationally Notable status: *Dytiscus lapponicus*, *Ilybius aenescens*, and *Gyrinus minute* and the IUCN British Red Data Book caddisfly species *Nemotaulius punctatolineatus*. A baseline survey of acid mire invertebrates on Dartmoor, England, made prior to restoration, found two water beetle species classed as nationally Scarce Category B by Foster (2010); *Paracymus scutellaris* and *Helochares punctatus* (Boyce, 2011). Verberk et al. (2006b) found the rare chironomid, *Lasiodiamesa gracilis*, in oligotrophic pools at their study site in the Netherlands. However, and perhaps unsurprisingly, peatlands with a trophic gradient have been shown to house more rare and endangered aquatic species than do purely ombrotrophic bogs. Studies from the Netherlands, looking at pools situated throughout a raised bog remnant with water chemistry ranging from oligotrophic to minerotrophic, reported many rare beetles including C*olymbetes paykulli* (Verberk et al., 2010a) and the seriously threatened species *Haliplus fulvicollis,* which was found in pools influence by seepage water (Verberk et al., 2001). A study undertaken in pristine raised bog in Estonia found six species of vulnerable, endangered or critically endangered Trichoptera, of which five were far more prevalent in transitional or lagg zones than in the ombrotrophic bog massif (van Kleef et al., 2012). However, the literature suggests that bog pools may be especially important for rare or endangered odonates, such as three of Scotland’s rarest species;

Aeshna caerulea (the Azure Hawker), *Somatochlora arctica* (the Northern Emerald) and *Leucorrhinia dubia* (the White-Faced Darter) (Maitland, 1999). Six species of critically endangered, endangered or vulnerable odonates were found in intact raised bog in Estonia, including *Coenagrion hastulatum* (the Northern damselfly), of which three were more prevalent in the bog massif (ombrotrophic) and three in the transitional or lagg zones (van Kleef et al., 2012). Towers (2004) recorded the presence of *C. hastulatum* (the Northern Damsefly) in Scotland and Drinan et al. (2013) the endangered species *Cordulia aenea* (the Downy Emerald) in Ireland.

2.2.4 Amphibians

Results from a Canadian study looking at artificial and natural bog pools identified four amphibian taxa associated with the pools; green frogs (*Rana clamitans melanota*), leopard frogs (*Rana pipiens*), wood frogs (*Rana sylvatica*) and the American toad (*Anaxyrus americanus*) (Mazerolle et al., 2006). Tadpoles, as well as metamorphosed juveniles and adults were present. Amphibian occurrence was much higher in artificial than natural bog pools, although there was no relationship detected between amphibian abundance and pool size, pool depth or pH. The only strong relationship found was a negative one between the occurrence of green frog tadpoles and cover of herbs and floating vegetation. In contrast, a study by Hunter et al. (2009) in the Kosciuszko National Park, New South Wales, Australia, found that the males of the critically endangered Southern Corroboree Frog (*Pseudophryne corroboree*) selected nest sites in the banks of larger and deeper pools, with a weaker positive relationship between occupied male nest sites and midday pool temperature. A study of amphibians living in a range of fens in a reserve near Nijmegen, the Netherlands, found six anuran species including the common frog (*Rana temporaria*) and the common toad (*Bufo bufo*) (Strijbosch, 1979). The results indicated that spawning did not take place in the most acidic water (pH 3.7), most likely due to the increased occurrence of the spawn being attacked by the freshwater mould *Saprolegnia*. Moulding decreased as pH increased and was virtually non-existent in water with a pH of ~6. In the British Isles, although amphibians such as the common toad (a UK BAP priority species), smooth (*Lissotriton vulgaris*) and palmate (*Lissotriton helveticus*) newts and the common frog are known to utilise pools on blanket bog (Littlewood et al., 2010), quantitative literature is rare. One example is Dibner et al. (2014), who analysed how the common frog utilised pools in mature plantation forests, clear-felled areas, unplanted blanket bogs, and roadside drainage ditches in the West of Ireland. The results indicated a clear preference for roadside drainage ditches as breeding sites. Other studies looking at, for example, pool occupancy rates or the relative importance of amphibians as top-level predators in the absence of fish, are needed to build on these interesting findings.

2.3 Pools created by restoration measures

2.3.1 Background

Globally, peatlands have been subjected to anthropogenic drainage for a variety of reasons. For example, in south-east Asia, vast swathes of tropical peatlands have been drained to facilitate agriculture and forestry, leading to increased CO_2 emissions (Hooijer et al., 2010). Harvesting peat for fuel or horticultural products is also a widespread practise and occurs in areas with some of the world's largest peat deposits such as Russia and Canada (Tuittila et al., 2000, Van Seters and Price, 2001, Poulin et al., 2004). In the UK drainage of upland blanket peat was actively encouraged by the Government after World War II and subsidised at 70% of the cost (Stewart and Lance, 1983). The closely-spaced drains across blanket peat landscapes were originally cut with the intention of drying out peat to develop upland terrain for agriculture; mainly improving sheep grazing and red grouse habitat, and for afforestation (Stewart and Lance, 1983, Holden et al., 2004). Drainage reached a peak in the 1960s and 1970s, especially in the English Pennines (Holden et al., 2004), with aerial photographs of England and Wales suggesting that in some areas over 50% of blanket bog and moorland has been drained and in Scotland some 5000 km^2 of uplands have been subjected to drain development (Coulson et al., 1990).

The British upland drainage policy is now widely regarded as having been unsuccessful (Coulson et al., 1990, Holden et al., 2007b) with no evidence that the original aims were met (e.g. Holden et al., 2007b). Furthermore, there is evidence that drainage was detrimental. As well as the erosion caused by the drainage itself, further degradation was triggered by the increased stocking rates of large grazing animals. Side effects of degraded peatlands included decreased carbon accumulation rates (Silvola et al., 1996, Baird et al., 2009) and increased dissolved organic carbon (DOC) loads and water discoloration in peatland streams (Wallage et al., 2006, Armstrong et al., 2010). Ecologically, drainage altered biodiversity by lowering the water table, resulting in a loss of vegetation adapted to the water-logged conditions and negative impacts on downstream river biodiversity (Ramchunder et al., 2012b). Thus, a process of drain blocking was started in the UK in the late 1980s with the main aim of encouraging water-table recovery and thus the establishment of peat-forming species, notably *Sphagnum* mosses (Armstrong et al., 2009).

The potential consequences of drain-blocking have been the subject of research which has concentrated mainly on hydrological aspects with a legal and / or more direct financial implication, such as levels of DOC and water discoloration (Wallage et al., 2006, Armstrong et al., 2010) which require treatment for potable supply. In contrast, the ecological implications have received scant attention, despite the stated aim of many schemes to restore pre-drainage ecological conditions (Parry et al., 2014). One study based in Northern England looked at the impact on stream macroinvertebrates and physicochemistry (Ramchunder et al., 2012b), another analysed the impact of drain-blocking on cranefly larvae in the peat adjacent to blocked drains (Carroll et al., 2011) and a third looked at vegetation colonisation in pools formed by drain-blocking (Peacock et al., 2013). With regards to macroinvertebrates, some studies have looked at the impact of peatland restoration on existing lentic waterbodies (Verberk et al., 2006a, Verberk et al., 2006b, Hannigan et al., 2011). However, there are only two reports dealing with the macroinvertebrate communities which inhabit drain-blocked pools in peat systems in the British Isles (Boyce, 2010, Ramchunder et al., 2012a) (but see van Duinen et al. (2003) for a study based on a restored raised bog in the Netherlands).

The need to analyse and quantify the potential ecological benefits of drain-blocking is urgent, as there is some evidence to suggest that open-water pools on areas of peatland may act as hot spots for emissions of greenhouse gases, especially methane (Baird et al., 2009, Holden, 2009). Another potential issue is that pools may increase the abundance of the dipteran family Cerapotogonidae (biting midges) which are known to spread diseases, such as the Schmallemberg virus, amongst sheep (DEFRA, 2013). These potentially detrimental impacts of drain-blocking need to be balanced with the possible ecological benefits as the new pools may provide valuable habitat for algae and invertebrates and also food and water for amphibian and bird species. Therefore any decision on possible drain-blocking methodologies needs to be informed by a solid evidence base.

2.3.2 Primary producers

Studies on vegetation in drain-blocked pools are scarce. Mazerolle et al. (2006) undertook a study on a previously mined and partially restored peatland near Quebec City (Canada) in which eight artificial pools were created and the vegetation growth monitored and compared to nearby natural pools. After four years the artificial pools still exhibited substantially less vegetation cover than the natural pools. In particular, mean *Sphagnum* cover was only 21.6% compared to 89.5% in the natural pools. In contrast, Peacock et al. (2013) studied 60 drain-blocked pools on a blanket bog in north Wales and found that pools re-vegetated quickly, displaying a mean total vegetation cover of 76% only eighteen months after restoration. This apparent discrepancy may be explained by varying levels of CO_2 in the water, as low levels have been shown to limit the growth of the aquatic *Sphagnum* species *S. cuspidatum* (Paffen and Roelofs, 1991). Levels of CO_2 may vary due to the abundance of methanotrophic bacteria living alongside the moss which oxidise methane to produce CO_2 (Raghoebarsing et al., 2005), but CO_2 data were not available for the two studies. Shallower pools in the North Wales study (Peacock et al., 2013) were dominated by *Eriophorum* sedges whereas deeper pools exhibited more *Sphagnum* coverage, and two pools exhibited substantial algal growth. In newly-created pools with limited vegetation cover algal growth can be substantial (Peacock et al., 2013) and may contribute significantly to the food web.

There is evidence that drain-blocked pools promote algal biodiversity, as artificial pools at Moor House NNR (English Pennines) were recently reported to house a species previously unreported in the British Isles; *Saturnella saturnus* (Figure 2.4) (Beadle et al., 2014). A study by Goodyer (2014) looked at how desmid communities reacted to both drainage and drain-blocking in Scottish blanket mires. Results showed that desmid species richness was very low in drained peatland, compared to nearby intact mire, but that it did recover, after drain-blocking, to ~ 70% of the diversity of nearby intact peatland after twelve years.

Figure 2.4.Photograph of the green alga *Saturnella saturnus*. Found for the first time in the British Isles in drain-blocked pools at Moor House NNR, Upper Teesdale, England © C.F. Carter (6cvw@freeuk.com).

2.3.3 Macroinvertebrates

A study by van Duinen et al. (2003) of various raised bogs in the Netherlands compared macroinvertebrate communities found in remnant pools (formed in old peat cuttings or buckwheat trenches abandoned 50+ years ago) and restored pools (created by rewetting measures no longer than 29 years previously). The pools housed five provisional red-list beetles species as defined by Drost et al. (1992) and the red-listed odonates *Leuchorrhinia dubia* (the White-Faced Darter) and C*oenagrion lunulatum* (the Crescent Bluet or Irish Damselfly), along with four red-listed caddisflies. In Canada, Mazerolle et al. (2006) found only Coleoptera, Hemiptera and Anisoptera in eight pools they had dug on an area of restored peatland four years previously. The species found were not reported as being rare or endangered, but the authors did note that the beetle species included several peatland specialists such as *Colymbetes paykulli* and *Hydrobius fuscipes*.

In southern England, the Exmoor Mire Restoration project, undertaken by South West Water, carried out a survey of invertebrates (terrestrial and aquatic) on areas of blanket peatland subjected to drain-blocking (Boyce, 2010). Four aquatic taxa were targeted by pond-netting; Odonata, Hemiptera, Coleoptera and Diptera (Tipuloidea – craneflies). Although no Red Data Book species were identified, the authors listed several key species including the acid-mire specialists *Sympetrum danae* (Black Darter dragonfly) and the water boatman species *Hespercorixa castanea.* Amongst the beetle species was the acid-mire obligate *Helochares punctatus*, which is classed as Nationally Scarce Category B (Foster, 2010). Ramchunder et al. (2012a) provided initial findings from a study looking at 20 natural and 20 drain-blocked pools in the English Pennines. Twenty six macroinvertebrate species had been identified to date including; Hemiptera, Coleoptera, Trichoptera, Plecoptera, Diptera (craneflies and chironomids) and Odonata (damselflies). These findings generally agree with the existing British Isles-based literature on natural pools, especially with regards to the dominance of chironomids, beetles and true bugs. The presence of stoneflies (Plecoptera) in this study was especially interesting as this taxa was listed in only one other study reviewed for this paper (Verberk et al., 2010a), when the occurrence of one species, *Nemoura cinerea*, was found to have increased following re-wetting measures in a raised bog remnant in the Netherlands. The species found in the British-based study was also from the genus Nemoura (*Nemoura cambrica*), and was found in both natural and artificial pools.

2.3.4 Amphibians

A study looking at amphibians in artificial pools, based in Canada, involved pools dug on peatland by the authors (Mazerolle et al., 2006). The results showed that use of artificial pools by amphibians was substantially higher than use of naturally-occurring pools; for example, the mean number of green frog tadpoles found in 70 natural bog pools was 2.1 ± 10.8, and in only eight man-made pools was 22.9 ± 64.8. These findings indicate that drain-blocked pools may provide a vital addition to the habitat range of these taxa, although the sampling took place in different years (1999-2000 for the natural pools and 2003 for the artificial pools) so differences due to other factors (e.g. weather) cannot be ruled out. However, a study by Dibner et al. (2014) in the West of Ireland also found that artificial waterbodies (in this case roadside drainage ditches) were utilised more by the common frog than other, natural waterbodies in the same area. One potential reason for this may be that drainage ditches provide useful connectivity within the landscape. If this is the case, then drain-blocked pools in drainage systems on areas of bog may well prove to be similarly useful.

2.4 Environmental influences on macroinvertebrate community composition

The factors which enable ponds to contribute so much to landscape-scale diversity; their isolated nature, small catchment areas and heterogeneous physico-chemical attributes (Williams et al., 2003, Biggs et al., 2005) also lead to low levels of inter-pool community similarity. This, along with the often stochastic nature of community assembly (Belyea and Lancaster, 1999) can make it difficult to compare pools and analyse the potential mechanisms driving the processes of colonisation and subsequent community assembly. However, some factors known to play a part in the community structure of lentic habitats are discussed here, with a view to explaining the pool macroinvertebrate communities described above (sections 2.2.3 and 2.3.3). These factors will be considered to identify which could be most influential in shaping community assembly in pools created by re-wetting measures on areas of bog. However, it must be noted that pool characteristics often combine to shape community structure, so there is some inevitable overlap between the sections.

2.4.1 Pool size / permanence

Ecologists have long observed a positive relationship between habitat area and the number of species found there, a phenomenon referred to as the ‘species-area’ curve (Connor and McCoy, 1979). One explanation for this is that larger areas usually encompass more habitat types (Williams, 1943). However, MacArthur and Wilson (1967) expanded upon this with the equilibrium theory of island biogeography, which argued that both the size and the isolation of an island play a part in the number of species present by helping to determine the balance between immigration and extinction. Lentic water bodies are effectively habitat islands, with smaller pools especially prone to stochastic extinction events such as extreme temperature fluctuations and desiccation. In this way, pool size and permanence are inextricably linked and together play a vital role in shaping their aquatic communities. However, it has also been posited that small, isolated waterbodies may be an exception to the theory of island biogeography, at least for certain taxa (Scheffer et al., 2006). These authors argue that the impact of species interactions, namely the absence of top predators (i.e. fish) from such habitats, means that the relative abundance and species richness of other taxa (e.g. macrophytes, macroinvertebrates and amphibians) can flourish. The absence of fish also promotes a more species-rich and complex pool vegetation structure. Thus, small, fishless waterbodies will house more macroinvertebrate taxa per unit area than larger lakes containing fish. However, although bog pools are fishless, they are known to be home to amphibians (Littlewood et al., 2010) and are frequented by moorland birds which may act as top-level predators.

Oertli et al. (2002) analysed data from 80 ponds across Switzerland, including bog pools, which were assigned to different size classes. Whilst increased size correlated with increased richness and abundance, the relationships were fairly weak for most taxa with the exception of Odonata and Gastropoda. Odonates are widely represented in peat pool studies where they have been found to dominate in larger, more permanent pools (Larson and House, 1990, Foster, 1995, Standen et al., 1998, Oertli et al., 2002, Mazerolle et al., 2006). This could be due to several factors such as increased availability of prey or oviposition sites, but may also be because their relatively longer, often semivoltine, life cycle requires the protection of permanent water coverage for the developing larvae, as is the case with *Aeshna juncea* (Common Hawker) (Johansson, 2000). However, another of the species commonly found in bog pool studies - *Sympetrum danae* (Black Darter) – has a univoltine life cycle (Johansson, 2000), so may be equally able to thrive in smaller pools.

For other species the relationship is less clear. Towers (2004) studied 22 natural bog pools in a complex at Forsinard, Scotland and found only a weak, non-significant relationship between pool size and species richness. The author theorised that this may be because all the pools across the size gradient had similar vegetation structures and also were in close proximity to each other, allowing cross-colonisation of an already impoverished species pool. Drain-blocked pools will also meet these criteria, being similar in structure and closely grouped together. The analysis of Towers (2004) did, however, show a change in community composition along a patch-size gradient, with at least one size-related character (perimeter, area or depth) always proving important in explaining community composition. For example, depth was the only significant variable explaining Dytiscid beetle assemblages in baited traps, probably as they actively use the water column for predation. Similarly, in a study by Mazerolle et al. (2006) in Canada the capture rates of Hemipterans in natural peat pools was positively correlated with pool perimeter, potentially because many Hemipterans (e.g. Gerridae) make use of the pool surface. A study by Hannigan and Kelly-Quinn (2012) highlighted the differences between peatland pools and *Sphagnum* hollows. The authors studied pools > 100 m^2, pools 10.1 – 100 m^2 and *Sphagnum* hollows on peatlands in Ireland and found that, whilst there was no significant difference between habitats in terms of taxon richness or abundance, community composition and structure differed significantly between the pools and hollows.

Several studies have found that small pools tend to house small beetles. Standen et al. (1998) showed that temporary pools in the Flow Country of Scotland were dominated by small beetles of the subfamily Hydroporinae. In another study in the Flow Country, Downie et al. (1998a) found no individuals from the anatomically largest subfamily (Dytiscinae) in the smallest pools in their study, which instead were dominated by the comparatively smaller Hydroporinae and Colymbetinae. A study by Foster (1995) of peat pools at Loch Fleet, Scotland, also found that shallow pools were dominated by small diving beetles (genus *Hydroporus*) whereas deep pools housed the comparatively larger diving beetles (genera *Agabus* and *Ilybius*). These findings may be suggestive of a level of niche differentiation, with smaller and larger beetles potentially dividing resources to avoid direct competition. All dytiscids are predators, both as larvae and adults, so will compete for the same food sources, but smaller species should be able to fulfil their nutritional requirements in a smaller water column. However, all beetles with a univoltine life cycle - that includes a summer larvae and overwintering adult phase (e.g. the larger *Agabus arcticus*) - will be able to take advantage of smaller, temporary pools in the summer for larval development.

Pools of different sizes may promote biodiversity due to their exploitation by species with different functional traits and life histories. Verberk et al. (2008) analysed macroinvertebrate datasets from a range of waterbodies located in the Korenburgerveen nature reserve (Netherlands), including bog pools. They found that, whilst large and small bog pools were relatively similar with regards to the life-history strategies of the macroinvertebrates inhabiting them, small, shaded bog puddles differed slightly as species needed to be able to react to more unstable water levels. Species addressed this in different ways, with resistant diapausing stages or with relatively long-lived adults capable of dispersal during dry periods. This indicates that even very small pools can be useful to a range of macroinvertebrates.

The above studies suggest that, whilst there is a relationship between increased pool size and changes in community composition, it is a complex one underpinned by other variables, both biotic and abiotic. The size of pools formed in drains will be constrained by the drain dimensions and the topography of the terrain. If, however, one of the objectives of blocking on a particular site is to encourage colonisation by a wide of aquatic macroinvertebrates, then land managers could consider creating a range of different size pools by manipulating the shape of the drains directly behind the dam, both vertically and horizontally. It seems reasonable to assume, for example, that the creation of larger pools may especially benefit taxa with semivoltine life cycles (i.e. life cycles that take more than one year to complete) by affording more stability and protection for the developing larvae. Such taxa include some species of dragonflies and damselflies which are amongst the most charismatic taxa to inhabit pools on blanket bog.

2.4.2 Habitat heterogeneity

The link between higher levels of habitat heterogeneity and increased biodiversity is a well-established ecological theory (Tews et al., 2004). The theory assumes that more complex habitats (usually referring to the range of vegetation structure present) provide more niches for species to exploit and therefore promote increased biodiversity. Previously, habitat heterogeneity has been regarded simply as part of the species-area curve theory (section 2.4.1) but increased size does not always lead to increased structural heterogeneity, and bog pools are a good example of this. For example, in British peat pools macrophytes are generally limited to a few species, mainly aquatic *Sphagnum* species and *Eriophorum* sedges (Lindsay, 1995, Peacock et al., 2013) and this relative homogeneity of vegetation was one theory posited by Towers (2004) to explain the lack of a species-area relationship in her work looking at bog pools of different sizes at Forsinard. In this section, we look at the influence on macroinvertebrate communities of (1) the structural complexity within an individual pool and (2) the diversity of habitats within the wider landscape.

Different taxa of aquatic beetles are known to make use of different mesohabitats such as pool surfaces (e.g. Gyrinidae), the water column e.g. (Dytiscidae) and steep-sided pool edges (e.g. larger species of Dytiscidae), whilst others utilise

Sphagnum carpets and vegetation mats (Foster and Bilton, 1998, Fairchild et al., 2000). Indeed, variance in the morphology of different beetle species (e.g. body shape, size, leg configuration) dictates their swimming capability, particularly the balance between velocity and manoeuvrability, and therefore whether the species is more suited to open water (i.e. pool middle) or more densely-vegetated habitats (i.e. pool margin) (Ribera et al., 1997). This was reflected in a study by Verberk et al. (2005) in the Netherlands, which found a clear link between invertebrate locomotion and microhabitat preference. However, Downie et al. (1998a) found no significant difference in either individual abundance or community composition between pool centre and edge for Coleoptera or Hemiptera in a study based in the Flow Country. In contrast, a study of peatland restoration measures in Canada by Mazerolle et al. (2006) found that capture rates of some macroinvertebrate taxa were influenced by different types of pool vegetation. Beetles and damselflies were negatively associated with tall shrubs and emergent vegetation, whereas Hemipterans were negatively associated with low shrubs and moss cover. Capture rates of damselflies increased amongst submerged and floating vegetation. Thus, encouraging the colonisation of different types of vegetation may increase macroinvertebrate diversity in drain-blocked pools, although the practicality of this process is untested. For example, Mazerolle et al. (2006) found that an attempt to encourage vegetation colonisation by stocking half of their artificial pools with aquatic vegetation, including *Sphagnum cuspidatum*, from nearby sources had no significant impact on subsequent vegetation growth compared to the unstocked pools.

Landscape heterogeneity, as opposed to within-pool heterogeneity, may also be a factor in levels of biodiversity. Verberk et al. (2006a and 2006b) looked at how restoration (re-wetting) measures impacted on macroinvertebrate communities in areas of raised bog with water-bodies along a trophic gradient (and therefore increased landscape heterogeneity) in the Netherlands. The authors found that re-wetting led to an overall decrease in biodiversity, with common species increasing in numbers and rarer, characteristic species declining. However, the study areas in this report were on raised bog with pockets of minerotrophic input amongst the ombrotrophic areas, meaning that there was more inherent heterogeneity (and therefore probably more macroinvertebrate diversity) than would be found on blanket bog, which tends to have a more constant nutrient status. Thus, the homogenising potential of re-wetting measures would be, by definition, greater on areas of heterogeneous raised bog than on its blanket counterpart. Also, many of the areas in England subjected to drain-blocking do not have naturally occurring pools prior to restoration, so there are far fewer existing aquatic populations which can be adversely impacted by the measures.

2.4.3 Pool age

Ecological succession, defined as 'the sequential replacement of species following a disturbance (a relatively abrupt loss of biomass or structure)' (Prach and Walker, 2011) is a well-established ecological theory (Connell and Slatyer, 1977). The communities of most habitats change through time due to many reasons, e.g. species-environment interactions (Chase, 2007), species-species interactions (Macarthur and Levins, 1967, Abrams, 1983) and stochastic or neutral factors such as birth, death, colonization, extinction and speciation (Hubbell, 2001). Community assembly is dictated by three main factors as discussed by Belyea and Lancaster (1999): dispersal constraints, environmental constraints and internal dynamics, and it is reasonable to assume that macroinvertebrate communities in newly-created pools will differ from those in long-established pools as a result of these factors. For example, pool age was found to be the most important factor determining beetle assemblage in 18 freshwater lowland ponds in Pennsylvania, USA (Fairchild et al., 2000), with predatory dytiscids prevailing in young ponds and herbivorous species in older ponds with more developed vegetation communities. However, a study in a heterogeneous bog remnant in the Netherlands found that deterministic processes and stochastic processes operated simultaneously, but that their relative importance varied for species with different life-history traits; habitat generalists were more influenced by stochastic processes (e.g. colonisation and extinction rates) and habitat specialists by deterministic processes (e.g. environmental conditions) (Verberk et al., 2010b).

The age of many natural peat pools is unknown, but drain-blocking measures provide an ideal opportunity to analyse community assembly in lentic habitats by monitoring floral and faunal succession in drain-blocked pools from the moment of pool creation. Also, as land managers usually keep detailed records about when drains are blocked, and pools form almost immediately behind the dams, pools can be reliably aged and chronosequence (space for time) studies may be undertaken.

There is some evidence that older pools house more rare and characteristic bog species than younger pools. A study by van Duinen et al. (2003) on areas of remnant and restored raised bog in the Netherlands, found that the older remnant water bodies (at least 50 years old) housed more fairly-rare, rare and very-rare species than the younger restored pools (no more than 29 years old), as well as more species classed as characteristic of raised bog systems. In a shorter-term study in Canada, Mazerolle et al. (2006) dug eight pools in an area of peatland formerly subjected to peat extraction but now undergoing restoration measures. After four years, invertebrate abundance and species richness was still substantially lower in the man-made pools as opposed to natural pools in nearby, relatively undisturbed peatlands. However, in a study on restored blanket bog in County Wicklow, Ireland, Hannigan et al. (2011) found no significant difference in macroinvertebrate communities between natural pools on an intact peatland and those on a bog restored fifteen years previously. Taken together as a timeline these three studies suggest that artificial pools may come to more resemble more established / natural pools with increased age, although this is likely to happen over a period of decades rather than years (so chronosequence studies may be more time-effective than those based on direct observation). Thus, it seems probable that the communities in drain-blocked pools could develop over time to provide suitable long-term habitats for aquatic species if they were allowed to persist. Of course, this also depends on the suitability of the pools themselves (environmental factors) and the availability of nearby ‘source’ communities (Van Duinen et al., 2007). Another point to note is that larger, deeper pools would be more likely to remain as open water systems so if the establishment of aquatic macroinvertebrate communities is a consideration in peatland restoration measures, then the creation of at least some larger pools should be considered.

2.4.4 Dispersal of aquatic invertebrates

Aquatic invertebrates are usually classed as either passive or active dispersers (Figure 2.5). Active dispersal is achieved by adults with flying capabilities whereas passive dispersal is accomplished via animal vectors or transport by wind (Bilton et al., 2001). A further type, temporal dispersal, could be defined as the ability to survive through periods of unsuitable environmental conditions (e.g. dormant propagules stored in sediment or diapause). Neighbouring pools are more likely to exhibit similar community composition then those further apart due to two main factors: (1) ponds closer together are likely to have similar environmental conditions which suit certain taxa and (2) invertebrate dispersal occurs in fragmented populations between reachable, suitable habitats, leading to the existence of meta-populations.

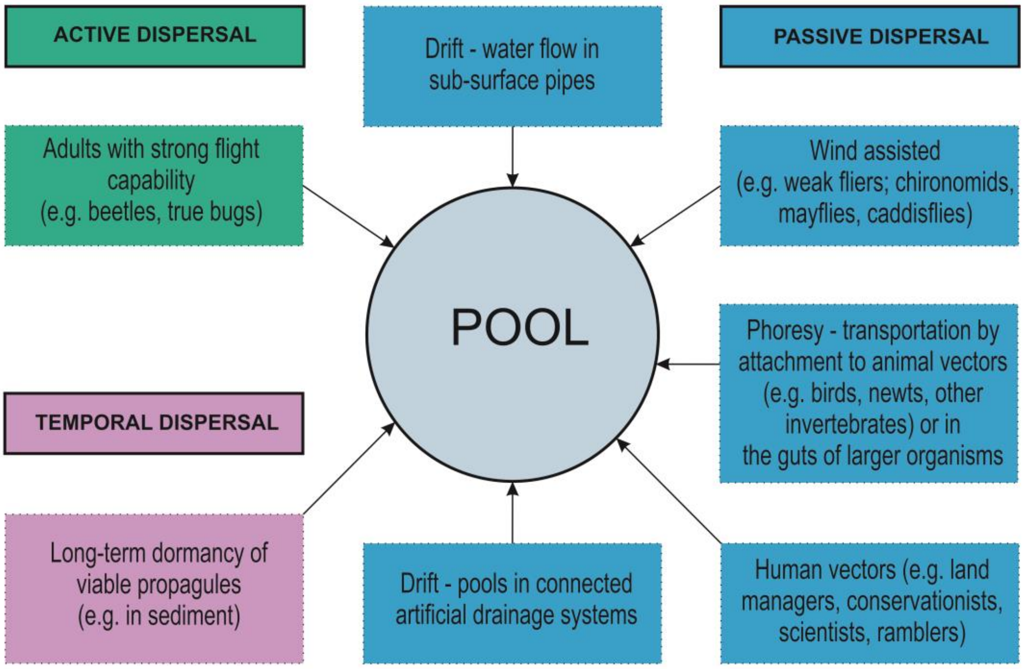

Figure 2.5. Potential dispersal mechanisms of macroinvertebrates inhabiting peat pools.

In England, although drain-blocked pools in the same drainage system are very close to each other, initially they do not often have a ‘source’ macroinvertebrate community close by, due to the lack of naturally-occurring pools. Instead, colonising invertebrates potentially come from tarns or sink holes, or valley bottom lakes and streams, but these are often sparse and isolated. It seems likely, therefore, that initial colonisation of drain-blocked pools may be slow but that once a few pools in a system are invaded then the capacity to spread out along the entire drainage system would increase. Also, the more drainage systems are blocked, the more pools are created and cross-colonisation between areas is facilitated. This is reflected in a study of lowland urban ponds which found a highly significant correlation between macroinvertebrate species richness and pond density (i.e. more species were found in ponds that were close together) (Gledhill et al., 2008). Furthermore, a study by (Verberk et al., 2006b) found that adjacent water-bodies in a heterogeneous bog remnant were more similar than environmental conditions would have anticipated. This suggests that invertebrates will disperse to nearby waterbodies even if environmental conditions are not ideal, so prioritising areas of drained bog close to existing waterbodies for blocking will facilitate the dispersal of invertebrates across the wider landscape.

Predatory dytiscids (Coleoptera) have been shown to be early colonisers of newly created pools (Fairchild et al., 2000). A likely explanation for this is that flight is an important element of the life cycle of the vast majority of adult water beetles. For example, the strong flight capacity of *Colymbetes paykulli*, a beetle restricted almost entirely to the cold-water of sphagnum bogs, was demonstrated by Mazerolle et al. (2006). This species colonised a man-made pool in Canada within two years of its creation when the nearest natural pools were 40km away. As with beetles, some adult hemipterans are able to actively disperse via flight and therefore may also be amongst the first to colonise drain-blocked pools. Evidence for this was provided by Mazerolle et al. (2006) who dug eight pools in an area of Canadian peatland. After four years, Hemiptera and Coleoptera accounted for almost the entire invertebrate community in the man-made pools, suggesting they are effective early colonisers.

Passive dispersal is a risky strategy, as an organism has no control over its final destination. Hence, many passive dispersers have evolved adaptations to increase their chances of success. These include physical features such as hooks or sticky appendages to facilitate adhesion to an animal vector, and also phenological adaptations which include timing the production of the bulk of small dispersing stages to coincide with bird migrations (Bilton et al., 2001). In the case of drain-blocked pools, passive dispersal via bird vectors could prove to be a successful mechanism as moorland birds are attracted to areas of blanket bog with many pools (Lavers and Haines-Young, 1996) and, due to the drainage systems in which they form, drain-blocked pools often occur in large numbers and in close proximity to each other.

2.4.5 Water chemistry and gases

One element of water chemistry which has been shown to be important in dictating community composition in at least some lentic habitats is pH (Batzer and Wissinger, 1996). However, studies concentrating specifically on peat bog pools have generally discounted pH as a contributory factor when explaining community composition (Standen et al., 1998, Towers, 2004). This is likely due to the fact that pH levels in peat bog pools are kept consistently low, typically <pH 4.5 in areas dominated by *Sphagnum* (Clymo, 1967). Readings from studies in the Flow Country, Scotland, vary very little, for example from just below 3.5 to just above 4.5 (Towers, 2004) and such restricted ranges are unlikely to account for much variation in species assemblages. In a more heterogeneous raised bog landscape, the pH range is greater and does contribute to higher levels of biodiversity (e.g.van Duinen, 2013).

Bog pool studies which measure pH levels do not always measure other chemical properties such as electrical conductivity (EC), nutrient levels or dissolved oxygen (Standen et al., 1998, Mazerolle et al., 2006). Towers (2004) measured EC and total dissolved solids (TDS) but did not relate either to community composition. Nutrient levels in peat pool water are generally low, with Hannigan et al. (2011) reporting that that levels of nitrite, nitrate and ammonia were too low to be detected (<0.001mg l^{-1}), with pools also exhibiting low conductivity, ranging from 50.5 to 55.67

µS cm^{-1}. It seems that such properties are seen as unimportant in defining bog pool communities, perhaps because readings are consistently so low and / or unvaried. However, in this respect as with pH, drain-blocked pools may differ from natural (ombrotrophic) pools if they have eroded down to the underlying mineral substrate.

2.4.6 Food webs and carbon cycling

The low levels of primary production in bog pools have traditionally been attributed to the low levels of nutrient availability, although a recent study by Karlsson et al. (2009) proposed that light availability (affected by coloured organic matter input) could be the main limiting factor in unproductive lakes. In bog pools, such allochthonous (external) sources of organic carbon are readily available because of the high levels of dissolved organic carbon (DOC) in the surrounding peat, a large part of which is made up of humic substances (Wallage et al., 2006). These substances drain into the pools providing a source of organic carbon for bacteria which is independent of the within-pool primary production and may mean that peat pools are net heterotrophic (i.e. they respire more carbon than is fixed via photosynthesis). Many studies looking at the ratios of gross primary production (GPP) and ecosystem respiration (R) in a range of lentic systems, using the dissolved oxygen change technique (Odum, 1956), have reported negative net ecosystem production (NEP) values, making them net heterotrophic and thus biological sources of carbon to the atmosphere (Cornell and Klarer, 2008, Coloso et al., 2008, Staehr et al., 2012a). If this proves to be the case with artificial peat pools then, from a climate change perspective, this would constitute a negative aspect which land managers would need to consider alongside the potential benefits to biodiversity afforded by pool creation.

Using isotopic analysis, van Duinen et al. (2013) set out to establish the relative contribution of different basal food sources in bog pools in Estonia. The results indicated that zooplankton relied mainly on bacteria, and insects on algae, with periphyton (dominated by green algae) estimated to sustain ~ ½ of the invertebrate food web (Figure 2.6). Methane oxidising bacteria (MOB) were believed to contribute to the food web both directly (i.e. consumed by zooplankton and chironomid larvae) and indirectly, by releasing carbon dioxide (CO_2) which was then assimilated by the algae in the pools and passed up the trophic levels (Figure 2.6). The potential importance of methane as a basis for food webs in lentic habitats was also suggested by a study of Australian billabongs, in which carbon isotope analysis found that macroinvertebrates were too ^{13}C-depleted to have derived their carbon purely from pool vegetation (Bunn and Boon, 1993). The authors hypothesised that methanotrophic bacteria may have been an important source of carbon despite the large biomass of littoral and fringing biomass in the pools. It seems likely then, that the presence of humic substances and methanotrophic bacteria may help to sustain substantial macroinvertebrate communities in drain-blocked pools before, and even after, large-scale vegetation colonisation.

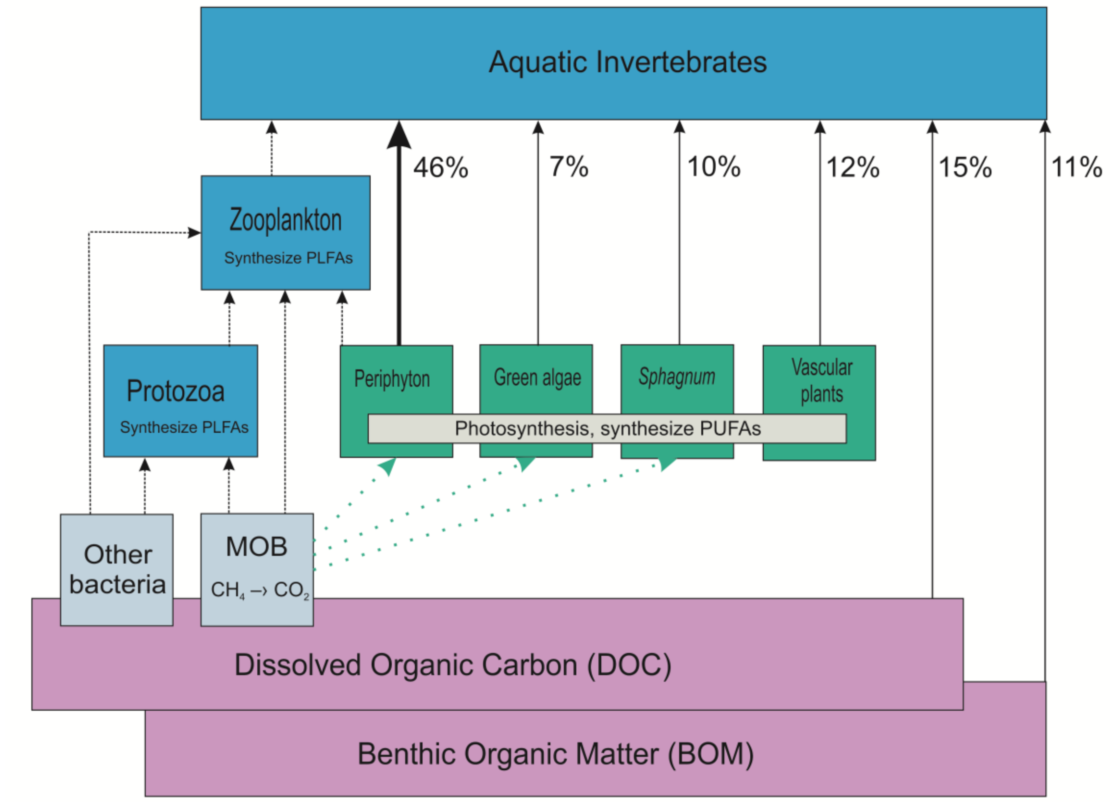

Figure 2.6. Schematic representation of the food web in raised bog pools. The percentages next to the black arrows indicate the mean estimated contribution of the basal food sources to the aquatic macroinvertebrates, as derived from isotopic analysis. The dashed arrows indicate possible additional trophic relations based on phospholipid-derived fatty acid (PLFA) data. The green dotted arrows indicate the possible role of methane-oxidizing bacteria (MOB) in the carbon supply to the primary producers. PUFAs, polyunsaturated fatty acids. (Reprinted with permission from van Duinen et al. (2013) Copyright 2014 The Society for Freshwater Science).

2.5 Conclusions

Natural peat pools house important communities of macroinvertebrates, including many acid-mire specialists, and rare and endangered species. Creating new, artificial pools on peatlands may have conservation benefits by extending the habitat range for such species. However, a distinction should be made between water-bodies on areas of blanket bog, such as those studied in the British Isles (e.g. Towers, 2004, Boyce, 2011, Hannigan et al., 2011) and the heterogeneous raised bog remnants studied in the Netherlands (e.g. Verberk et al., 2006a), with the latter having more inherent biodiversity due to the different water and vegetation types studied. Whereas large-scale re-wetting has proved to be somewhat detrimental to diversity in the Netherlands, this may not be the case on areas of blanket bog such as those in the British Isles, where the re-wetting measures are unlikely to impact on existing water-bodies and instead will generally create new freshwater habitat. The creation of drain-blocked pools in areas without natural pool systems is also likely to attract moorland birds and amphibians therefore benefitting the wider ecosystem.

In areas of blanket peat, pool size and water level stability appear to be major factors in defining species assemblages, with smaller, astatic pools home to different communities than larger, permanent pools. Therefore, land managers looking to create pool systems for the benefit of macroinvertebrates should consider creating an array of pools of different sizes by manipulating the physical dimensions of the drains immediately behind the dams. Guidelines on the actual size ranges for drain-blocked pool systems that would help to promote aquatic biodiversity could be deduced from empirical studies. More studies on amphibians are also needed to determine the main physico-chemical variables underpinning their pool selection behaviour, so that this can be taken into account during drain-blocking planning. Amphibians may also be important as top-level predators in these fishless pools, yet this theory is also as yet untested.

The literature on naturally-occurring lentic water bodies suggests that drain-blocked pools should be net heterotrophic, and that both algae and allochthonous sources of organic carbon should form an important basal element of the food webs in these systems. Further studies to ascertain the rates of GPP, R and NEP would help to elucidate the issue, as would analysis of the carbon isotopes found in the various food sources and consumers. If the pools prove to be biological carbon sources then this would need to be considered alongside the potential ecological benefits to biodiversity. Whether more heterogeneous vegetation cover promotes macroinvertebrate diversity is unclear from the literature. However, as the morphology and life-history traits of different species makes them suited to either open-water or more densely-vegetated areas, it seems likely that a heterogeneous vegetation structure which includes open water areas would be beneficial. However, the practicality of inducing *Sphagnum* to grow in pools poses problems and the process of seeding pools with *Sphagnum* is still in its infancy.

The literature suggests that macroinvertebrates will attempt to colonise nearby waterbodies even when environmental conditions are not ideal. Therefore, land managers should consider prioritising catchments for drain-blocking which are near to existing water bodies, such as streams, tarns and sinkholes, then working outwards. This will maximise the chances of successful dispersal by existing biotic communities. Monitoring could begin as soon as the pools form, to look at initial community assembly and ascertain how long it takes for different taxa to colonise the pools. If long-term monitoring is not an option, then pools belonging to different age classes could be sampled to analyse how the communities change over time. The literature from the Netherlands looking at raised bog pools suggests that older pools tend to house more diverse communities, including more species classed as rare or characteristic (van Duinen et al., 2003). It remains unknown if this is the case in blanket bog pools.

Drain-blocked pools could prove to be an important addition to the ecological landscape of blanket mires, not just for aquatic species but for terrestrial biota as well. Baseline datasets on the taxa that inhabit them are vital not just for current understanding but also to enable monitoring in the face of climate change and the increased likelihood of extreme weather events such as drought (Dai, 2013). The large number of pools created by these measures should act as a buffer against such disturbances and may eventually provide refuge for taxa from more marginal habitats which respond to the changing climate by migrating upwards and polewards (Walther et al., 2002). Peatland rewetting measures constitute a rare case of freshwater habitat creation and their biodiversity should therefore be carefully managed and monitored to maximise the potentially large-scale ecological benefits.

Chapter 3: Macroinvertebrate biodiversity in natural and artificial peatland pools

3.1 Introduction

Small, lentic water bodies such as ponds and ditches are known to make an important contribution to catchment-scale biodiversity (Williams et al., 2003, Biggs et al., 2005). Not only do they sustain a high number of rare and uncommon macroinvertebrate species compared to larger lakes and rivers, but the abiotic and biotic dissimilarity between sites leads to high rates of beta diversity (Oertli et al., 2005, Davies et al., 2008). As habitat islands, ponds act as stepping stones in the landscape, enhancing connectivity between water-bodies and facilitating the existence of meta-communities (Caudill, 2003, Cottenie and De Meester, 2005, McAbendroth et al., 2005) and this role will only become more important in the face of climate change and associated species migrations both upwards and polewards (Walther et al., 2002, Rosset and Oertli, 2011). Ponds also act as good model systems for large-scale surveys and experimental manipulation, due to factors such as their abundance, small size, environmental heterogeneity and response to anthropogenic influences (De Meester et al., 2005).

Although there is no defined size range for a pond or pool, it is generally accepted that they range from 1 m^2 to either 2 ha (Biggs et al., 2005) or 5 ha (Céréghino et al., 2008). In the UK, in the year 2000, there were an estimated 400,000 inland freshwater bodies ranging in size from 25m^2 to 5 ha (25 to 50,000 m^2), which accounted for 97% of the total number of all discrete standing water bodies (Biggs et al., 2005, Oertli et al., 2005). However, the number of even smaller pools (1 to 25 m^2) is unknown and perhaps unquantifiable, due to their transitory nature and to the limitations of the current mapping technology, although large numbers must exist across the country. Although ponds are not mentioned in the EU Water Framework Directive (Davies et al., 2008), their numbers are increasing on a global scale as a result of peatland rewetting schemes (Chapter 2); a rare case of freshwater habitat creation at a time of increasing threat from damaging anthropogenic influences (Dudgeon et al., 2006).

Peatland rewetting schemes have taken place in, for example, Canada (Ketcheson and Price, 2011, McCarter and Price, 2015), the Netherlands (van Duinen et al., 2003, Verberk et al., 2010a), Ireland (Hannigan et al., 2011, Wilson et al., 2013) and countries in Northern Europe such as Estonia, Sweden and Finland (Tuittila et al., 2000, Vasander et al., 2003). Drain-blocking in the UK was instigated in the early 1990s, mainly as a response to European legislation concerning the protection of priority habitats (Holden et al., 2004). The main aim of drain-blocking is to encourage water table recovery and thus the establishment of peat-forming species, notably *Sphagnum* mosses. The process involves installing dams in the drains, generally using peat turves (Armstrong et al., 2009) resulting in the creation of small pools of water, usually ≤3 m^2 (personal observation). Sometimes, the drain is reprofiled, with the steep edges pulled inwards to form a slope and the vegetation redistributed to cover bare peat. This theoretically results in shallower channel profile with a correspondingly shallower, smaller pool behind the dam (Parry et al., 2014) (Figure 3.1a). Sometimes the peat used to make the dam is dug out from the side of the drain, creating a larger, square-shaped pool which protrudes out resulting in a series of 'L-shaped' pools along the drain (Figure 3.1b). In contrast, natural peat pools tend to be shallow, with a large surface area to depth ratio and irregular margins (Figure 3.1c).

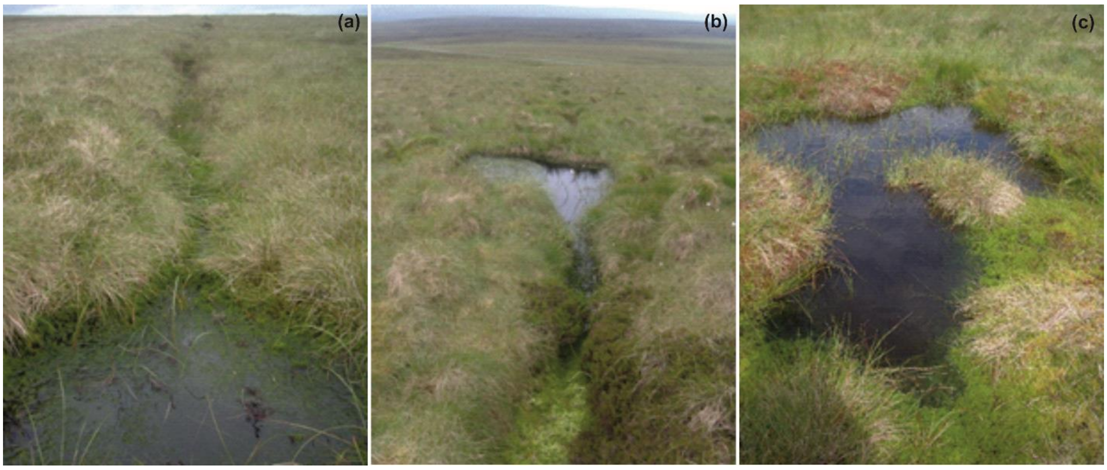

Figure 3.1. Photographs of reprofiled, L-shaped and natural pools (a) a reprofiled drain with a rounded pool (Geltsdale RSPB Reserve), (b) an L-shaped pool in an un-profiled drain (Yad Moss) and (c) a natural pool on intact blanket bog (Harwood Fell). All sites in Cumbria, UK.

Drain-blocked pools on peatland now number in the hundreds of thousands across the UK, and there may even be several million. For example, using a calculation based on the total length of drains blocked and the average spacing between dams, it is estimated that ~500,000 pools have been created in the North Pennines AONB alone since 1995 (Alistair Lockett, North Pennines AONB, pers. comm.). However, little is known about the ecology of these artificially created dam pools. In areas of peatland where natural pools are more abundant, such as in the Flow Country in Scotland, their macroinvertebrate communities are fairly well-studied (Foster, 1995, Downie et al., 1998a, Standen et al., 1998, Standen, 1999, Towers, 2004). There is also a body of work looking at the characteristics of lentic peatland water bodies in Ireland (Hannigan and Kelly-Quinn, 2012, Drinan et al., 2013, Baars et al., 2014). Internationally, there is a wider body of literature looking at the effect of peatland restoration on aquatic macroinvertebrate communites, such as in Ireland (Hannigan et al., 2011), in Canada (Mazerolle et al., 2006) and especially in the Netherlands (i.e. (van Duinen et al., 2003, Verberk et al., 2006a, Verberk et al., 2006b, van Kleef et al., 2012). However, these studies did not look specifically at the ecology of pools which form in drains as a result of blocking. Indeed, there are only two UK-based studies looking at the macroinvertebrate communities of drain-blocked pools (Boyce, 2010, Brown et al., submitted), with the first of these looking at selected taxa only (Coleoptera, Odonata and Heteroptera).

A review of the macroinvertebrate diversity found in peat pools, both natural and drain-blocked, suggested that pool size was a more important factor in dictating biodiversity and community composition than was, for example, water chemistry (see Chapter 2). This is due partially to the relatively homogeneous nature of peat pool water chemistry (Hannigan and Kelly-Quinn, 2014) and also to the species-area curve theory (Connor and McCoy, 1979, Towers, 2004). However, in very small water bodies such as those formed by drain-blocking, water permanence also comes into play. Small volume pools are more susceptible to drying, which shapes community structure by acting on species persistence (Wellborn et al., 1996) and recolonisation dynamics (Jeffries, 2011). Furthermore, there is some evidence that Odonates select sites based on predictable visual clues linked to hydroperiod, especially the extent of vegetation cover (Buchwald, 1992, Urban, 2004). However, it is unclear whether the restricted size range of drain-blocked pools would result in different levels of biodiversity or community composition.

The aim of this study was to assess the suitability of drain-blocked pools as habitat for aquatic macroinvertebrates. This was achieved by comparing the environmental characteristcs and macroinvertebrate communities of drain-blocked and natural pools, and also by comparing pools created using two different blocking methodologies (i.e. reprofiled drains and L-shaped pools). These two restoration methodologies were chosen due to their prevalence in drain-blocking programs in the study area (the English Pennines). The two methods should also create pools with different physical properties, as reprofiling is intended to encourage smaller, shallower pools with more vegetation cover (Parry et al., 2014). Three hypotheses were tested:

H_1 – Physically, the blocked pools were expected to be deeper than the natural pools and to hold more water, with the L-shaped pools expected to be larger than the reprofiled pools due to the reprofiling methodology (Parry et al., 2014). Water chemistry was predicted to be similar between all pool types (Hannigan et al., 2011, Brown et al., submitted).

H_2 – Pool communities in all pool types were expected to be dominated by chironomids, beetles and hemipterans, as these have been shown to be the most common taxa found in small, peatland water bodies (Chapter 2). Differences in macroinvertebrate biodiversity and community composition between the pool types were expected to be small due to the homogeneous nature of peatland water chemistry (Hannigan et al., 2011, Brown et al., submitted).

H_3 - Any differences in biodiversity or community compsoition were predicted to be driven more by the physical dimensions of the pool than water chemistry (Chapter 2). For example, larger, deeper pools should house more species and individuals (Oertli et al., 2002, Towers, 2004), and be more attractive to larger beetle taxa and species with semi-voltine life cycles such as odonates (Larson and House, 1990, Foster, 1995, Downie et al., 1998a).

3.2 Methods

3.2.1 *Study sites*

A total of 60 pools were sampled; 20 reprofiled, 20 L-shaped and 20 natural. All pools were located at sites in the Pennines, northern England (Table 3.1, Figure 3.2). Potential sites were identified via communications with land management agencies and by viewing on-line satellite and aerial images, then site visits were carried out to confirm the blocking method and suitability of the sites and the pools (e.g. site accessibility, pool size, etc) before a final site list was compiled. Natural pools are rare in the Pennines and only one truly-natural pool complex was identified (Butterburn Flow, pers.comm Richard Lindsay). The other natural pools were isolated features in otherwise intact peatlands. All chosen pools had a surface area ≤ 3m^2. Artificial pools were also controlled for age, with all pools ≤ 6 years old. Sampling was undertaken between 16th July and 1st August 2012 and the sampled pools at each site were selected randomly on site. All sites had blanket peat cover, with vegetation dominated by *Eriophorum* spp. and *Calluna vulgaris* (L.), with varying amounts of *Sphagnum* spp. cover.

Table 3.1. Details of the study sites and the number of pools sampled at each.

Site Name	Pool Type	No. of pools	Lat Long	Altitude (m)	Drains Blocked
Butterburn Flow	Natural	9	55° 4' 34''N, 2° 30' 22''W	280	n/a
Geltsdale	Natural	4	54° 53' 39''N, 2° 36' 42''W	600	n/a
Harwood Fell	Natural	2	54° 41' 46''N, 2° 20' 26''W	620	n/a
Widdybank Fell	Natural	5	54° 39' 50''N, 2° 16' 43''W	525	n/a
Geltsdale	Reprofiled	10	54° 52' 55''N, 2° 36' 21''W	590	2008
Stean Moor	Reprofiled	10	54° 8' 59'' N, 1° 54' 44'' W	390	2009-2010
Langdon Common	L-shaped	5	54° 42' 16''N, 2° 13' 42''W	540	2009
Tynehead Fell	L-shaped	10	54° 42' 34''N, 2° 20' 48''W	560	2007
Yad Moss	L-shaped	5	54° 43' 15''N, 2° 20' 36''W	615	2006

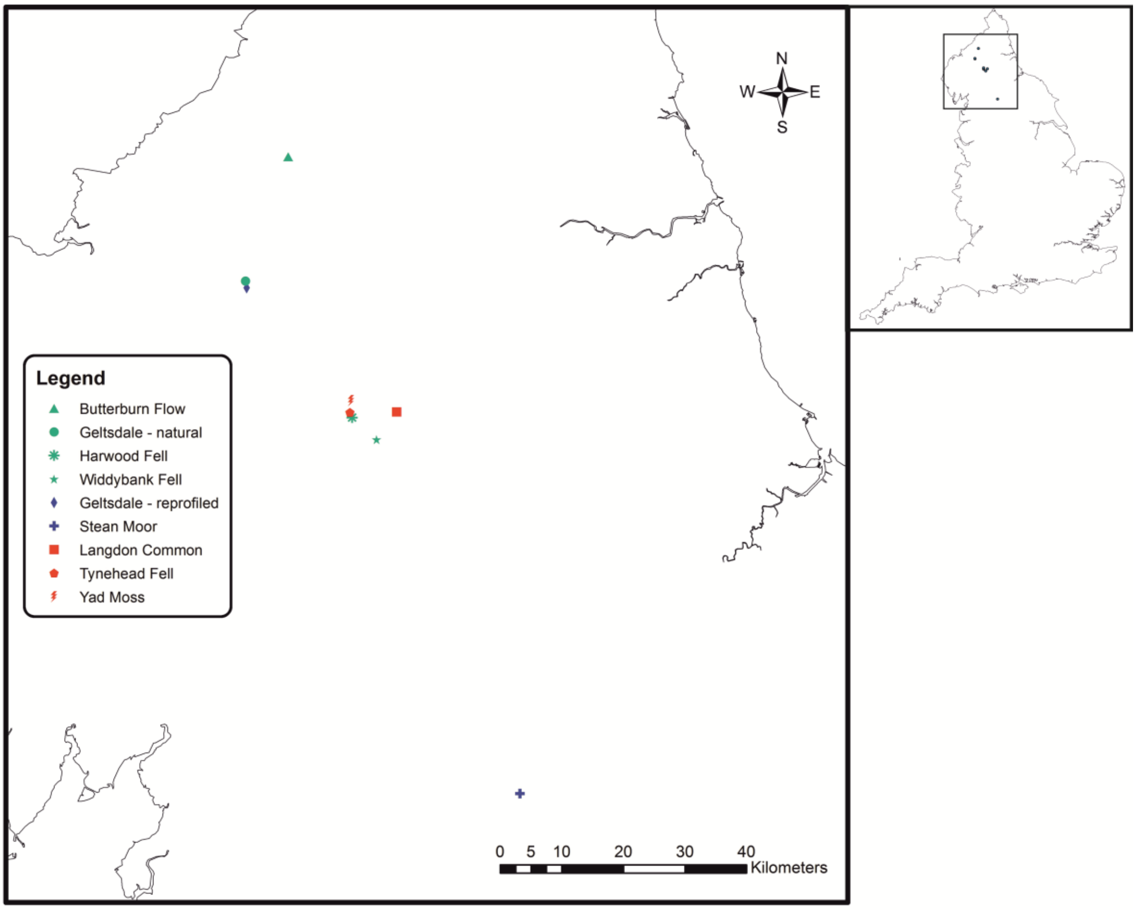

Figure 3.2. Map of the study sites

3.2.2 Sampling methodology

For each pool, the altitude (m) and OS grid reference were recorded using a Garmin eTrex Handheld GPS Navigator. The long axis, short axis and perimeter were measured and depth measurements were taken at regular intervals, the exact number being appropriate to the pool size (although always >40 measurements). The approximate water volume was estimated by multiplying the surface area (calculated by multiplying the long and short axes) by the mean depth. Each pool was sketched and photographed and % vegetation cover was estimated. Upper water column (top 10cm) electrical conductivity (EC), dissolved oxygen (DO), water temperature and pH readings were taken in the field using a portable HACH HQ30d meter. Additionally, a 50 mL water sample was collected for further analysis in the laboratory, where it was passed through a 0.45-µm filter and subsequently analysed for total nitrogen (TN), total phosphorus (TP), dissolved organic carbon (DOC), major anions (Cl, SO_4) and a range of metals and cations (Al, Ca, Fe, K, Mg, Na, Si). The rationale behind collecting such a wide range of ionic data was mainly to provide a more complete picture of the water chemistry of ombrotrophic peat pools than that provided by the papers reviewed in Chapter 2, which tended to collect data on the more 'standard' variables collected in aquatic studies, such as pH, EC, nutrients and DOC. All the ions sampled have some biological relevance, for example Fe, as well as being a macro-nutrient element, can also be toxic to freshwater biota at elevated levels, as can Al (Wren and Stephenson, 1991, van der Welle et al., 2006). In peaty areas, sulphate (SO_4) can be reduced to toxic sulfide, which can be detrimental to freshwater biota (van der Welle et al., 2006). The other ions are all either macro- or micro-elements which are essential, by varying degrees, to freshwater plants and animals (Jackson and Jackson, 2000). Therefore, ions were sampled mainly to provide baseline data but also to ascertain whether they helped to explain any patterns in macroinvertebrate biodiversity. Water colour was measured using an UV/VIS spectrophotometer, but because water colour absorbance at 254 nm and levels of DOC were very highly, positively correlated (Spearman Rank $r_s = 0.92$, $p < 0.001$), water colour was excluded from subsequent analyses.

Macroinvertebrate samples were collected using a long-handled pond-net (250-µm mesh). Biggs et al. (1998) suggested that pools should be sampled for three minutes with time being divided between mesohabitats. The pools in this study were very small so two minutes were divided equally between observed mesohabitats (i.e. open water, floating vegetation, littoral vegetation, bottom sediments) and a further one minute was spent searching for surface dwelling taxa. Samples were preserved in

70 % methylated spirits and transported to the laboratory. The pond net methodology was chosen as it is recommended by Pond Action (Biggs et al., 1998) and allows for a comprehensive survey of the entire pool system in one sampling effort. Furthermore, in a previous study of blocked pools in the Pennines, pond-netting had been shown to capture a wide range of both active and sessile invertebrates (Brown et al., submitted). One alternative method would have been the combined use of activity traps (either baited or unbaited) along with sediment samples (e.g. Towers, 2004). However, this was ruled out mainly for pratical reasons (i.e. the need for repeated visits to remote sites) but also to avoid within-trap predation in the period between the trap being laid and collected. After sorting, macroinvertebrates were identified to species level (where possible) under a light microscope (up to x40 magnification) using standard keys (see Pawley et al., 2011 and references therein). Where Chironomidae abundance totalled >50 individuals, Chironomidae were sub-sampled (n=50) (Rees et al., 2008) for identification to the lowest possible taxonomic resolution. Individuals were immersed in a solution of 10% potassium hydroxide and heated to 70°C for 10 minutes. The chironomids were then transferred into a solution of 95% glacial acetic acid for five minutes, then 80% methylated spirits for five minutes before being stored 100% methylated spirits. Individuals were mounted on slides using Euparal and identified using a compound microscope and following Cranston (1982) and Brooks et al. (2007).

3.2.3 Statistical analysis

For the purposes of statistical analysis, taxonomic adjustment was applied when it was not possible to identify individuals to species level, mainly because they were too small. In such cases, when only one adult species had been identified in that genus or family, then the small individual was attributed to that species. For example, only one species of stonefly (*Nemoura cambrica*) was identified, so all the *Nemoura* spp. individuals were classed as *N. cambrica*. In other cases, for example with the Dytsicidae larvae, it was possible that the larval pool, as well as including young of the adult species identified in the particular pool, also represented species found in the wider dataset or even other species not found in any of the pools, as bog pool beetles are much more diverse than bog pool stoneflies. Therefore, Dytiscidae larve were included in the analysis as a separate category. Appendix A provides a complete list of taxa identified and further details of the taxonomic adjustment undertaken.

Analyses were carried out to look for differences between (1) the natural and blocked (reprofiled and L-shaped combined) pools and (2) the natural, reprofiled and L-shaped pools. Principal Component Analysis (PCA) was used to examine variance in the environmental variables with data standardised using Z-scores prior to analysis (Clarke and Gorley, 2015). Principal components (PCs) with Eigenvalues >1 were retained and % variance of each recorded. Generalised linear models (GLMs) were used to determine significant differences in PC scores between pool types, with the most appropriate error distribution determined by maximum likelihood estimates (MLEs).

Biodiversity was analysed for all taxa (after taxonomic adjustment) and also for the two most taxonomically rich and abundant groups; the Chironomidae and Coleoptera. For each pool, the following biodiversity metrics were calculated: (i) the number of macroinvertebrate taxa (taxon richness), (ii) number of individuals (abundance), (iii) diversity (1-Simpson's Diversity Index λ):

$$1 - (\lambda = \Sigma\, n_i(n_i-1)/N(N-1)$$

where N is the total number of individuals in a sample and n_i is the number of individuals of taxon *i*, with a resulting figure of between 0 and 1; the higher the score the more diverse the sample, and (iv) dominance (Berger-Parker Index 'D'). The Berger-Parker Index is a measure of taxon evenness / dominance and expresses the number of individuals in the most abundant taxon (N_{max}) as a percentage of overall abundance (N):

$$D = N_{max}/N$$

The higher the resulting figure (between 0 and 1) the higher the dominance and the lower the evenness in the sample (Magurran, 2004). The 1-Simpsons index was chosen over the Shannon index because of the latter's assumption that all species from an infinitely large community are represented in the sample being analysed. When this assumption is not met it gives rise to a source of error which increases along with a declines in the proportion of species represented (Magurran, 2004).

To test for spatial autocorrelation, Moran's I values were calculated for each variable (both environmental and biological) in the dataset (Dormann et al., 2007). In this chapter, spatial autocorrelation was found for seven of the environmental variables (EC, TN, DOC, Al, Ca, Mg and Na) and for the biodiversity metrics of taxonomic richness and abundance for the Coleoptera dataset. Where variables were not spatially autocorrelated, GLMs were used to compare between pool types, with the most appropriate error distribution determined by maximum likelihood estimates (MLEs); this was typically negative-binomial for count data (O'Hara and Kotze, 2010). Where spatial autocorrelation was present, generalised linear mixed models (GLMMs) were used with pool as a random factor, in preference to GLMs (Dormann et al., 2007). For the GLMMs, where the data were not normally distributed, the penalised quasilikelihood (PQL) method was used to specify the distribution of the residuals (Bolker et al., 2009).

In the case of the environmental variables, 95 test results were reported, increasing the chance of false discoveries (i.e. type I errors; accepting results as significant when they are not). Therefore, q values were estimated from the original p values using the QVALUE package in R (Storey, 2002). The biodiversity datasets reported far fewer results (n = 20) so, although there was still a chance of slightly elevated type I error reporting, it was not thought necessary to calculate q values.

To analyse the community structure of the pools, nMDS was undertaken in PRIMER-E. nMDS was used because of its non-parametric approach to multivariate analysis of ecological properties (Clarke, 1993), it being especially useful for datasets containing large numbers of zeros (e.g. abundance data). As there were several 'rare' taxa included in the analysis (i.e. 19 of the 58 taxa occurred in only one or two pools), the biotic data were square-root transformed prior to analysis, thus reducing the distortion that a small number of large values can cause and slightly elevating the importance of the rare species. At the other end of the dataset, 21 taxa were found in ≥ 10 pools, with 13 of those taxa found in >20 pools. Therefore, more robust transformation (e.g. fourth root or log(X+1)) was deemed unnecessary as it would have under-represented the importance of these more common taxa. All subsequent analysis was based on a Bray-Curtis coefficient triangular similarity matrix. The ANOSIM routine was used to test for significant differences in community similarity between the pool types (Clarke and Green, 1988). The ANOSIM routine provides a global R statistic ranging between 0 and 1 (where 0 is completely the same and 1 is completely different). The best 2-dimensional nMDS solution was overlain with the environmental variables which correlated most strongly (>0.5) to the biotic ordination co-ordinates (MDS1 and MDS2) using Pearson's correlations in the 'overlays' facility (Clarke and Gorley, 2015). To aid visual interpretation, the Chironomidae nMDS ordination was reduced to a subset by removing five outlying pools (four from Butterburn Flow and one from Stean Moor); these pools were outliers as they contained either no chironomids or very small populations of taxa rarely found in this study. The SIMPER routine was used to define community composition by highlighting the taxa which contributed most to the overall similarity of the each pool type and also to the average dissimilarity between the pool types (Clarke, 1993). Finally, GLMs were used to look for relationships between the four biodiversity metrics and the environmental variables, to ascertain which were most important in driving biodiversity in the pools. All GLMs and GLMMs were performed using R 3.1.2.

3.3 Results

3.3.1 Environmental characteristics

There were several significant differences between the blocked (combined) and natural pools (Table 3.2). Physically, the blocked pools were significantly deeper with a larger water volume. The natural pools had, on average, larger perimeters and also exhibited more vegetation cover than the blocked pools, although neither of these differences was significant. With regards to the water chemistry, the natural pools had significantly higher levels of DO, whereas the blocked pools had significantly higher levels of DOC, Al and Fe(Table 3.2). When the blocked pools were separated into reprofiled and L-shaped, many of the significant differences seen between the blocked and natural pools remained significant, but further distinctions were elucidated (Table 3.2).

Table 3.2. Environmental variables and GLM / GLMM results. Medians (and interquartile range) of the different pool types; (blocked = reprofiled + L-shaped), along with GLM / GLMM results reporting the differences for each variable between the pool types. Overall results refer to natural v reprofiled v L-shaped. Significant results ($q > 0.05$) are highlighted bold. † indicates a GLMM as opposed to a GLM.

	Pool Type				**GLM / GLMM Results**				
Variable	**Natural**	**Blocked combined**	**Re-profiled**	**L-shaped**	**Blocked v natural**	**Overall**	**Natural v Reprofiled**	**Natural v L-shaped**	**Reprofiled v L-shaped**
Depth (cm)	9 (9)	20 (11)	26 (10)	18 (10)	t = 5.04 **q < 0.001**	**q <0.001**	t = 5.41 **q <0.001**	t = 4.08 **q = 0.001**	t = -1.85 q = 0.07
Perimeter (cm)	534 (231)	504 (200)	393 (222)	542 (175)	t = 2.08 q = 0.05	**q = 0.001**	t = 3.69 **q = 0.001**	t = 0.24 q = 0.38	t = -3.45 **q = 0.002**
Volume (m^3)	0.17 (0.32)	0.34 (0.48)	0.26 (0.53)	0.37 (0.38)	t = -2.21 **q = 0.04**	q = 0.07	t = -1.50 q = 0.11	t = -2.31 **q = 0.03**	t = -0.81 q = 0.22
Vegetation cover (%)	28.00 (85.25)	16.00 (81.25)	10.00 (83.75)	45.00 (82.50)	t = 0.87 q = 0.21	q = 0.22	t = 1.29 q = 0.14	t = 0.26 q = 0.38	t = 1.03 q = 0.19
DO ($mg\ L^{-1}$)	10.28 (2.91)	8.85 (4.12)	7.77 (6.43)	8.92 (1.08)	t = 3.48 **q = 0.002**	**q <0.001**	t = 4.94 **q <0.001**	t = 1.60 q = 0.10	t = -3.34 **q = 0.002**
† EC ($\mu s\ cm^{-1}$)	26.15 (12.13)	31.75 (15.90)	39.90 (21.03)	30.25 (5.98)	t = -1.39 q = 0.13	q = 0.15	t = -1.71 q = 0.08	t = -0.76 q = 0.23	t = 0.98 q = 0.20
pH	4.40 (0.26)	4.34 (0.18)	4.29 (0.18)	4.36 (0.29)	t = -0.25 q = 0.38	q = 0.21	t = 0.47 q = 0.32	t = -0.92 q = 0.21	t = -1.39 q = 0.13
† TN ($mg\ L^{-1}$)	1.01 (1.02)	1.05 (1.60)	1.83 (2.46)	0.87 (0.82)	t = 0.36 q = 0.35	q = 0.06	t = -0.91 q = 0.21	t = 1.56 q = 0.11	t = -2.47 **q = 0.03**
TP ($mg\ L^{-1}$)	0.03 (0.05)	0.03 (0.08)	0.06 (0.11)	0.02 (0.04)	t = -0.08 q = 0.42	q = 0.43	t = -0.13 q = 0.40	t = 0.01 q = 0.09	t = 0.14 q = 0.40
† DOC ($mg\ L^{-1}$)	20.40 (15.93)	36.95 (22.25)	42.51 (44.30)	35.75 (7.03)	t = -5.75 **q < 0.001**	**q <0.001**	t = -6.28 **q <0.001**	t = -4.06 **q = 0.001**	t = 2.24 q = **0.04**
† Al ($mg\ L^{-1}$)	0.03 (0.04)	0.09 (0.14)	0.14 (0.13)	0.07 (0.13)	t = -3.13 **q = 0.01**	**q = 0.004**	t = -3.71 **q = 0.002**	t = -1.82 q = 0.07	t = 1.89 q = 0.07
† Ca ($mg\ L^{-1}$)	0.24 (0.20)	0.50 (0.56)	0.37 (0.66)	0.50 (0.46)	t = -2.14 q = 0.05	q = 0.09	t = -1.56 q = 0.10	t = -2.11 q = 0.05	t = -0.55 q = 0.30
Fe ($mg\ L^{-1}$)	0.14 (0.29)	0.75 (3.43)	2.10 (4.99)	0.68 (1.35)	t = -3.47 **q = 0.002**	**q < 0.001**	t = -5.09 **q < 0.001**	t = -2.51 **q = 0.02**	t = 3.64 **q = 0.002**
K ($mg\ L^{-1}$)	0.06 (0.08)	0.03 (0.03)	0.03 (0.03)	0.03 (0.05)	t = 1.70 q = 0.09	q = 0.15	t = 1.70 q = 0.08	t = 1.22 q = 0.15	t = -0.49 q = 0.32
† Mg ($mg\ L^{-1}$)	0.18 (0.08)	0.23 (0.35)	0.30 (0.50)	0.23 (0.29)	t = -2.03 q = 0.06	**q = 0.03**	t = -2.80 **q = 0.01**	t = -1.73 q = 0.08	t = 1.10 q = 0.18
† Na ($mg\ L^{-1}$)	1.57 (0.38)	1.66 (0.42)	1.73 (0.45)	1.64 (0.27)	t = -0.88 q = 0.21	q = 0.16	t = -1.45 q = 0.12	t = 0.09 q = 0.42	t = 1.36 q = 0.13
Si ($mg\ L^{-1}$)	0.06 (0.04)	0.11 (0.18)	0.14 (0.28)	0.11 (0.13)	t = -2.01 q = 0.06	**q = 0.04**	t = -2.60 **q = 0.02**	t = -0.92 q = 0.21	t = 1.68 q = 0.09
Cl ($mg\ L^{-1}$)	1.62 (0.40)	1.35 (1.35)	1.57 (1.81)	1.11 (0.71)	t = -2.38 q = 0.38	q = 0.21	t = -0.76 q = 0.23	t = 0.35 q = 0.35	t = 1.11 q = 0.17
SO_4 ($mg\ L^{-1}$)	0.34 (0.40)	0.19 (0.30)	0.23 (0.29)	0.14 (0.16)	t = 0.66 q = 0.26	q = 0.21	t = -0.07 q = 0.42	t = 1.21 q = 0.15	t = 1.27 q = 0.14

For example, whilst both blocked pool types still had larger water volumes than the natural pools, the difference was only significant between the L-shaped and natural pools. The L-shaped pools were shown to have longer perimeter lengths than the natural pools, with the reprofiled pools perimeters being significantly shorter than either of the other pool types. Similarly, the natural pools were found to have less vegetation cover than L-shaped pools but still more than the reprofiled pools. Chemically, the natural pools still exhibited the highest levels of DO, but both the natural and L-shaped pools had significantly higher levels than the reprofiled pools. Both blocked pool types had significantly higher concentrations of DOC and Fe than the natural pools, but in both cases concentrations in the reprofiled pools were also significantly higher than in the L-shaped ones. Three water chemistry variables; Al, Mg and Si, all followed the same pattern, with levels being highest in the reprofiled pools, then L-shaped pools and lowest in the natural pools, with the difference between reprofiled and natural pools being significant. Concentrations of TN, which were not significantly different between the blocked (combined) and natural pools, were shown to be significantly lower in the L-shaped pools than in the reprofiled pools (Table 3.2).

The PCA generated five PCs with Eigenvalues >1 with the first two PCs accounting for 55.2% of the total variation (Table 3.3). The strongest loadings on PC1 were negative; Fe (-0.314) and Mg (-0.347). Two loadings on PC2 were also below -0.3; DOC and Al, with strong positive loadings for DO, K and SO_4. When the PC scores were analysed by pool type the blocked pools were associated with the negative values on both PC1 and PC2, and this association was driven mainly by the negative scores of the reprofiled pools (Figure 3.3). In contrast, the natural pools displayed positive mean scores on both PC1 and PC2. Although the PC1 scores for the natural and blocked (combined) pools were not significantly different, the reprofiled pools had significantly lower (more negative) scores than the natural pools (t = -2.55, p = 0.01) (Figure 3.3a). The PC2 scores were significantly different between the natural and blocked (combined) pools (t = 4.32, p < 0.001), and also between the natural and reprofiled (t = -5.21, p < 0.001), natural and L-shaped (t = 2.62, p = 0.01) and reprofiled and L-shaped (t = -2.59, p = 0.01) pool types (Figure 3.3b).

Table 3.3. PCA metrics. Scores, Eigenvalues and % variance explained for the five PCs with Eigenvalues >1. Scores > 0.3 and < -0.3 are highlighted to aid interpretation.

Variable	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Mean Depth	0.064	-0.267	0.285	**-0.495**	0.246
Perimeter	0.188	0.259	-0.030	**-0.384**	-0.216
Volume	0.170	-0.055	0.230	**-0.607**	0.023
Veg cover	-0.142	0.172	**-0.300**	-0.133	-0.517
DO	0.199	**0.355**	-0.180	-0.140	-0.041
EC	-0.238	0.082	-0.289	-0.160	0.269
pH	-0.100	0.201	**0.436**	0.045	**-0.346**
TN	-0.285	0.084	-0.215	-0.110	0.171
TP	-0.142	0.119	-0.215	-0.105	**0.422**
DOC	-0.221	**-0.393**	-0.205	-0.103	-0.028
Al	-0.246	**-0.335**	-0.098	-0.124	-0.195
Ca	-0.282	-0.010	-0.069	-0.268	-0.252
Fe	**-0.314**	-0.165	0.171	-0.018	-0.071
K	-0.142	**0.416**	-0.134	-0.170	0.041
Mg	**-0.347**	-0.084	0.006	-0.065	-0.131
Na	-0.271	0.203	0.130	0.055	0.271
Si	-0.257	0.096	**0.415**	0.051	0.061
Cl	-0.295	0.113	0.082	0.102	-0.079
SO_4	-0.222	**0.312**	0.278	-0.057	0.123
Eigenvalues	7.61	2.88	2.06	1.73	1.06
%Variation	40	15.2	10.8	9.1	5.6

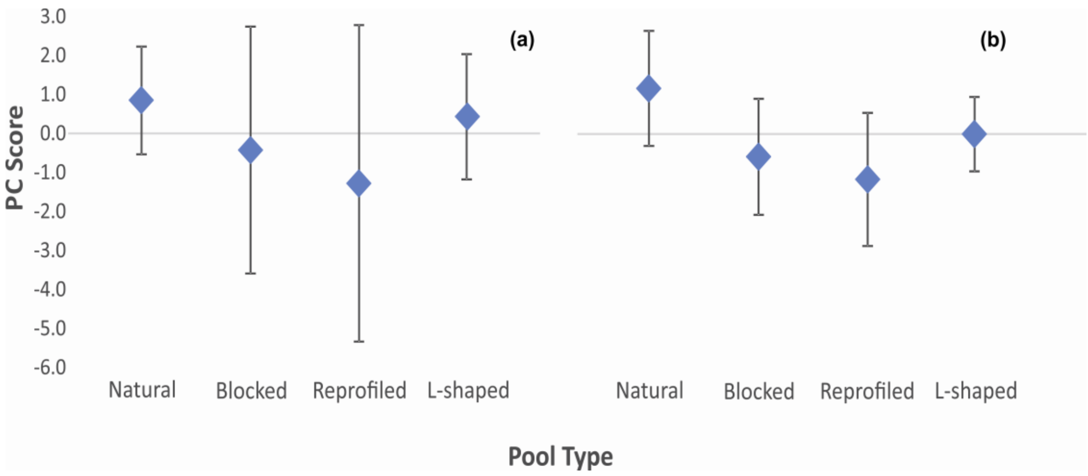

Figure 3.3. PCA metrics. Mean PC scores (+/- 1 st. dev) for each pool type; (a) PC1 and (b) PC2.

3.3.2 Macroinvertebrate biodiversity

Altogether 13160 individuals were collected and 64 macroinvertebrate taxa were identified, although the number of taxa included for statistical analysis after taxonomic adjustment was 58 (Appendix A). The richest taxonomic orders were Diptera (27 taxa, of which 21 were Chironomidae) and Coleoptera (18 adult species and 4 larval taxa). Overall, Chironomidae were by far the most abundant taxon, accounting for 74% of all individuals (Table 3.4). The total abundance of chironomids was highest in the L-shaped pools and lowest in the natural pools (Table 3.4, Figure 3.4a). The only other taxa to account for >5% of the overall relative abundance were beetles (adults and larvae combined) at 16.6% and hemipterans (adults and nymphs) which accounted for 7.38% of overall abundance. Beetles were most abundant in the reprofiled pools and least abundant in the L-shaped pools, whilst hemipterans and trichopterans were far more abundant in both blocked pool types than in the natural pools. Plecoptera, although rare, were found almost exclusively in the reprofiled pools, whilst Odonata were found exclusively in the L-shaped pools (Table 3.4). The relative abundance of Chironomidae was similar between the natural and blocked pools, with the largest difference falling between the two blocked pool types; the reprofiled pools had the smallest relative abundance and the L-shaped pools the largest (Table 3.4, Figure 3.4b). The relative abundance of Coleoptera was much higher in the natural pools than the blocked, whilst the opposite was true of the relative abundance of Hemiptera (Table 3.4, Figure 3.4 b).

On average, the blocked pools had higher levels of taxonomic richness and abundance than the natural pools although the differences were not significant, and the average values for the two diversity indices were almost identical (Table 3.5, Figure

Table 3.4. Total and relative abundance metrics of the different taxa found in the pool types along with their relative contribution to overall abundance. Chironomidae are separated from other Diptera to highlight their major contribution to the overall abundance figures.

Taxon	Natural	Blocked	Reprofiled	L-shaped	Total	% Contribution overall
Chironomidae	2241 (70.92%)	7514 (75.14%)	3216 (68.78%)	4298 (80.73%)	**9755**	74.13
Coleoptera	743 (23.51%)	1442 (14.42%)	874 (18.69%)	568 (10.67%)	**2185**	16.60
Hemiptera	99 (3.13%)	872 (8.72%)	496 (10.61%)	376 (7.06%)	**971**	7.38
Trichoptera	19 (0.60%)	116 (1.16%)	61 (1.30%)	55 (1.03%)	**135**	1.03
Collembola	42 (1.33%)	19 (0.19%)	11 (0.24%)	8 (0.15%)	**61**	0.46
Other Diptera	9 (0.29%)	6 (0.06%)	1 (0.02%)	5 (0.09%)	**15**	0.11
Plecoptera	0 (0.00%)	13 (0.13%)	12 (0.26%)	1 (0.02%)	**13**	0.10
Megaloptera	6 (0.19%)	7 (0.07%)	5 (0.10%)	2 (0.04%)	**13**	0.10
Odonata	0 (0.00%)	10 (0.10%)	0 (0.00%)	10 (0.19%)	**10**	0.08
Hydracarina	1 (0.03%)	1 (0.01%)	0 (0.00%)	1 (0.02%)	**2**	0.02
Total	**3160**	**10000**	**4676**	**5324**	**13160**	**100.00**

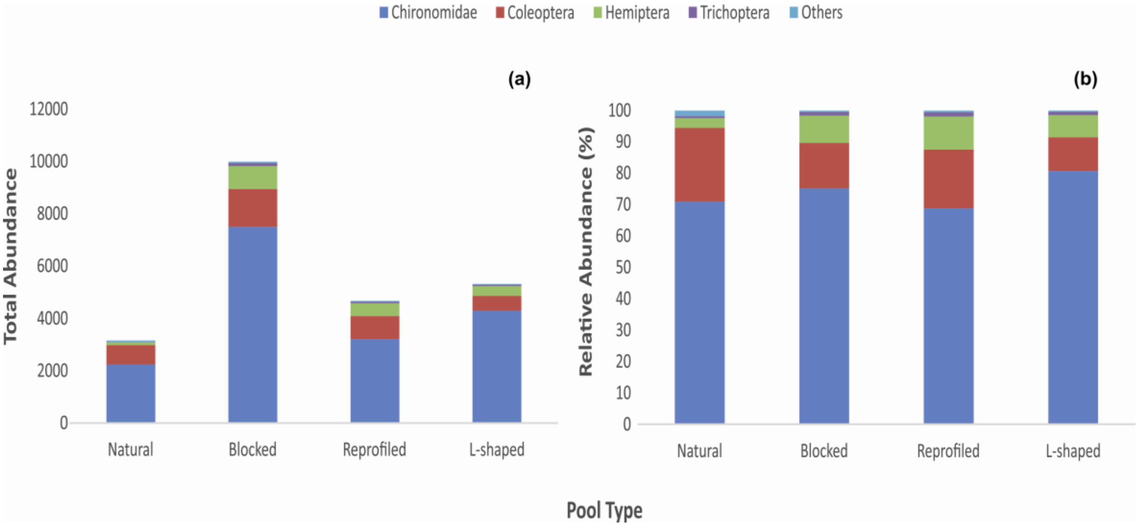

Figure 3.4. Total and relative abundance metrics. (a) Total abundance and (b) relative abundance of the macroinvertebrate orders found in the pool types. Orders accounting for <1% of the overall relative abundance are grouped together as 'others'.

3.5). However, when the blocked pools were split into the two sub-categories, the reprofiled pools were found to house significantly more taxa than both the natural and

L-shaped pools. The L-shaped pools housed the highest average abundance of macroinvertebrates but there was no significant difference in abundance between the three pool types. The L-shaped pools displayed significantly lower Simpson's diversity and higher Berger-Parker scores than both reprofiled and natural pools.

Table 3.5. Biodiversity metrics and GLM results. Means (± st.dev) for the different pool types (blocked = reprofiled + L-shaped), along with GLM results reporting the differences between the pool types. Overall results refer to natural v reprofiled v L-shaped. Significant results are highlighted bold.

	Pool Type				GLM Results				
Variable	**Natural**	**Blocked**	**Re-profiled**	**L-shaped**	**Blocked v natural**	**Overall**	**Natural v reprofiled**	**Natural v L-shaped**	**Reprofiled v L-shaped**
Taxon Richness	10.25 (5.04)	11.48 (3.74)	13.05 (3.50)	9.90 (3.34)	t = -1.06 p = 0.29	**p = 0.03**	t = 2.20 **p = 0.03**	t = 0.28 p = 0.78	t = 2.47 **p = 0.02**
Abundance	158 (160)	250 (213)	234 (198)	266 (230)	t = -1.85 p = 0.07	p = 0.18	t = 1.36 p = 0.18	t = -1.81 p = 0.08	t = -0.45 p = 0.65
1-Simpsons	0.75 (0.10)	0.72 (0.13)	0.78 (0.09)	0.66 (0.13)	t = 0.84 p = 0.41	**p = 0.001**	t = 0.97 p = 0.34	t = 2.56 **p = 0.01**	t = 3.53 **p = 0.001**
Berger Parker	0.41 (0.12)	0.43 (0.15)	0.36 (0.12)	0.50 (0.15)	t = -0.48 p = 0.64	**p = 0.002**	t = -1.30 p = 0.20	t = -2.21 **p = 0.03**	t = -3.51 **p = 0.001**

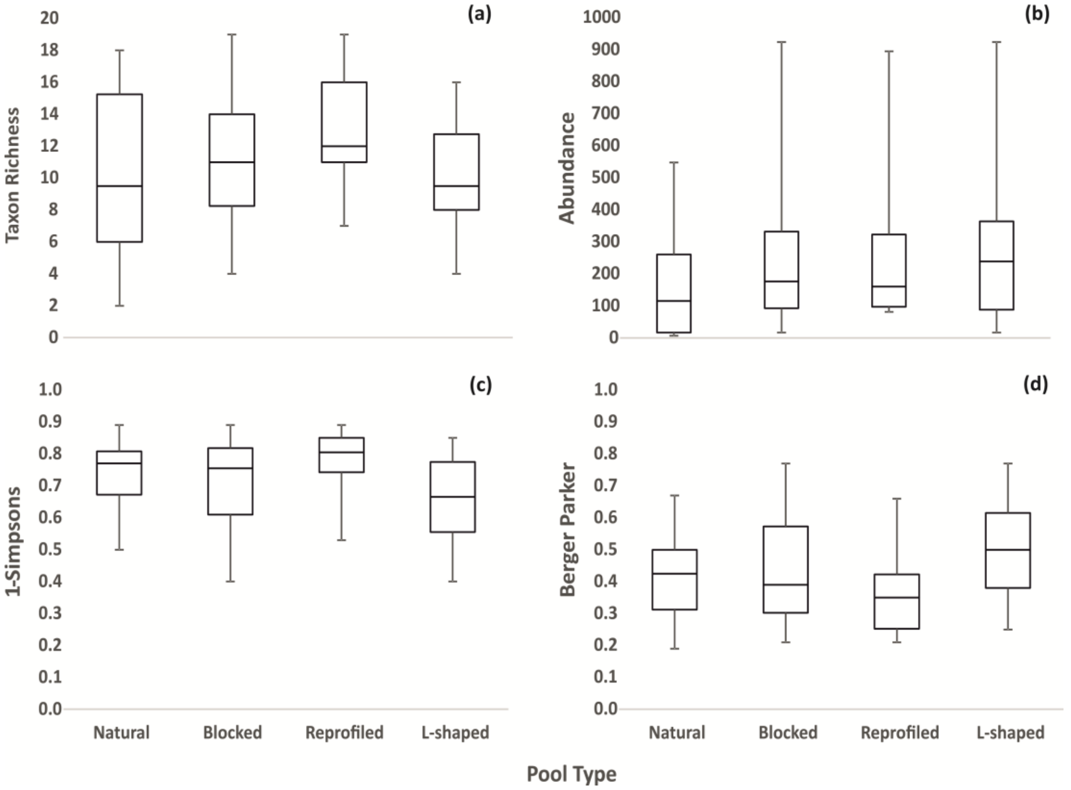

Figure 3.5. Biodiversity metrics for the pool types; (a) Taxon richness, (b) Abundance, (c) Simpsons Diversity Index (λ-1) and (d) Berger-Parker Dominance Index (D). Error bars denote +/- 1 St. Dev.

3.3.3 Macroinvertebrate community composition

The nMDS ordination showed some degree of separation between the natural and blocked (combined) pools and, to a lesser extent, between the reprofiled and L-shaped pools (Figure 3.6a). The most distinct grouping was formed by the Butterburn Flow pools, and the two reprofiled sites (Geltsdale and Stean Moor) were also shown to be fairly distinct from each other. The ANOSIM tests reported a significant difference in macroinvertebrate community similarity between the natural and blocked pools (ANOSIM, Global R = 0.300, p = 0.001), which was still significant when comparing the natural, reprofiled and L-shaped pools but with a reduced R statistic (R = 0.213, p = 0.001). Pairwise comparison of the reprofiled, L-shaped and natural pools revealed that the biggest difference lay between the natural and reprofiled pools (R = 0.325, p = 0.001), followed by the natural and L-shaped pools (R = 0.185, p = 0.003). The L-shaped and reprofiled pools were the most similar (R = 0.134, p = 0.004) (Figure 3.6a).

SIMPER analysis showed that the blocked pools were, on average, more similar to each other than the natural pools, which were the least similar of all four pool types (Table 3.6). The top three taxa contributing to similarity in the blocked pools were Dytiscidae larvae, followed by two chironomid taxa; *P. obvius* and *Z. mucronata*. For natural pools Dytiscidae larvae were followed by two beetle taxa; *H. tristis* and *H. obscurus*. When the blocked pools were broken down into the two sub-categories, the reprofiled pools displayed the highest level of similarity and the L-shaped pools were slightly less similar (Table 3.6). Whilst Dytiscidae larvae again contributed most to the similarity of each pool type, the other main defining species differed between pool types. For L-shaped pools the remaining similarity was accounted for by three chironomid taxa; *Z. mucronata*, *P. obvius* and *Macropelopia*. In the in the reprofiled pools the list of defining taxa was headed by the chironomids *P. obvius and C. plumosus*, but also included the hemipteran *C. wollastoni*, Tanytarsini spp. and the beetle species *A. bipustulatus* and *H. gyllenhalii* (Table 3.6).

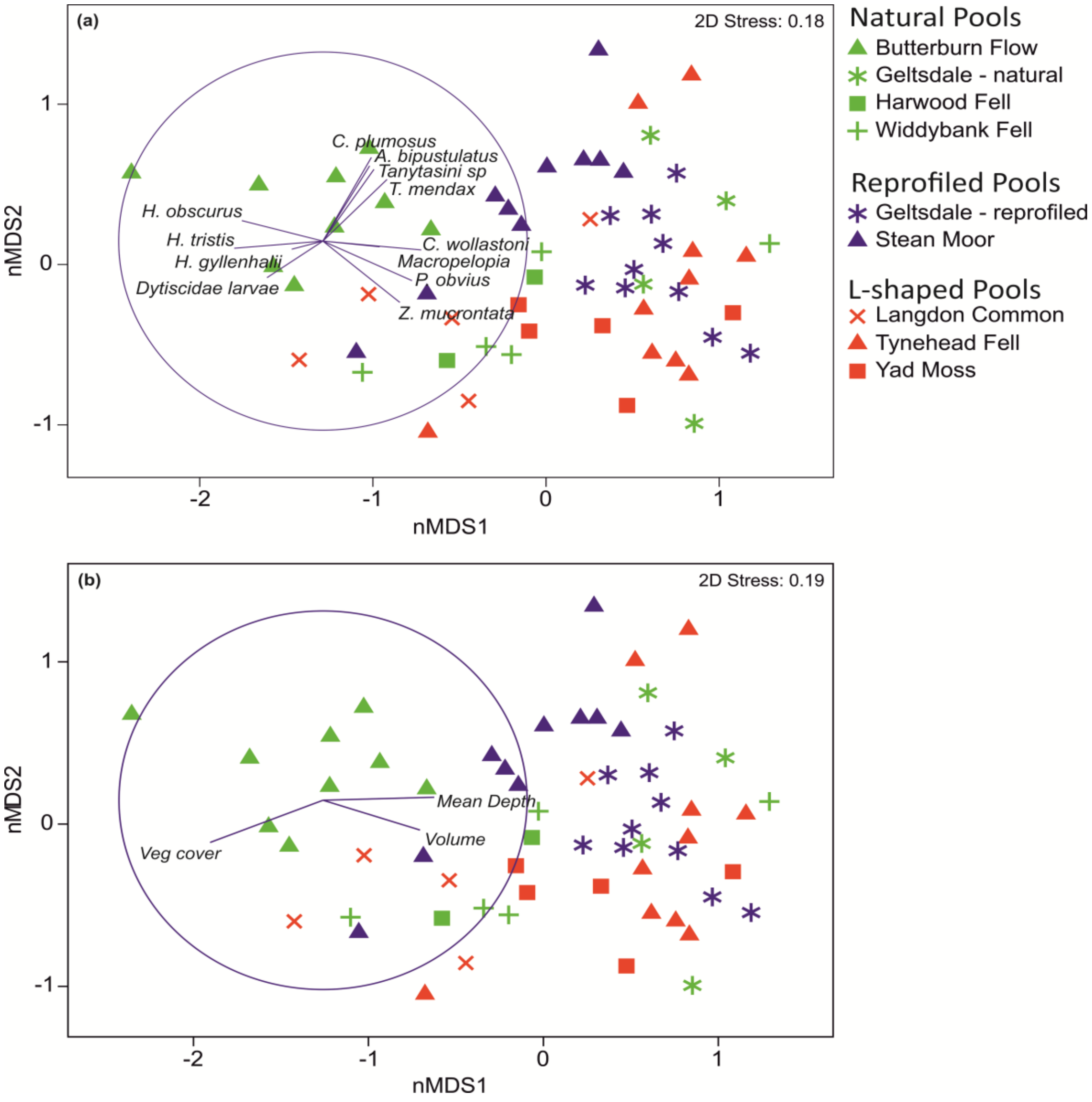

Figure 3.6. nMDS ordination showing the similarity between the different pool types and sites (a) overlaid with taxa highlighted by the SIMPER analysis (see tables 3.6 & 3.7) and (b) overlaid with environmental variables which resulted in Pearson's correlations of >0.5 with either nMDS ordination axis.

The average dissimilarity between the natural and blocked pools was high (72.46%) and was almost exactly the same for the natural v reprofiled (72.62%) and the natural v L-shaped pools (72.30%) (Table 3.7). The biggest contributor to the average dissimilarity between the natural and blocked pools was Dytiscidae larvae, which were more abundant in the natural pools, as was the adult beetle *H. tristis*. However, several chironomid taxa also contributed to the differences, with *C. plumosus* more abundant in the reprofiled pools and *Z. mucronata* in the L-shaped pools. These two taxa were also among the main contributors to the lower average dissimilarity between the two blocked pool types (64.33%) (Table 3.7.)

Table 3.6. SIMPER analysis – intra-pool type similarity. Defining taxa for each pool type (i.e. contributing up to 70% of the overall similarity); average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Type	Taxon	Av. Abund.	% Contrib.	% Cum
Natural Average similarity: 30.77%	*Dytiscidae* larvae	4.23	35.31	35.31
	Hydroporus tristis	2.42	16.43	51.73
	Hydroporus obscurus	1.82	9.49	61.22
	Zalutscia mucrontata	2.01	7.97	69.19
	Psectrocladius obvius	1.18	5.38	74.57
Blocked Average similarity: 37.48%	Dytiscidae larvae	3.51	20.74	20.74
	Psectrocladius obvius	2.88	16.33	37.07
	Zalutscia mucrontata	2.88	14.01	51.07
	Callicorixa wollastoni	1.93	8.41	59.49
	Chironomus plumosus	2.02	7.05	66.54
	Macropelopia	1.54	5.57	72.11
Reprofiled Average similarity: 42.91%	Dytiscidae larvae	3.40	17.19	17.19
	Psectrocladius obvius	3.14	15.72	32.91
	Chironomus plumosus	2.74	11.52	44.43
	Callicorixa wollastoni	2.38	9.52	53.95
	Tanytasini spp	1.78	7.07	61.01
	Agabus bipustulatus	1.16	5.77	66.78
	Hydroporus gyllenhalii	1.63	5.6	72.38
L-shaped Average similarity: 35.85%	*Zalutscia mucrontata*	3.94	27.49	27.49
	Dytiscidae larvae	3.62	22.78	50.28
	Psectrocladius obvius	2.62	14.98	65.26
	Macropelopia	1.63	7.09	72.34

Table 3.7. SIMPER analysis - inter-pool type dissimilarity. Taxa which contribute at least 5% to the overall difference between pool types; average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Types	**Taxon**	**Av. Abund.**	**Av.Abund**	**% Contrib.**	**% Cum.**
		Natural	**Blocked**		
Groups Natural & Blocked Average dissimilarity: 72.46%	Dytiscidae larvae	4.23	3.51	8.32	8.32
	Zalutscia mucrontata	2.01	2.88	7.65	15.97
	Hydroporus tristis	2.42	0.43	6.40	22.37
	Psectrocladius obvius	1.18	2.88	6.21	28.58
	Chironomus plumosus	1.22	2.02	5.78	34.37
	Hydroporus obscurus	1.82	0.05	5.09	39.46
		Natural	**Reprofiled**		
Groups Natural & Reprofiled Average dissimilarity: 72.62%	Dytiscidae larvae	4.23	3.40	7.35	7.35
	Chironomus plumosus	1.22	2.74	6.32	13.66
	Hydroporus tristis	2.42	0.18	6.25	19.91
	Psectrocladius obvius	1.18	3.14	6.24	26.15
	Zalutscia mucrontata	2.01	1.83	6.05	32.20
	Callicorixa wollastoni	0.67	2.38	5.47	37.68
	Tanytarsus mendax	1.18	1.74	5.41	43.09
		Natural	**L-shaped**		
Groups Natural & L-shaped Average dissimilarity:= 72.30%	Dytiscidae larvae	4.23	3.62	9.30	9.30
	Zalutscia mucrontata	2.01	3.94	9.26	18.56
	Hydroporus tristis	2.42	0.69	6.55	25.11
	Psectrocladius obvius	1.18	2.62	6.19	31.29
	Hydroporus obscurus	1.82	0.05	5.38	36.67
	Chironomus plumosus	1.22	1.30	5.24	41.92
	Macropelopia	0.89	1.63	5.06	46.98
		Reprofiled	**L-shaped**		
Groups Reprofiled & L-shaped Average dissimilarity = 64.33%	*Zalutscia mucrontata*	1.83	3.94	9.45	9.45
	Dytiscidae larvae	3.40	3.62	8.65	18.11
	Chironomus plumosus	2.74	1.30	8.16	26.27
	Psectrocladius obvius	3.14	2.62	6.78	33.05
	Callicorixa wollastoni	2.38	1.47	6.03	39.07
	Macropelopia	1.44	1.63	5.35	44.43
	Tanytarsus mendax	1.74	0.90	5.32	49.75
	Tanytasini sp	1.78	1.05	5.18	54.93

3.3.4 Chironomidae biodiversity and community composition

Overall, Chironomidae taxon richness was higher in the blocked pools than the natural pools, with both blocked types displaying higher average taxon richness than their natural counterparts. However, the only significant difference lay between the natural and reprofiled pools (Table 3.8, Figure 3.7). Chironomid abundance was also higher in the blocked pools, with the L-shaped pools containing more chironomids, on average, than the reprofiled pools, although none of the differences were significant

Table 3.8. Chironomidae biodiversity metrics and GLM results. Means (± st.dev) for the different pool types (blocked = reprofiled + L-shaped), along with GLM results reporting the differences between the pool types. Overall results refer to natural v reprofiled v L-shaped. Significant results are highlighted bold.

	Pool Type				**GLM Results**				
Variable	**Natural**	**Blocked**	**Re-profiled**	**L-shaped**	**Blocked v natural**	**Overall**	**Natural v reprofiled**	**Natural v L-Shaped**	**Reprofiled v L-shaped**
Taxon Richness	3.80 (3.44)	5.18 (2.18)	5.60 (2.06)	4.75 (2.27)	t = -1.89 p = 0.06	p = 0.10	t = 2.14 **p = 0.04**	t = -1.13 p = 0.26	t = 1.01 p = 0.32
Abundance	112 (147)	188 (206)	161 (197)	215 (216)	t = -1.61 p = 0.11	p = 0.23	t = 0.96 p = 0.34	t = -1.74 p = 0.09	t = -0.77 p = 0.44
1-Simpsons	0.48 (0.31)	0.60 (0.20)	0.70 (0.11)	0.51 (0.22)	t = -1.69 p = 0.10	**p = 0.007**	t = 2.82 **p = 0.01**	t = -0.39 p = 0.70	t = 2.62 **p = 0.01**
Berger Parker	0.66 (0.27)	0.55 (0.20)	0.47 (0.18)	0.63 (0.19)	t = 1.65 p = 0.11	**p = 0.01**	t = -2.63 **p = 0.01**	t = 0.40 p = 0.69	t = -2.36 **p = 0.02**

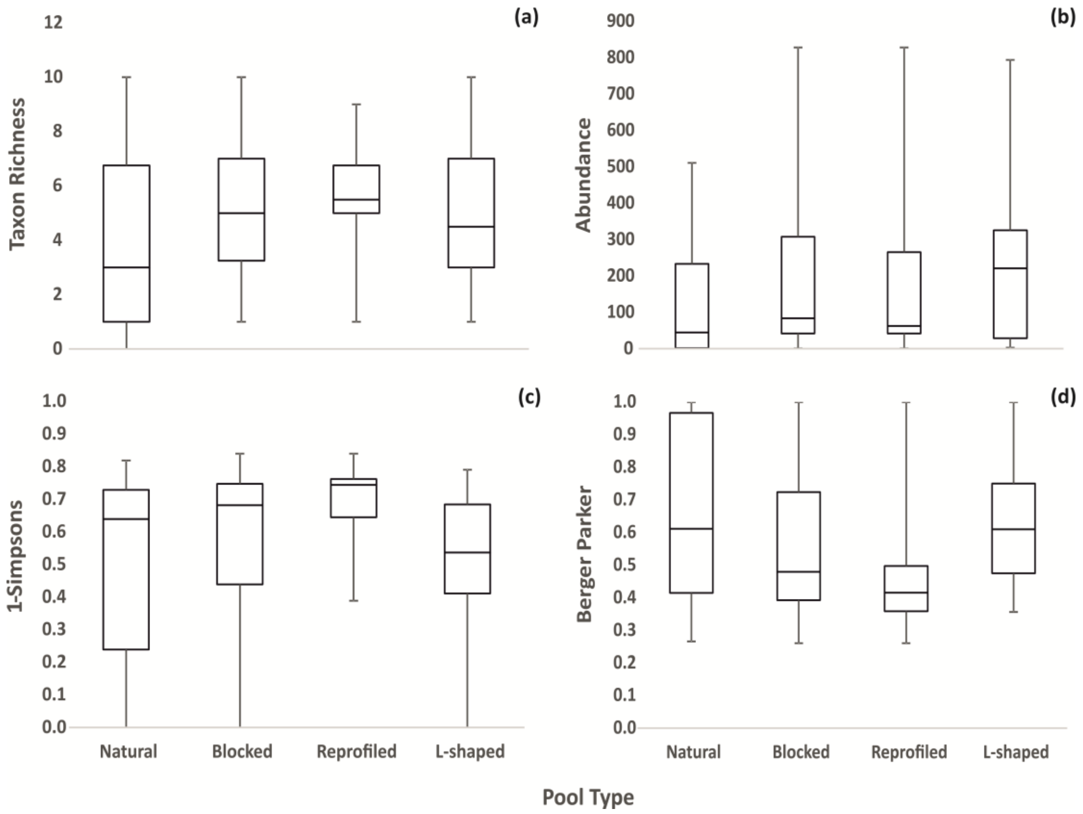

Figure 3.7. Chironomidae biodiversity metrics for the pool types; (a) Taxon richness, (b) Abundance, (c) Simpsons Diversity Index (λ-1) and (d) Berger-Parker Dominance Index (D). Error bars denote +/- 1 St. Dev.

(Table 3.8, Figure 3.7). The diversity indices suggested that the blocked pools were more diverse than the natural pools, as both blocked types returned higher 1-

Simpsons and lower Berger-Parker scores. In both cases, the significant differences lay between the reprofiled pools (which had the highest 1-Simpsons and lowest Berger-Parker scores) and the other two pool types (Table 3.8, Figure 3.7).

The nMDS ordination suggested little differentiation between the pools types with regards to chironomid community composition (Figure 3.8). This was reflected in the ANOSIM tests which reported a significant difference in macroinvertebrate community similarity between the natural and blocked pools but with a low Global R statistic (ANOSIM, Global R = 0.191, p = 0.005). When comparing between the three pool types the R statistic reduced still further (R = 0.098, p = 0.001). Pairwise comparisons revealed that the biggest difference lay between the reprofiled and L-shaped pools (R = 0.165, p = 0.001), followed by the reprofiled and natural pools (R = 0.101, p = 0.005). The L-shaped and natural pools were the most similar and were the only pairing not to be significantly different from each other (R = 0.037, p = 0.07) (Figure 3.6a).

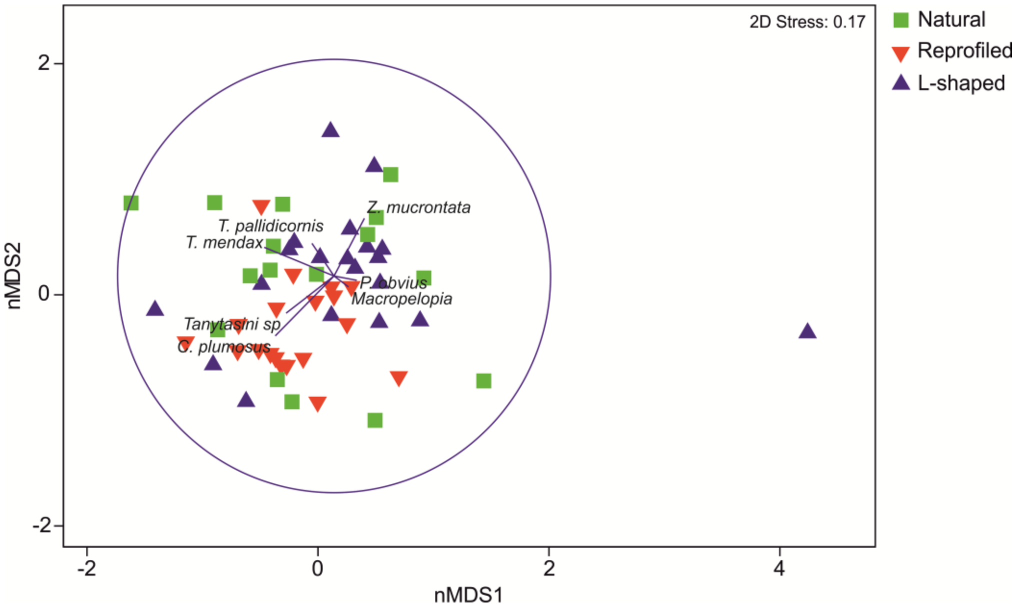

Figure 3.8. Chironomidae nMDS ordination showing the similarity between the different pool types and overlaid with taxa highlighted by the SIMPER analysis (see tables 3.9 & 3.10)

SIMPER analysis showed that chironomid community composition was by far the least similar in the natural pools (16.87%), whereas the blocked (combined) pools resembled each other more (37.27%) (Table 3.9). Of the two blocked types, the reprofiled pools displayed the highest similarity (43.52%). *Z. mucronata* and *P. obvius* were the most abundant taxa in both the natural and L-shaped pools, whereas the reprofiled pools were defined most by *P. obvius* and *C. plumosus*. The average dissimilarity between the natural and blocked pools was high (74.21%), with similar figures for the natural v reprofiled (73.83%) and natural v L-shaped pools (74.59%) (Table 3.10). Average abundances were generally lower in the natural pools with limited exceptions, for example *Z. mucronata* was more abundant in the natural than the reprofiled pools, and both *T. mendax* and *T. pallidicornis* were both more abundant in the natural than the L-shaped pools. The reprofiled and L-shaped pools had a lower average dissimilarity (65.59%) with *Z mucronata* being more abundant in the L-shaped pools and *C. plumosus* more abundant in the reprofiled pools (Table 3.10)

Table 3.9. Chironomidae SIMPER analysis - intra-pool type similarity. Defining taxa for each pool type (i.e. contributing up to 70% of the overall similarity); average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Type	Taxon	Av. Abund.	% Contrib.	% Cum.
Natural Average similarity: 16.87%	*Zalutscia mucrontata*	3.01	33.22	33.22
	Psectrocladius obvius	2	21.11	54.34
	Chironomus plumosus	1.8	15.31	69.65
	Tanytarsus mendax	1.42	7.54	77.19
Blocked Average similarity: 37.27%	*Psectrocladius obvius*	3.8	30.51	30.51
	Zalutscia mucrontata	3.55	22.94	53.45
	Chironomus plumosus	2.69	14.86	68.31
	Tanytasini *sp*	1.85	9.66	77.97
Reprofiled Average similarity: 43.52%	*Psectrocladius obvius*	4.5	32.62	32.62
	Chironomus plumosus	3.77	24.51	57.13
	Tanytasini *sp*	2.43	13.66	70.79
L-shaped Average similarity: 37.02%	*Zalutscia mucrontata*	5.03	46.24	46.24
	Psectrocladius obvius	3.09	23.81	70.05

Table 3.10. Chironomidae SIMPER analysis - inter-pool type dissimilarity. Taxa which contribute at least 5% to the overall difference between pool types; average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Types	**Taxon**	**Av.Abund**	**Av.Abund**	**Contrib%**	**Cum.%**
		Natural	**Blocked**		
Groups Natural & Blocked Average dissimilarity: 74.21%	*Zalutscia mucrontata*	3.01	3.55	16.98	16.98
	Psectrocladius obvius	2.00	3.80	15.03	32.00
	Chironomus plumosus	1.80	2.69	12.54	44.54
	Macropelopia	1.23	1.70	9.18	53.72
	Tanytarsus mendax	1.42	1.50	8.99	62.71
	Tanytasini sp	0.99	1.85	8.22	70.94
		Natural	**Reprofiled**		
Groups Natural & Reprofiled Average dissimilarity: 73.83%	*Psectrocladius obvius*	2.00	4.50	16.38	16.38
	Chironomus plumosus	1.80	3.77	14.53	30.91
	Zalutscia mucrontata	3.01	2.06	12.96	43.87
	Tanytarsus mendax	1.42	2.03	10.39	54.26
	Tanytasini *sp*	0.99	2.43	9.54	63.80
	Macropelopia	1.23	1.62	8.59	72.39
		Natural	**L-shaped**		
Groups Natural & L-shaped Average dissimilarity: 74.59%	*Zalutscia mucrontata*	3.01	5.03	20.95	20.95
	Psectrocladius obvius	2.00	3.09	13.68	34.64
	Chironomus plumosus	1.80	1.62	10.57	45.20
	Macropelopia	1.23	1.78	9.76	54.97
	Tanytarsus mendax	1.42	0.97	7.61	62.58
	Tanytasini *sp*	0.99	1.27	6.92	69.49
	Tanytarsus pallidicornis	1.25	1.17	6.72	76.22
		Reprofiled	**L-shaped**		
Groups Reprofiled & L-shaped Average dissimilarity: 65.59%	*Zalutscia mucrontata*	2.06	5.03	16.80	16.80
	Chironomus plumosus	3.77	1.62	13.85	30.65
	Psectrocladius obvius	4.50	3.09	12.18	42.83
	Tanytasini *sp*	2.43	1.27	8.90	51.74
	Tanytarsus mendax	2.03	0.97	8.26	59.99
	Macropelopia	1.62	1.78	8.04	68.03
	Tanytarsus pallidicornis	1.50	1.17	6.98	75.01

3.3.5 Coleopteran biodiversity and community composition

Average Coleopteran taxon richness was highest (and practically identical) in the natural and reprofiled pools, and was significantly lower in the L-shaped pools (Table 3.11, Figure 3.9). There was no significant difference in beetle abundance between the pool types, although it was highest in the reprofiled and lowest in the L-shaped pools. The natural pools displayed significantly higher 1-Simpsons and significantly lower Berger Parker scores than the blocked pools, although the lower blocked (combined) figures were mainly due to the low scores for the L-shaped rather than the reprofiled pools (Table 3.11, Figure 3.9).

Table 3.11. Coleoptera biodiversity metrics and GLM/GLMM results. Means (± st.dev) for the different pool types (blocked = reprofiled + L-shaped), along with GLM/GLMM results reporting the differences between the pool types. Overall results refer to natural v reprofiled v L-shaped. Significant results are highlighted bold. † indicates GLMM as opposed to GLM.

	Pool Type				**GLM Results**				
Variable	**Natural**	**Blocked**	**Re-profiled**	**L-shaped**	**Blocked v natural**	**Overall**	**Natural v reprofiled**	**Natural v L-shaped**	**Reprofiled v L-shaped**
† Taxon Richness	4.80 (1.77)	3.98 (1.85)	4.80 (1.91)	3.15 (1.39)	t = 1.66 p = 0.10	**p = 0.004**	t = 0.00 p = 1.00	t = 3.07 **p = 0.003**	t = 3.07 **p = 0.003**
†Abundance	37 (41)	36 (42)	44 (43)	28 (39)	t = 0.10 p = 0.92	p = 0.50	t = 0.57 p = 0.57	t = 0.78 p = 0.44	t = 1.34 p = 0.18
1-Simpsons	0.63 (0.20)	0.49 (0.23)	0.57 (0.20)	0.41 (0.24)	t = 2.25 **p = 0.03**	**p = 0.005**	t = -0.79 p = 0.43	t = 3.17 **p = 0.003**	t = 2.37 **p = 0.02**
Berger Parker	0.57 (0.17)	0.69 (0.21)	0.60 (0.22)	0.77 (0.17)	t = -2.20 **p = 0.03**	**p = 0.002**	t = 0.59 p = 0.55	t = -3.28 **p = 0.002**	t = -2.69 **p = 0.009**

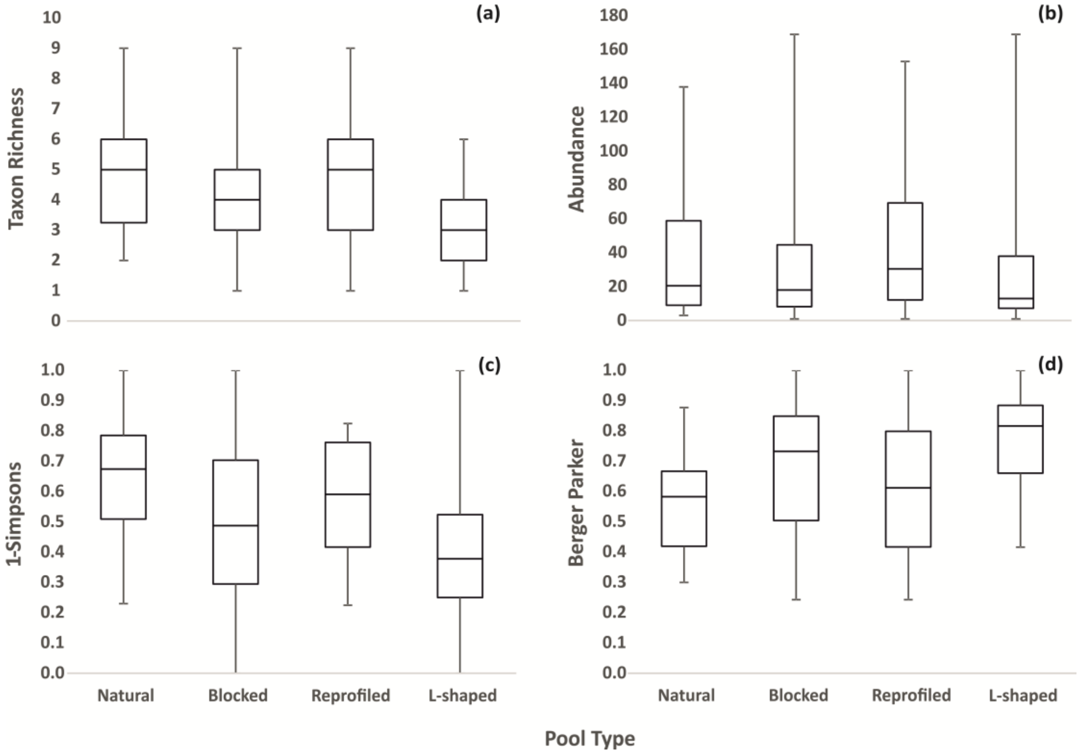

Figure 3.9. Coleoptera biodiversity metrics for the pool types; (a) Taxon richness, (b) Abundance, (c) Simpsons Diversity Index (λ-1) and (d) Berger-Parker Dominance Index (D). Error bars denote +/- 1 St. Dev.

The nMDS ordination suggested some overlap between the pool types with regards to beetle community composition, with the natural pools forming the most distinct cluster (Figure 3.11). ANOSIM reported a significant difference in community composition between the natural and blocked (combined) pools (ANOSIM, Global R = 0.430, p = 0.001). Analysis of the three pool types was still significant but with a reduced Global R statistic (R = 0.258, p = 0.001). Pairwise comparisons revealed that the main difference lay between the natural and reprofiled pools (R = 0.390, p = 0.001), followed by the natural and L-shaped pools (R = 0.261, p= 0.001), with the two blocked pool types having the most similar composition (R = 0.147, p = 0.007).

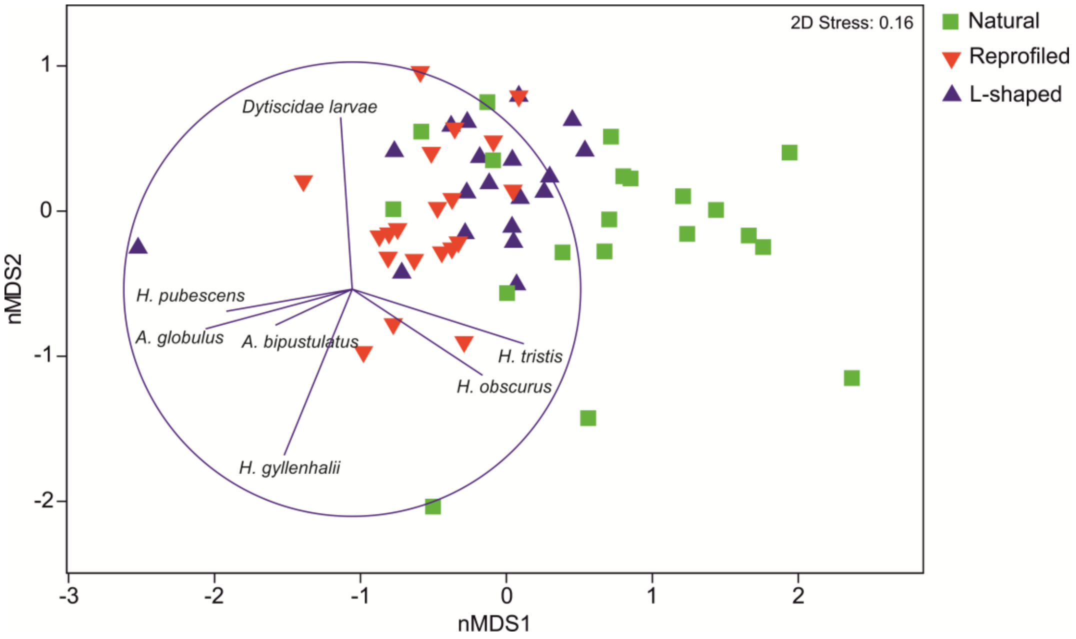

Figure 3.11. Coleoptera nMDS ordination showing the similarity between the different pool types and overlaid with taxa highlighted by the SIMPER analysis (see tables 3.12 & 3.13)

SIMPER analysis showed that the natural pools were, on average, the least similar to each other (average similarity = 46.83%) (Table 3.12). Dytiscidae larvae were by far the most important contributors to community similarity in each pool type, with

Table 3.12. Coleoptera SIMPER analysis - intra-pool type similarity. Defining taxa for each pool type (i.e. contributing up to 70% of the overall similarity); average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Type	Taxon	Av. Abund.	% Contrib.	% Cum.
Natural Average similarity: 46.83%	Dytiscidae larvae	6.41	55.15	55.15
	Hydroporus tristis	3.08	20.09	75.24
Blocked Average similarity: 60.54%	Dytiscidae larvae	7.98	71.53	71.53
Reprofiled Average similarity: 62.02%	Dytiscidae larvae	7.58	60.02	60.02
	Agabus bipustulatus	2.79	14.01	74.03
L-shaped Average similarity: 62.15%	Dytiscidae larvae	8.37	81.29	81.29

Table 3.13. Coleoptera SIMPER analysis - inter-pool type dissimilarity. Taxa which contribute at least 5% to the overall difference between pool types; average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Types	Taxon	Av. Abund	Av. Abund	% Contrib.	% Cum.
		Natural	**Blocked**		
Groups Natural & Blocked Average dissimilarity: 56.14%	*Hydroporus tristis*	3.08	0.75	13.76	13.76
	Dytiscidae larvae	6.41	7.98	13.64	27.40
	Hydroporus obscurus	2.38	0.09	12.02	39.42
	Hydroporus gyllenhalii	1.14	2.35	11.48	50.90
	Agabus bipustulatus	1.12	2.09	11.26	62.16
	Hydroporus pubescens	0.49	1.69	8.30	70.46
		Natural	**Reprofiled**		
Groups Natural & Reprofiled Average dissimilarity: 58.05%	*Hydroporus tristis*	3.08	0.35	13.41	13.41
	Agabus bipustulatus	1.12	2.79	12.07	25.48
	Hydroporus gyllenhalii	1.14	2.75	11.66	37.13
	Dytiscidae larvae	6.41	7.58	11.42	48.55
	Hydroporus obscurus	2.38	0.06	11.08	59.63
	Hydroporus pubescens	0.49	2.12	9.05	68.68
	Anacaena globulus	0.22	1.45	6.52	75.20
		Natural	**L-shaped**		
Groups Natural & L-shaped Average dissimilarity: 54.23%	Dytiscidae larvae	6.41	8.37	16.02	16.02
	Hydroporus tristis	3.08	1.15	14.14	30.16
	Hydroporus obscurus	2.38	0.12	13.02	43.18
	Hydroporus gyllenhalii	1.14	1.95	11.28	54.46
	Agabus bipustulatus	1.12	1.39	10.40	64.86
	Hydroporus pubescens	0.49	1.26	7.50	72.36
		Reprofiled	**L-shaped**		
Groups Reprofiled & L-shaped Average dissimilarity: 40.92%	*Agabus bipustulatus*	2.79	1.39	19.20	19.20
	Hydroporus gyllenhalii	2.75	1.95	16.51	35.71
	Hydroporus pubescens	2.12	1.26	16.00	51.71
	Dytiscidae larvae	7.58	8.37	14.51	66.22
	Anacaena globulus	1.45	0.51	11.08	77.30

only two other taxa being flagged up by the analysis; *Hydroporus tristis* for the natural pools and *Agabus bipustulatus* for the reprofiled pools. The two blocked pool types were the most similar to each other (average dissimilarity = 40.92%), with four adult species being more abundant in the reprofiled pools and only Dytiscidae larvae more abundant in the L-shaped pools (Table 3.13). Dytiscidae larvae were slightly less abundant in the natural pools than in both blocked pool types, as were all the adult species apart from *Hydroporus tristis* and *Hydroporus obscurus*.

3.3.6 Macroinvertebrate biodiversity and environmental variables

There were only two significant relationships between the pool environmental characteristics and the four biodiversity metrics. Vegetation cover (t = -4.60, p < 0.001) and Cl (t = -2.78, p = 0.001) were both negatively related to abundance. Levels of Cl were also borderline negatively related to taxon richness (t = -1.97, p = 0.05).

3.4 Discussion

This study has provided a novel insight into the environmental characteristics and macroinvertebrate biodiversity of drain-blocked and natural pools on areas of UK blanket bog. It also highlights some differences in biodiversity between pools formed using different blocking methods, which may be useful to land managers when planning future drain-blocking projects. This section now discusses these findings in the context of other studies.

3.4.1 Environmental characteristics

In support of H_1, the blocked pools were found to be deeper and to hold significantly more water than natural pools. The natural pools were very shallow (mean depth = 9cm) but similar depths were reported by Brown et al. (submitted) who reported a mean depth of 7cm for pools on areas of intact blanket bog in the Pennines. However, in other areas of the UK where natural pools system occur the pools are often much larger and deeper than those in the Pennines. For example, the largest pool studied in the Flow Country (Scotland) by Belyea and Lancaster (2002) had a surface area of 1930 m^2. However, regardless of size, natural peat pools generally have a large surface area to depth ratio (Foster and Fritz, 1987, Towers, 2004) as they tend to spread outwards rather than downwards after initial formation (Belyea and Lancaster, 2002) and this was reflected in the relatively large perimeters and shallow depths of the natural pools in my study. In contrast, the depth of drain-blocked pools is mainly pre-determined by the dimensions of the drainage ditch in which they form, although this can be altered to a certain extent by the blocking method (e.g. reprofiling).

Reprofiled pools displayed the lowest levels of vegetation cover despite reprofiling being intended to encourage vegetation growth within the drain. However, the vegetation cover varied widely between the two reprofiled sites, with extremely low levels at Geltsdale (median = 0, IQR = 1.75%) but relatively high levels at Stean Moor (median =82.5, IQR = 71%). The lack of vegetation cover at Geltsdale could be due to the pools there being the deepest in the study, as deeper pools can experience lower levels of light penetration which may inhibit vegetation growth (Ramchunder et al., 2009). Indeed, Peacock et al. (2013) found a strong negative correlation between pool depth and *Eriophorum* cover in recently blocked pools, although also a weaker but positive correlation between pool depth and *Sphagnum* cover, as floating mats of mosses are not reliant on light reaching the pool bottom. However, as the Geltsdale (natural) pools also had low vegetation cover (median = 6, IQR = 19%) but were much shallower than their reprofiled counterparts, there could be a different, unknown, site-specific cause.

The water chemistry of the pools was typical of that found in ombrotrophic peatland surface waters, with low pH, conductivity and ionic concentrations and high levels of DOC (Hannigan and Kelly-Quinn, 2014, Brown et al., submitted). However, levels of Cl and Na were found to be far lower than in a range of waterbodies in Irish bogs, i.e. at Owenirragh mean levels of Cl and Na were 22.25 and 10.69 mg L^{-1} respectively, but this was probably due to the relatively large influx of marine-derived ions in precipitation to the Irish bogs (Hannigan and Kelly-Quinn, 2014). Furthermore, whilst the levels of DOC found in this study were very similar to those reported by Brown et al. (submitted) (e.g. median 34.4 mg L^{-1} for blocked pools, also in the UK Pennines) they were higher than those reported by Peacock et al. (2013) in drain-blocked pools in Wales (mean 22.09 mg L^{-1}) and also in the majority of ombrotrophic waterbodies in Ireland (ranging from mean 10.71 to 31.31 mg L^{-1}) (Hannigan and Kelly-Quinn, 2014).

Whilst other studies comparing natural pools and those created by rewetting measures have reported no significant differences with regards to water chemistry (Hannigan et al., 2011, Brown et al., submitted) this study found several significant differences, thus not supporting the second part of H_2. Perhaps the most noticeable was for levels of DOC, with the natural pools having significantly lower concentrations than either of the blocked types, and the L-shaped pools having significantly lower concentrations than the reprofiled pools. Whilst blocked pools at Forsinard (Scotland) have also been found to exhibit higher levels of DOC than their natural counterparts (Ed Turner, pers.comm), this is in contrast to the findings of Brown et al. (submitted) who reported that natural pools in the Pennines had higher DOC levels than blocked pools. Also, Wallage et al. (2006) found that soil water from peat surrounding blocked drains had significantly lower levels of DOC than either drained or even intact peatlands. The authors theorised that this could be due to a store exhaustion process whereby drainage exposed the peat to atmospheric oxygen, leading to increased enzyme activity which accelerated DOC production, with subsequent rewetting resulting in any remaining labile carbon being 'flushed' from the system. One possible reason for the high levels of DOC in drain-blocked pools in my study is the 'enzyme-latch' mechanism, whereby the enzymes which were 'switched on' by water table drawdown were not subsequently 'switched off' as the water table recovered (Freeman et al., 2001). Furthermore, the 'exhausted' store of DOC could have been supplemented with alternative sources made available by any changes in the hydrological regime caused by the drainage and subsequent blocking (Wallage et al., 2006). It should be noted that one natural pool site, Butterburn Flow, exhibited by far the lowest DOC levels in this study (median = 14.57, IQR = 6.26 mg L^{-1}) whilst one of the reprofiled sites, Stean Moor, exhibited extremely high levels of DOC (median = 75.10, IQR = 35.70 mg L^{-1}), so these two sites may have skewed the average figures for their respective pool types. Levels of Fe were also found to be significantly different between all three pool types, being highest in the reprofiled and lowest in the natural pools. This is most likely due to the corresponding levels of DOC, which can act as a mobiliser of metals and pollutants (Wallage et al., 2006). Stean Moor also exhibited very high levels of Fe (median = 5.31, IQR = 6.28 mg L^{-1}), much higher than the

Environment Agency's current long-term EQS for dissolved Fe in freshwaters of 1 mg L^{-1} (Johnson et al., 2007).

Another significant difference in water chemistry was the levels of DO, with reprofiled pools having significantly lower levels than either the natural pools or the L-shaped pools. However, again, major differences were apparent between the two reprofiled sites, with the lowest DO levels by far found at Stean Moor (median = 2.83, IQR = 1.97 mg L^{-1}). This could be due to the much smaller average perimeter (and by implication surface area) of the Stean Moor pools, which potentially allowed for less diffusion of atmospheric O_2 per unit area.

3.4.2 Macroinvertebrate biodiversity and community composition

The dominance of chironomids, beetles and hemipterans in all the pool types supported the first part of H_2. Chironomids especially were numerically dominant, which agrees with other peatland pool studies (Standen et al., 1998, Towers, 2004, Hannigan et al., 2011, Hannigan and Kelly-Quinn, 2012, Baars et al., 2014). In this study chironomids were also the richest taxon, which is not always reflected in the literature because identification is sometimes only performed to family level (e.g. Hannigan and Kelly-Quinn, 2012). Peatland pool studies which have not reported large abundances of chironomids have usually employed sampling methods more suited to catch strong swimmers (e.g. funnel traps) (Downie et al., 1998a, Mazerolle et al., 2006). Chironomids probably thrive in small pools due to the scarcity of large predators and their ability to adapt their diet regardless of their preferred food source (Armitage et al., 1995). For example, chironomids can consume methanotrophic bacteria (Jones et al., 2008) and predatory taxa, such as Tanypods, will consume detritus (Baker and McLachlan, 1979) and algae (Ruse, 2002). The prevalence of chironomid larvae in this study is potentially beneficial for moorland birds, which feed on the emerged adult flies (Buchanan et al., 2006).

Beetles were the second most abundant and taxonomically rich taxa in this study, further supporting H_2. Amongst the adult species identified, *Enochrus affinis* and *Enochrus ochropterus* are categorised as 'notable'; defined as 'scarce in Great Britain and thought to occur in fewer than 100 10km squares of the National Grid' (Chadd and Extence, 2004). *E. affinis* is also classed as an acid-mire obligate, and several other species identified are classified as acid mire specialists (e.g. *Hydroporus gyllenhalii* and *Hydroporus obscurus*) or acid mire preferentials (e.g. *Helophorus flavipes* and *Hydroporus tristis*) (Boyce, 2004) (Appendix A). The hemipteran populations consisted mainly of Gerridae and Corixidae nymphs, with only two adult species identified; *Gerris costae* (an acid mire spcialist) and *Callicorixa wollastoni* (an acid mire preferential) (Boyce, 2004). This low level of hemipteran richness was unexpected. For example, Crisp and Heal (1998) found seven corixid species in peatland pools in the Pennines, of which *C. wollastoni* was the most common, and Brown et al. (submitted) reported eleven hemipteran taxa. However, both of these studies were carried out over longer periods of time which may have facilitated the capturing of a larger, more seasonally representative, species dataset.

Whilst chironomids and hemipterans were more abundant in the blocked pools, the abundance of beetles was greater in the natural pools than in the L-shaped pools. Indeed, both of the 'notable' beetles species; *E. affinis* and *E*. *ochropterus*, were found exclusively at Butterburn Flow, as was by far the largest population of *H. obscurus.* The existence of species found exclusively (or almost exclusively) at Butterburn Flow helps to explain the marked difference in community similarity between that and all the other sites in the study. It is also perhaps suggestive of differences in community composition between natural pools found in real complexes and those which are more isolated features in the landscape (i.e. the other natural pools in this study). Furthermore, Butterburn Flow generally had much lower taxonomic richness and abundance than the other sites, so the presence of *E. affinis* and *E. ochropterus* exclusively at this less diverse site demonstrates the important role that ponds play in supporting biodiversity at a landscape level (Williams et al., 2003, Biggs et al., 2005). Beetles of the genus *Enochrus* belong to the family Hydrophilidae, which feed on plants or decaying plant matter and are poor swimmers; both of these characteristics help to explain their presence at the shallow, sphagnum-filled pools at Butterburn Flow as opposed to some of the deeper, less vegetated pools.

Other important species identified in the study as a whole included the Brown Hawker dragonfly (*Aeshna juncea*), an acid mire preferential, and the acid mire obligate *Limnephilus coenosus*, a cased caddisfly (Boyce, 2004). Interestingly, *L. coenosus* was fairly equally distributed amongst the pool types, whereas the one other trichopteran species identified, the caseless *Plectrocnemia conspersa*, was not found in any of the natural pools but was particularly abundant at Tynehead Fell (L-shaped) and Geltsdale (reprofiled). As Brown et al. (submitted) also reported *P. conspersa* as present in artificial pools but absent from natural pools, this suggests that this species may be an early coloniser amongst the Trichoptera, an order generally perceived to have low dispersal abilities compared to, for example, larger beetle species such as *Dytiscus* (Van Duinen et al., 2007). However, in a study analysing community assembly in a stream created for fly fishing in Sweden, *P. conspersa* was one of the only taxa found in nearby reference sites not to have colonised the new stream by the end of the sampling period (18 months) (Malmqvist et al., 1991).

When comparing the natural and blocked pools for all taxa combined, there were no significant differences in any of the biodiversity metrics, supporting the second part of H_2 which predicted similar biodiversity across the pool types. This agrees with the findings of Hannigan et al. (2011) who found no significant differences between pools on intact mountain blanket bog and those on blanket bog restored fifteen years previously. However, when the blocked pool types were split into reprofiled and L-shaped, several significant differences became apparent. Although there was still no significant difference in macroinvertebrate abundance, the reprofiled pools displayed significantly higher taxonomic richness than either the L-shaped or the natural pools. This wasn’t just for all taxa combined; the reprofiled pools exhibited elevated chironomid taxon richness and diversity (as indicated by the diversity indices) than either of the other two pool types. Furthermore, the Coleoptera analysis showed that, while the L-shaped pools hosted the least abundant and diverse beetle communities, the reprofiled pools were on a par with natural pools with regards to beetle taxon richness and even had slightly higher 1-Simpsons and lower Berger-Parker scores, suggesting higher beetle diversity. One reason for this increased biodiversity in reprofiled pools may be that the reprofiling method involves redistributing the existing vegetation along the reprofiled drain edges, which potentially leads to a more complex and heterogeneous submerged vegetation structure within the pools (Tews et al., 2004). However, when looking at the richness and abundance statistics for the individual sites, it became clear that the averages for the natural sites were reduced substantially by the very low figures for Butterburn Flow. In contrast, the other three natural sites displayed high taxon richness (three out of the top four scores) and abundance (three out of the top five scores). This agrees more with Mazerolle et al. (2006) who found that arthropod richness and abundance in natural pools was much higher than in pools dug specifically for the study, four years previously. However, these authors did not report figures for dipterans which makes comparisons difficult, considering the high number of chironomids found in my study. There was less variation between the pools in the L-shaped category, which displayed significantly lower 1-Simpsons and higher Berger-Parker scores than either the reprofiled or natural pools. Overall, the data suggest that the blocking method of reprofiling may be conducive to greater taxon richness and biodiversity than the creation of L-shaped pools, although data from more blocked sites are needed to confirm the differences seen in this study.

Although community composition was significantly different between all pool types the global R statistic was generally low, again supporting the second part of H_2. The pool types found to be least similar for all taxa combined (with the largest Global R statistic) were the natural and reprofiled pools. After Dytiscidae larvae, the top three defining taxa in the natural pools were beetles, rather than the chironomids which played a larger role in defining the reprofiled pool communities. These differences in defining taxa between the pool types perhaps suggests a shift in community composition over time from chironomids to beetles, as the natural pools would have been older than the blocked pools although their exact age was undetermined. The Coleoptera nMDS analysis certainly suggested a shift in beetle community composition between the reprofiled and natural pools, as these were the least similar to each other despite being almost equally diverse (as indicated by the biodiversity metrics). This may be explained by the fact that some beetles are considered to be potential early colonisers due to their capacity for flight (Fairchild et al., 2000) and lentic species have been shown to have wider distributional ranges than lotic species (Ribera and Vogler, 2000). Interestingly, the SIMPER analysis highlighted that most of the more commonly-occurring adult beetle species, with the exception of *H. tristis* and *H. obscurus*, as well as Dytiscidae larvae, were more abundant in the blocked pools. This suggests that the high beetle diversity in the natural pools was driven more by the rarer species, such as those belonging to the genus *Enochrus*, which, in turn, provides tentative support for the findings of van Duinen et al. (2003) that numbers of rare species increase with time (assuming that the natural pools were indeed older than the blocked pools).

3.4.3 Relationships between environmental variables and biodiversity metrics

H_3 posited that the physical dimensions of the pools would influence biodiversity more than water chemistry, but was not supported by the results of the GLMs looking for relationships between the environmental variables and the four biodiversity metrics. Only two significant relationships were found, both negative, between abundance and (i) vegetation cover and (ii) concentrations of Cl. The strongly negative relationship between vegetation cover and abundance could be because vegetation impedes the activity of some species of beetles and hemipterans which use the water column to hunt for food. For example, Mazerolle et al. (2006) reported that capture rates of beetles and hemipterans were negatively associated with the presence of certain vegetation types, whereas the occurrence of damselflies increased among submerged and floating vegetation. However, in the case of my research, the low abundance in highly-vegetated pools was probably at least partly due to the sampling method, as pools that were full of *Sphagnum* were more difficult to sweep. It was especially difficult to sample the bottom sediments, which is where the majority of chironomids (by far the most abundant taxa) would be found. The significant negative relationship between abundance and Cl (as well as the borderline significant negative relationship between taxon richness and Cl) is less easy to explain. Nothing in the literature could explain why increased Cl, especially at relatively low background concentrations, would be detrimental to biodiversity. Furthermore, when analysing the data by site rather than by pool type, the least diverse sites did not have the highest Cl concentrations (or vice versa). Therefore, this result, although significant, should probably be regarded as an outlier. The large range of Fe concentrations found in the pools did not translate into any significant relationships between levels of Fe and the biodiversity metrics, suggesting that the highest Fe concentrations were not detrimental to biodiversity. However, this may be because the taxa most impacted by high Fe (fish and crustaceans) (Johnson et al., 2007) are not present in the pools.

The lack of a relationship between pool size and increased biodiversity disagrees with the long-established ecological theory of the species-area curve (Connor and McCoy, 1979), although this is perhaps unsurprising considering the restricted size range of the pools in this study. Although my study performed no analysis with regards to individual species, it was noted that the two odonate species; the Common Hawker and the Large Red damselfly, were found almost exclusively at Yad Moss. Yad Moss had the largest pool perimeters and water volume, and the permanence this implies would benefit species such as *A. juncea* whose life cycles are known to vary between uni- and semi-voltine (Johansson, 2000). Similarly, the largest diving beetle identified in this study; *A. bipustulatus*, was only absent from two sites; Butterburn Flow (the shallowest pools) and Langdon Common (the third shallowest pools) perhaps indicating its preference for deeper waters. Other studies have also reported that larger diving beetles are more common in larger, deeper peat pools, with smaller pools housing smaller beetles such as Hydroporinae (Foster, 1995, Downie et al., 1998a, Standen et al., 1998).

3.4.4 Conclusions

In conclusion, the pools formed in blocked drains appear to provide suitable habitat for a wide range of aquatic macroinvertebrates, with communities very similar to those found in natural peat pools. Whilst studies in the Netherlands have shown rewetting measures to be detrimental to aquatic macroinvertebrate biodiversity, these were analysing remnants of heterogeneous raised bog, in which the background levels of biodiversity were inherently higher due to the increased environmental gradient present (van Duinen et al., 2003, Verberk et al., 2010a). In contrast, the aquatic lentic landscape of areas such as the English Pennines was restricted mainly to isolated tarns and sink-holes before the advent of drain-blocking, so has benefitted from the pool creation with little risk to existing macroinvertebrate populations. Furthermore, the benefits to aquatic biodiversity afforded by drain blocking will extend spatially, by providing sustenance to fauna higher up the food chain (e.g. moorland birds) and possibly also temporally, by providing future refugia for species forced to migrate upwards and northwards in the face of climate change (Walther et al., 2002, Rosset and Oertli, 2011). The persistence of larger drain-blocked pools, and the habitat they provide for aquatic invertebrates, may also help to supply an alternative food source for moorland birds, as the abundance of terrestrial invertebrates declines in the face of climate change (Carroll et al., 2015).

The findings tentatively suggest that the blocking method of reprofiling may lead to higher taxonomic richness and diversity than the creation of L-shaped pools. However, if encouraging the presence of charismatic species such as dragonflies is important, then the creation of larger pools is recommended. Although no rare or endangered species were identified, the number of acid mire obligates, specialists and preferentials found confirms that the creation of aquatic habitat in the Pennines is facilitating the persistence of taxa that rely, to differing extents, on the existence of such habitat. This is important in a global context due to the proportionately large expanse of blanket bog located in the British Isles.

Chapter 4: The establishment of macroinvertebrate communities in artificial peatland pools

4.1 Introduction

Re-wetting measures on areas of peatland have created new freshwater habitat on a global scale, usually in the form of small pools (see Chapter 2). Although some studies have looked at macroinvertebrate communities in these artificial peatland pools, most commonly created by inserting dams into drainage ditches, (Boyce, 2010, Brown et al., submitted), little is known about how these communities initially form and subsequently change over time. However, the monitoring of newly created habitat provides an opportunity to address this research gap, and is vital to inform conservation goals of peatland restoration with regards to biodiversity (Prach and Walker, 2011).

Community assembly in any given habitat depends on three main factors; dispersal constraints, environmental constraints and internal dynamics (Belyea and Lancaster, 1999). Firstly, in the case of peatland pools, taxa from surrounding freshwater habitats need to reach the pool; these can be either strong or weak fliers who actively disperse, or taxa which are dispersed passively by vectors such as the wind or other organisms (Bilton et al., 2001, Bohonak and Jenkins, 2003). Dispersal, along with other events such as birth, death, extinction, and speciation, have been described as a neutral factors in community assembly (i.e. the assumption that individual organisms, regardless of species, have essentially the same chance of producing reproducing, dying, migrating and speciating), and some theorise that these neutral processes drive community change (Hubbell, 2001). However, other authors argue that niche or deterministic factors, such as the suitability of the prevailing environmental conditions and biological interactions (e.g. predation and competition), are as or more important in driving community assembly (Macarthur and Levins, 1967, Abrams, 1983, Purves and Turnbull, 2010, Brown and Milner, 2012). Taken together, neutral and deterministic processes facilitate the existence of metacommunities (i.e. a network of local communities between which multiple, potentially interacting species are able to disperse), which collectively sustain a wider species pool than may exist in any one specific location (Wilson, 1992, Mouquet and Loreau, 2002, Leibold et al., 2004).

Several studies have looked at the initial colonisation of newly-created freshwater habitats (Malmqvist et al., 1991, Milner et al., 2007, Louette et al., 2008, Ruhí et al., 2009, Cañedo-Argüelles and Rieradevall, 2011, Jeffries, 2011) and others have carried out chronosequence (space-for-time) studies looking at streams, pools and lakes of different ages (Barnes, 1983, Gee et al., 1997, Fairchild et al., 2000, Milner et al., 2000, Ruse, 2002). One of the most consistent findings is the early colonisation of aquatic habitat by Diptera, especially Chironomidae (Barnes, 1983, Malmqvist et al., 1991, Flory and Milner, 2000, Cañedo-Argüelles and Rieradevall, 2011). Chironomids are, at best, weak fliers and are most effectively dispersed by the wind during swarm events. However, this dispersal technique is highly effective and, when combined with a short life cycle, enables the rapid colonisation of new habitats (Armitage et al., 1995). There is also evidence for a change in chironomid community structure over time, with a shift from early-colonising Tanytarsini to Chironomini with increasing age (Barnes, 1983, Ruse, 2002). In acid ponds, however, Orthocladiinae and Tanytarsini are known to dominate, with very few Chironomini present (Barnes, 1983).

Other taxa such as Cladocera, Coleoptera, Plecoptera, Ephemeroptera, Heteroptera, Trichoptera, Odonata and Oligochaeta have also been reported to colonise new still waters within the first year after creation (Malmqvist et al., 1991, Louette et al., 2008, Ruhí et al., 2009, Cañedo-Argüelles and Rieradevall, 2011, Jeffries, 2011). However, the initial sharp rise in the number of species can be followed, fairly quickly, by a slower increase with Barnes (1983) reporting that the rate of new taxa colonising ball clay ponds in Dorset (UK) levelled out to less than one taxon per year after the first two years. However, the study found a difference between the Diptera species curve, which levelled out after one year, and the non-Diptera curve, which continued to increase until the third year (Barnes, 1983). As a consequence, most studies report no significant relationships between pool age and biodiversity metrics (Gee et al., 1997, Louette et al., 2008, Cañedo-Argüelles and Rieradevall, 2011). However, the community composition and relative abundance of taxa does appear to change over time. Hemipterans have been reported to reduce in relative abundance with pool age, whilst Trichoptera increase steadily (Barnes, 1983) and Odonata are generally more abundant in later successional stages (Barnes, 1983, Malmqvist et al., 1991, Cañedo-Argüelles and Rieradevall, 2011). Despite their capacity for active flight, Coleoptera have been reported by some studies as being amongst the later colonisers (Malmqvist et al., 1991, Cañedo-Argüelles and Rieradevall, 2011), although one study of small, temporary ponds dug in a seasonally flooded field in Northumberland (UK) reported the dytiscid beetle *Agabus bipustulatus* within seven days of pool creation (Jeffries, 2011). The community composition of beetle species has been shown to differ in pools of different ages, with predatory dysticids in pools created < 10 yrs previously as part of wetland destruction mitigation measures, to herbivorous curculionids and chrysomelids in a range of nearby, older reference ponds (Fairchild et al., 2000).

Changes in macroinvertebrate community composition over time have been linked to the development of new microhabitats (e.g. colonisation by different macrophytes), the increase in biological interactions such as predation and competition, and the relative dispersal abilities of colonising taxa (Barnes, 1983, Malmqvist et al., 1991, Fairchild et al., 2000, Cañedo-Argüelles and Rieradevall, 2011). The identity of the early-colonising or remnant (i.e. present after a disturbance) taxa can also shape the subsequent community and is known as a priority effect. Priority effects include both physical (e.g. habitat modification) and biological (e.g. competition or predation) processes (Ledger et al., 2006, Jeffries, 2011). The mechanisms driving community assembly can also be viewed within the context of the three biotic models of succession; facilitation, tolerance and inhibition, originally proposed by Connell and Slatyer (1977) for plants and sessile animals. This framework has since been used to explain the community assembly of aquatic fauna, for example Brown and Milner (2012) found that tolerance was a key mechanism underpinning primary succession in a glacial stream invertebrate community, as evidenced by the continual addition of new traits to the macroinvertebrate community whilst none were lost. However, it is likely that there will be elements of all three processes found in peatland pools; facilitation (e.g. the arrival of prey species such as chironomid larvae will facilitate the settlement of prey), tolerance (e.g. species with similar traits cohabiting) and inhibition (e.g. an increase in vegetation cover will inhibit the movement of taxa such as Hemiptera).

Stochastic disturbances (e.g. drought or inundation) also drive community change, and the small pools formed by drain-blocking are more susceptible to events such as drought and desiccation, overheating and freezing. Although the small size of drain-blocked pools will not deter the majority of invertebrates from colonising, pool permanence is likely to be a major factor determining species persistence (Wellborn et al., 1996). For example, water-level instability can disrupt developmental cycles, resulting in failure to metamorphose or to reach a drought-resistant stage (Urban, 2004). Furthermore, small pools on areas of UK moorland are at high altitude and freeze for long periods over winter, which may lead to anoxia and reduced nutrient levels in the water below. Thus, the small size of drain-blocked pools may act as a filter, decreasing the overall diversity and leading to more similar community composition than in less disturbed pools (Chase, 2007).

The aim of this study was to analyse macroinvertebrate community assembly in drain-blocked pools in the Pennines (northern England). This was achieved by (a) monitoring a set of newly created pools for the first eighteen months of their lifespan and (b) undertaking a longer-term chronosequence survey of pools belonging to different age classes (<3 years, 5-8 years and 10+ years). The hypotheses were:

H_1. Chironomids would be early colonisers (Malmqvist et al., 1991, Flory and Milner, 2000, Cañedo-Argüelles and Rieradevall, 2011) due to their high dispersal abilities and short life cycles (Armitage et al., 1995).

H_2. Taxon richness and abundance would rise most sharply within the first two years after pool creation but would start to level out thereafter, leading to no significant differences in biodiversity metrics between the oldest age classes (Barnes, 1983, Gee et al., 1997, Cañedo-Argüelles and Rieradevall, 2011).

H_3. Macroinvertebrate community structure and the relative abundance of taxa would change over time due to factors such as the different dispersal abilities of taxa, biological interactions between the invading taxa and temporal changes in the habitat structure (e.g. vegetation) (Barnes, 1983, Malmqvist et al., 1991, Fairchild et al., 2000, Cañedo-Argüelles and Rieradevall, 2011). However, inter-pool community similarity was predicted to increase with pool age, due to the susceptibility of small pools to stochastic events. For example, desiccation events select for drought-tolerant taxa (Urban, 2004, Chase, 2007).

4.2 Methods

4.2.1 Study sites

Initial community assembly in newly-blocked drains was monitored at Moor House NNR (Table 4.1), where the drainage ditches had been blocked in December 2012. Regular sampling (every two months) was undertaken from April 2013 to June 2014 (pool age 4 to 18 months), apart from over winter 2012/2013 when inclement weather hindered site access or resulted in frozen pools. Five drainage ditches were selected and, on each occasion, one pool from each drain was sampled for macroinvertebrates and environmental characteristics. Different pools were sampled on each sampling visit. This dataset is referred to from here on as the *Moor House pools*.

For the chronosequence survey, six sites were selected (five plus Moor House), two for each age category (time since blocked); <3 years, 5-8 years and 10+ years, with all sites located within the English Pennines (Table 4.1, Figure 4.1). At each site, five drainage ditches were selected and one pool from each was sampled in June 2013. Sampling was repeated in June 2014, giving a total of ten pools per site and twenty pools per age class. Different pools were sampled in the second year to avoid any

Table 4.1. Study sites descriptions. Details of the sampling sites including age class and time since blocked.

Site Name	Lat Long	Drains Blocked	Age Class	Pool Age 2013 (years)	Pool Age 2014 (years)	Altitude (m)
Moor House	54° 41' 27"N 2° 22' 56"W	2012	<3yrs	0.5	1.5	572
Tennant Gill	54° 7' 39"N 2° 11' 28"W	2011	<3yrs	1.5	2.5	506
Cold Fell	54° 52' 55''N 2° 36' 21''W	2008	5-8yrs	5	6	590
Yad Moss	54° 43' 15''N 2° 20' 36''W	2006	5-8yrs	7	8	615
Halton lea	54° 54' 28"N 2° 32' 51"W	2012	10+yrs	10	11	393
Oughtershaw Beck	54° 13' 59"N 2° 14' 12"W	1999	10+yrs	14	15	401

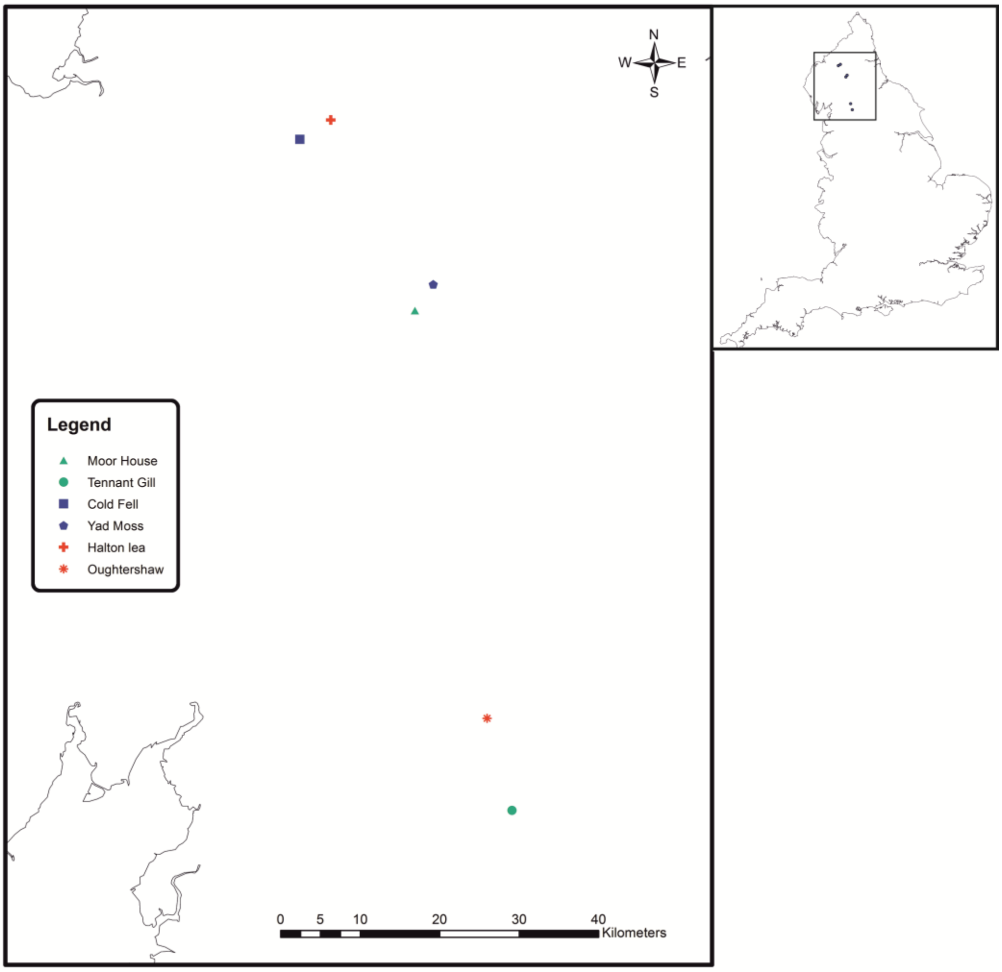

Figure 4.1. Map of study sites

sampling artefacts from the first effort (the pools were so small that sampling could be likened to a disturbance event, with associated population manipulation). However, pools sampled in the second year were all located within the same drains as those sampled in year one. This dataset is referred to as the *chronosequence pools*. Potential sites were identified via communications with land management agencies and by viewing on-line satellite and aerial images, then site visits were carried out to confirm the suitability of the sites and the pools (e.g. site accessibility, pool size, etc). All chosen pools had a surface area ≤3 m^2. The sampled pools at each site were selected randomly on the day. The two June sampling efforts from the Moor House pools were included in the Chronosequence dataset as part of the <3 years pools. All sites had blanket peat cover, with vegetation dominated by *Eriophorum* spp. and *Calluna vulgaris* (L.), with varying amounts of *Sphagnum* spp. cover. Climate data were not available for all the sites but data from a weather station at Moor House NNR (NY 754329) are considered as typical for the north Pennines; mean annual precipitation from 2000 to 2012 was 2001 mm, with a corresponding mean monthly temperature of 6.28 °C (ECN, 2014).

4.2.2 Sampling methodology

The sampling methodology for environmental characteristics and macroinvertebrates was the same as outlined in Chapter 3.

4.2.3 Statistical analysis

For the Chronosequence dataset, analyses were carried out to look for differences between the three age classes. Detailed explanations of the analyses can be found in section 3.2.3 of Chapter 3 but included; (1) Principal Component Analysis (PCA) to help examine variance in the environmental variables, (2) the calculation of four biodiversity metrics; taxon richness, abundance, the 1-Simpson's Diversity Index (λ) and the Berger-Parker Index (D), (3) the use of generalised linear models (GLMs) and generalised linear mixed models (GLMMs) to compare the environmental and biodiversity variables between the age classes and (4) nMDS ordination, ANOSIM and SIMPER analysis in PRIMER-E to analyse the community composition of both the Moor House and the chronosequence datasets. Biodiversity analysis was again carried out for all taxa combined and also for the two most taxonomically rich and abundant taxa; Chironomidae and Coleoptera. To aid visual interpretation of the nMDS ordinations some outlying pools were removed: three >3 years pools from the overall nMDS, four pools from the Chironomidae nMDS (one >3 years, two 5-8 years and one 10+ years) and four >3 years pools from the Coleopteran nMDS. All GLMs / GLMMs were performed using R 3.1.2. As in Chapter 3, the environmental and biodiversity datasets were tested for spatial autocorrelation but in this case only two environmental variables were found to be spatially autocorrelated. Further to this, for the Moor House pools, Spearman Rank correlations were used to look for relationships between pool age (time since blocked) and the four biodiversity metrics. Spearman Rank tests were used in preference to GLMs due to the pool age variable being categorical and were carried out in Minitab 17.

4.3 Results

4.3.1 Environmental characteristics

Physically, the 5-8 years pools were the deepest, with the largest perimeters and the greatest water volume (Table 4.2); they were significantly deeper than the <3 years pools and had significantly larger water volumes than both the other age classes. The 10+ years pools had significantly smaller perimeters than either the <3 or 5-8 years pools. Vegetation cover differed significantly between all three age classes, with the <3 years pools having by far the lowest cover and the 10+ years pools the highest. With regards to the water chemistry, the most marked difference was in levels of DO, with the <3 years pools exhibiting significantly lower levels than either of the other two age classes, which had very similar levels to each other. EC was significantly higher in the 10+ years pools than for either other age class, and pH was significantly higher in the <3 years pools than the 5-8 or 10+years pools. The 5-8 years pools had significantly lower concentrations of K and Si than either of the other two age classes, and the 10+ pools had significantly higher concentrations of Mg, Na and Cl than the other two classes (Table 4.2).

The PCA generated five PCs with Eigenvalues > 1, with the first two PCs accounting for 40.9% of the variation (Table 4.3). The strongest loading on PC1 was a negative one for Na (-0.423). PC2 had two strong loadings for physical characters: depth (0.431) and volume (0.400). When the PC scores were analysed by age class the <3 years pools were associated with positive scores on PC1 and negative scores on PC2, the 5-8 years pools were positive on both PC1 and PC2, and the 10+ years pools were associated with negative scores on both but more strongly so on PC1 (Figure 4.2). Overall, the PC1 scores were significantly different between all three age classes ($p < 0.001$), whereas the difference between the PC2 scores was only significant if we accept $p = 0.05$. For the PC1 scores, the 10+ pools were significantly different from both the <3 years ($t = -3.40$, $p = 0.001$) and the 5-8 years ($t = 4.21$, $p < 0.001$) pools. For the PC2 scores, only the <3 and 5-8 years pools were significantly different from each other ($t = 2.47$, $p = 0.02$) (Figure 4. 2).

Table 4.2. Environmental variables and GLM/GLMM results. Medians (plus interquartile range), of the different age classes, along with GLM/GLMM results reporting the overall differences and differences between the age classes. Significant results at q<0.05 are highlighted in bold. † signifies GLMM as opposed to GLM.

	Age Class			**GLM Results**			
Variable	**<3yrs**	**5-8yrs**	**10+yrs**	**Overall**	**<3yrs v 5-8yrs**	**<3yrs v 10+ yrs**	**5-8yrs v 10+yrs**
† Depth (cm)	18 (15)	28 (11)	19 (21)	**q = 0.02**	t = 3.42 **q = 0.002**	t = 1.92 q = 0.05	t = 1.50 q = 0.10
Perimeter (cm)	521 (311)	595 (327)	370 (157)	**q = 0.001**	t = 0.88 q= 0.23	t = -3.17 **q = 0.004**	t = 4.05 **q = 0.001**
Volume (m^2)	0.40 (0.74)	0.74 (0.59)	0.25 (0.51)	**q = 0.01**	t = 2.07 **q = 0.04**	t = -1.14 q = 0.17	t = 3.21 **q = 0.003**
Vegetation cover (%)	13 (23)	97.5 (100)	100 (0)	**q < 0.001**	t = 3.54 **q = 0.002**	t = 6.84 **q < 0.001**	t = -3.30 **q = 0.003**
DO (mg L^{-1})	6.58 (2.31)	9.34 (4.49)	9.16 (2.55)	**q = 0.001**	t = -3.78 **q < 0.001**	t = -3.57 **q = 0.002**	t = -0.23 q = 0.37
EC (µs cm^{-1})	36.95 (10.02)	44.65 (14.50)	46.30 (45.00)	**q = 0.003**	t = 0.94 q = 0.22	t = 3.48 **q = 0.002**	t = -2.53 **q = 0.01**
pH	4.20 (0.22)	4.04 (0.35)	4.00 (0.45)	**q = 0.02**	t = 2.55 **q = 0.01**	t = 2.35 **q = 0.02**	t = 0.21 q = 0.38
TN (mg L^{-1})	1.01 (0.38)	0.88 (0.50)	0.80 (0.60)	q = 0.34	t = -0.88 q = 0.23	t = -0.66 q = 0.27	t = -0.22 q = 0.37
TP (mg L^{-1})	0.03 (0.02)	0.02 (0.01)	0.03 (0.02)	**q = 0.02**	t = -0.38 q = 0.35	t = 1.85 q = 0.05	t = -2.00 **q = 0.04**
DOC (mg L^{-1})	34.68 (12.12)	38.28 (19.01)	33.07 (17.23)	q = 0.35	t = 0.54 q = 0.31	t = 0.85 q = 0.23	t = -0.31 q = 0.36
Al (mg L^{-1})	0.06 (0.09)	0.07 (0.04)	0.06 (0.10)	q = 0.23	t = -1.23 q = 0.16	t = -0.07 q = 0.42	t = -1.16 q = 0.17
Ca (mg L^{-1})	0.46 (0.51)	0.24 (0.25)	0.34 (0.22)	**q = 0.02**	t = -2.79 **q = 0.01**	t = -1.84 q = 0.05	t = -0.95 q = 0.22
Fe (mg L^{-1})	0.34 (1.40)	0.47 (0.37)	0.49 (1.61)	q = 0.23	t = -0.78 q = 0.24	t = 0.56 q = 0.30	t = -1.34 q = 0.13
† K (mg L^{-1})	0.17 (0.77)	0.06 (0.10)	0.20 (0.44)	**q = 0.01**	t = -3.07 **q = 0.004**	t = -0.31 q = 0.36	t = -2.76 **q = 0.01**
Mg (mg L^{-1})	0.38 (0.12)	0.32 (0.10)	0.43 (0.20)	**q = 0.002**	t = -1.40 q = 0.12	t = 2.32 q **= 0.02**	t = -3.70 **q = 0.001**
Na (mg L^{-1})	2.80 (0.61)	3.21 (0.65)	3.74 (1.89)	**q < 0.001**	t = 0.66 q = 0.27	t = 4.62 **q <0.001**	t = -3.96 **q = 0.001**
Si (mg L^{-1})	0.12 (0.12)	0.05 (0.04)	0.13 (0.26)	**q = 0.002**	t = -2.63 q **= 0.01**	t = 0.86 q = 0.23	t = -3.22 **p = 0.003**
Cl (mg L^{-1})	2.56 (3.72)	3.89 (3.52)	5.68 (5.72)	**q = 0.001**	t = 1.33 q = 0.26	t = 11.47 **q = 0.001**	t = -10.14 q = **0.01**
SO_4 (mg L^{-1})	0.26 (0.25)	0.26 (0.39)	0.35 (0.51)	q = 0.42	t = -0.25 q = 0.37	t = 0.02 q = 0.42	t = -0.28 q = 0.37

Table 4.3. PCA metrics. PC scores, eigenvalues and % variance explained for the five PCs with Eigenvalues >1, produced from the environmental dataset. Scores > 0.4 and < -0.4 are highlighted to aid interpretation.

Variable	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Depth	-0.096	**0.431**	-0.105	0.144	-0.100
Perimeter	0.173	0.328	-0.129	0.262	-0.261
Volume	0.082	**0.400**	-0.151	0.347	-0.250
Veg	-0.143	0.031	0.170	0.296	**0.506**
DO	0.018	0.098	0.245	**0.503**	0.253
EC	-0.332	0.064	0.256	-0.048	-0.020
pH	0.053	-0.347	-0.255	0.162	-0.216
TN	-0.179	0.062	-0.395	-0.266	0.149
TP	-0.116	-0.114	0.112	0.109	-0.033
DOC	-0.212	0.250	-0.181	-0.177	0.381
Al	-0.289	-0.083	-0.359	0.073	0.151
Ca	0.006	-0.392	-0.207	0.145	-0.102
Fe	-0.299	-0.116	-0.346	0.191	0.137
K	-0.227	0.082	-0.047	-0.205	-0.379
Mg	-0.370	-0.157	0.200	0.073	-0.202
Na	**-0.423**	0.077	0.155	-0.006	-0.083
Si	-0.231	0.043	-0.304	0.302	-0.125
Cl	-0.369	0.001	0.275	0.020	-0.253
SO_4	0.024	-0.346	0.053	0.326	-0.017
Eigenvalues	4.57	3.21	2.85	1.95	1.51
%Variation	24.0	16.9	15.0	10.2	7.9

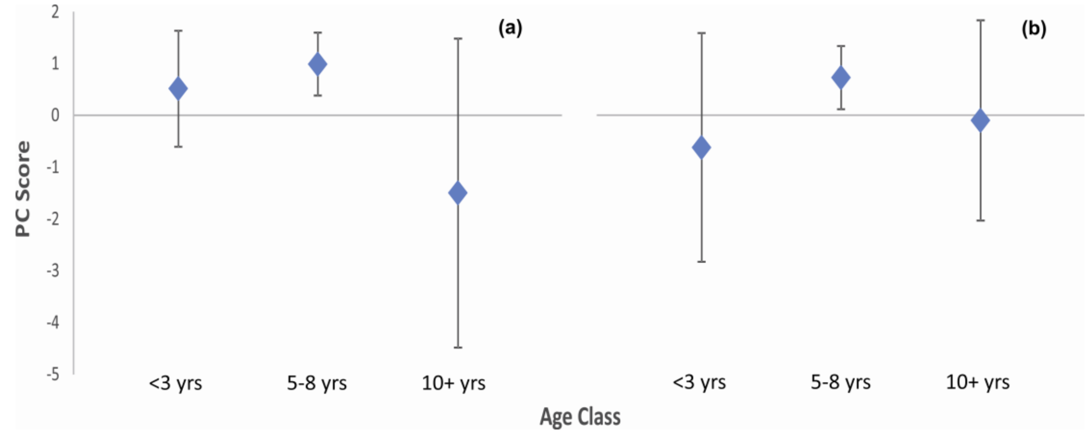

Figure 4.2. PCA metrics. Mean PC scores (+/- 1 st. dev) for each pool type; (a) PC1 and (b) PC2.

4.3.2 Macroinvertebrate biodiversity

Over the two studies, 11492 macroinvertebrates belonging to 76 taxa were collected and identified, although this figure was reduced to 68 after taxonomic adjustment (Appendix A). Chironomidae were the dominant taxon in both datasets, accounting for 22 of the 45 taxa identified at Moor House, and 27 of the 72 taxa in the chronosequence pools. Beetles were also well-represented in both studies with eight adult species found at Moor House, rising to 16 in the wider study (Appendix A).

Macroinvertebrate abundance changed substantially in the first 18 months since drain-blocking, with the largest increase between June and August 2013, when total numbers jumped from 31 to 995 (Figure 4.3a). In this time period, total abundance reached a peak in December 2013 (n = 1075) mainly due to the large numbers of Chironomidae (n = 842) and Plecoptera (n = 164). In the Moor House pools, four taxa each accounted for > 1% of overall abundance, with chironomids being by far the largest contributors (79.48%), followed by Hemiptera (8.48%), Coleoptera (5.87%) and Plecoptera (5.78%). Chironomids were by far the most abundant taxa in each sampling effort, both in total (Figure 4.2a) and relative abundance (Figure 4.3b). The only other taxa to reach double figures for relative abundance in any one sampling period were Hemiptera (28.35%), and Coleoptera (13.19%), both in June 2014, and Plecoptera (15.26%) in December 2013. Chironomidae, Plecoptera, Trichoptera and other Diptera were all found on the first sampling occasion (4 months), whereas Coleoptera and Hemiptera were absent until six months and then only constituted one or two individuals. The first oligochaetes appeared after ten months, and no odonates were found.

Analysis of the chronosequence pools showed that seven taxa each accounted for > 1% of overall abundance; Chronomidae (47.0%), Coleoptera (34.4%), Hemiptera

(6.0%), Plecoptera (4.4%), other Diptera (3.7%), Trichoptera (2.1%) and Odonata (1.70%). The total abundance of macroinvertebrates was greatest in the 5-8 age class and lowest in the 10+ age class, mainly due to the paucity of chironomids in the oldest pools (Figure 4.3c). Only one taxon, Hemiptera (adults and nymphs), was most abundant in the <3 years age class. Three taxa were most abundant in the 5-8 years age class; Chironomidae, Plecoptera and Trichoptera. In the 10+ age class, Coleoptera (adult and larvae), other Diptera, Odonata, Oligochaeta and Collembola were all more abundant than in either of the younger age classes (Figure 4.3c). The taxon with the highest relative abundance in both the <3 years and 5-8 years pools was Chironomidae, whereas more than half of the individuals in the 10+ year pools were Coleoptera (Figure 4.3d). The relative abundance of other Diptera was also much higher in the 10+ years pools, and both the total and relative abundance of Odonata increased with pool age (Figures 4.3c, 2d).

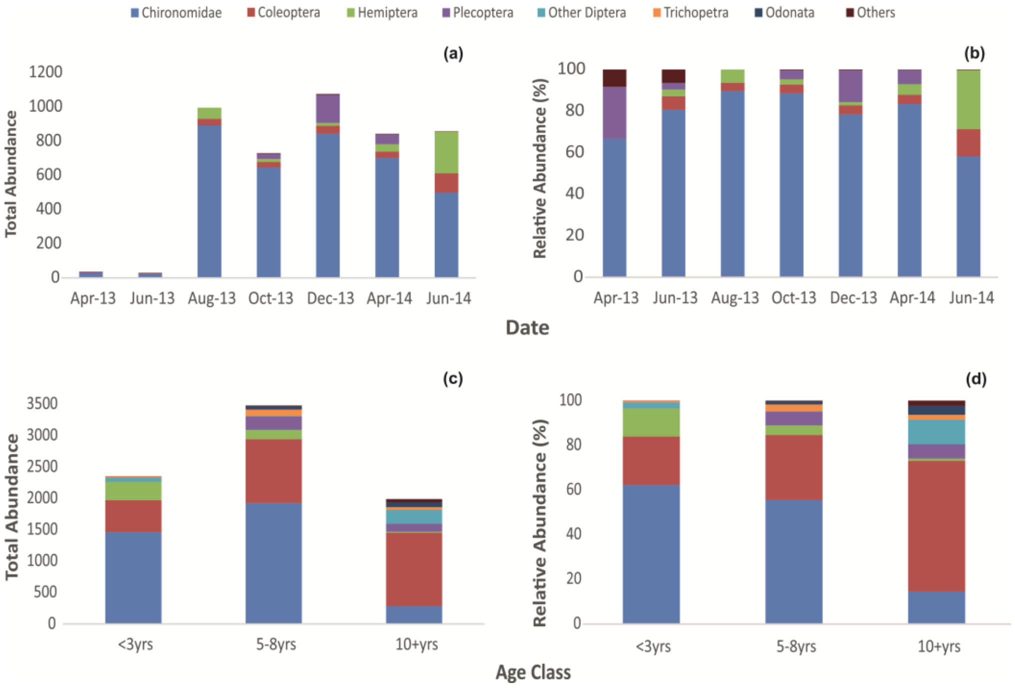

Figure 4.3. Total and relative abundance metrics of taxa accounting for >1% of total abundance in (a) and (b) the Moor House pools and (c) and (d) the Chronosequence pools.

Thirteen of the 45 taxa identified in the Moor House pools were found in the first sampling effort (4 months) (Figure 4.4a). The species curve continued to rise quite sharply until ten months, although it was still increasing at the end of the study. The chronosequence species curve also showed a sharp rise at the start, with 44 of the 72 taxa found within the first 2.5 years (Figure 4.4b). The curve continued to rise, levelling off at about ten years, although three new taxa were found for the first time in the oldest pools (15 years): the Diptera *Pedicia* sp. and *Tabanidae* sp., along with the cased caddisfly *Limnephilus centralis*. In the chronosequence pools, the chironomid *Chironomus plumosus* was widespread and abundant in pools up to the age of 5 years, but completely absent from pools aged 7+ years. Similarly, two adult hemipterans; *Gerris costae* and *Callicorixa wollastoni* were not fund in any pools aged 8+ years. No one taxon was found throughout the entire dataset, but the beetle *Agabus bipustulatus* was present in every pool age except 6 months and 15 years.

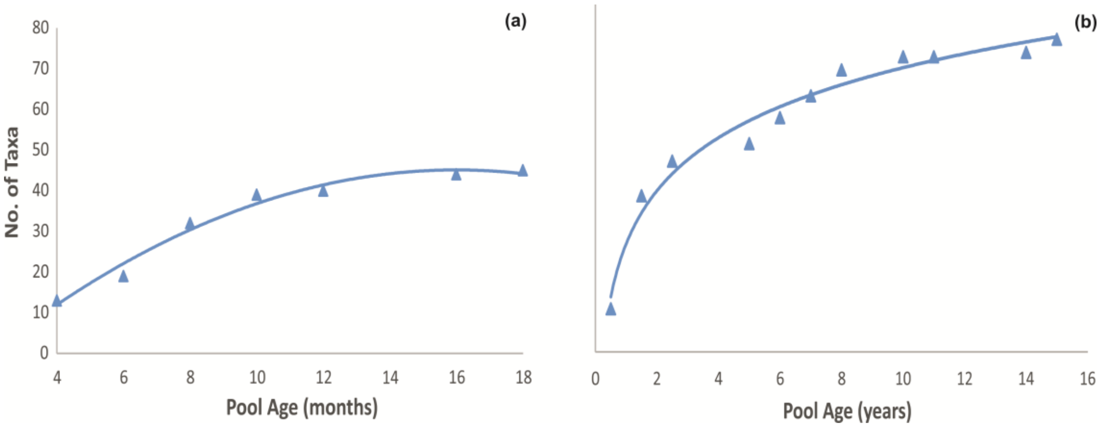

Figure 4.4. Species curves for (a) the Moor House pools and (b) the chronosequence pools.

In the Moor House pools, both taxon richness and abundance increased significantly with pool age over the 18 months (Table 4.4, Figures 4.5a, b), although mean abundance reached a peak at 12 months (December 2013) and mean taxon richness at 16 months (April 2014). The main rise in both taxon richness and abundance was seen between 6 and 8 months (June and August 2013). The relationship between pool age and Berger-Parker was also significant (although not linear), but that between pool age and 1-Simpsons was not (Table 4.4, Figures 4.5c, d).

Table 4.4. Biodiversity metrics (Moor House pools). Means (± st.dev) for the different pool ages along with Spearman Rank results reporting the differences between the pool ages.

	4	**6**	**8**	**10**	**12**	**16**	**18**	**Spearman Rank**	
Variable	**Apr**	**Jun**	**Aug**	**Oct**	**Dec**	**Apr**	**Jun**	**Rs**	**p-value**
Taxon Richness	3.80 (2.68)	2.60 (1.52)	9.00 (3.74)	7.80 (1.64)	9.20 (1.10)	11.20 (1.64)	10.40 (2.07)	0.75	**< 0.001**
Abundance	7 (5)	6 (5)	199 (118)	146 (94)	215 (138)	168 (78)	171 (46)	0.60	**< 0.001**
1-Simpsons	0.71 (0.26)	0.76 (0.33)	0.64 (0.16)	0.45 (0.15)	0.70 (0.11)	0.81 (0.07)	0.72 (0.10)	0.05	0.77
Berger Parker	0.57 (0.21)	0.64 (0.28)	0.50 (0.16)	0.73 (0.11)	0.47 (0.12)	0.31 (0.12)	0.44 (0.14)	-0.38	**0.02**

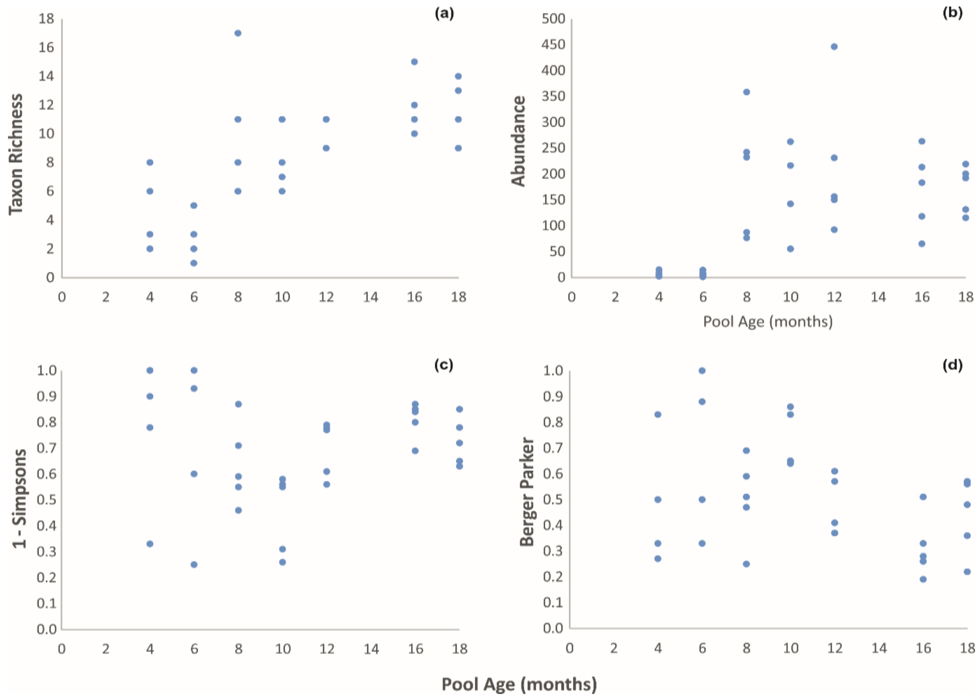

Figure 4.5. Relationships between pool age biodiversity metrics (Moor House pools) (a) taxon richness, (b) abundance, (c) 1-Simpsons and (d) Berger Parker for the Moor House pools. N = 5 per pool age, with some replicates having the same values

For the chronosequence pools, there was no linear relationship between pool age (in years) and any of the four biodiversity metrics (Figure 4.6). However, both taxon richness and abundance rose sharply between 0.5 and 1.5 years, with richness displaying a downwards trend after five years but with a slight rise again at 15 years. The relationship for abundance was less defined but suggested a peak between five and seven years (Figures 4.6a, b). There were no discernible patterns in either 1-Simpsons or Berger Parker over the time series (Figures 4.6c, d).

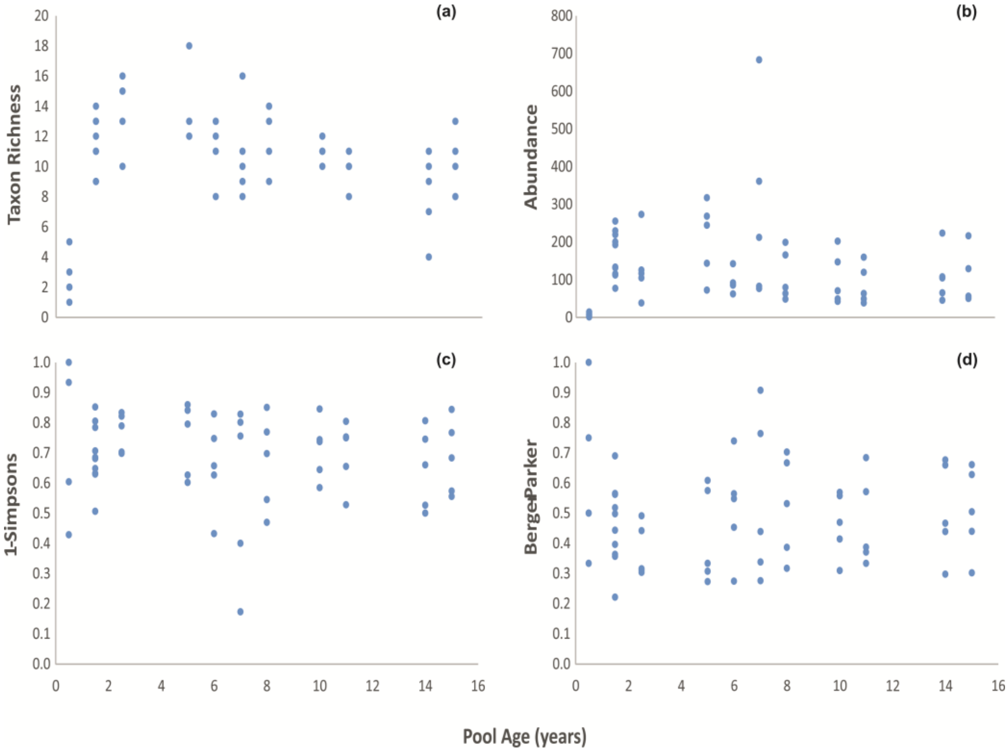

Figure 4.6. Relationships between pool age and biodiversity metrics (chronosequence pools) (a) taxon richness, (b) abundance, (c) 1-Simpsons and (d) Berger Parker for the chronosequence pools.

There were no significant differences in either taxon richness or macroinvertebrate abundance between the three chronosequence age classes, although the test for abundance was borderline significant (Table 4.5). However, the 5-8yr pools displayed significantly higher taxon richness than the <3 years pools (Table

4.5, Figure 4.7a), and the 10+ years pools had significantly lower abundance than the 5-8 years pools, which had the highest average abundance (Table 4.5, Figure 4.7b). There was no significant difference in either of the biodiversity indices: 1-Simpsons and Berger Parker (Table 4.5, Figures 4.7c, d).

Table 4.5. Biodiversity metrics (chronosequence pools). Means (st.dev) for the different age classes in the chronosequence pools, along with GLM results reporting the overall differences and those between the three age classes. Results at p<0.05 are highlighted in bold.

	Age Class			GLM Results			
Variable	**<3yrs**	**5-8yrs**	**10+yrs**	**Overall**	**<3 v 5-8yrs**	**<3 v 10+yrs**	**5-8 v 10+yrs**
Taxon Richness	9.35 (4.53)	11.45 (2.46)	9.70 (1.95)	p = 0.08	t = 2.09 **p = 0.04**	t = 0.35 p = 0.73	t = -1.74 p = 0.09
Abundance	118 (89)	174 (151)	99 (61)	p = 0.05	t = 1.65 p = 0.11	t = -0.71 p = 0.48	t = 2.35 **p = 0.02**
1-Simpsons	0.73 (0.15)	0.66 (0.18)	0.69 (0.11)	p = 0.32	t = -1.47 p = 0.15	t = -1.01 p = 0.32	t = 0.46 p = 0.65
Berger Parker	0.48 (0.18)	0.50 (0.19)	0.49 (0.13)	p = 0.94	t = 0.35 p = 0.73	t = 0.10 p = 0.92	t = -0.24 p = 0.81

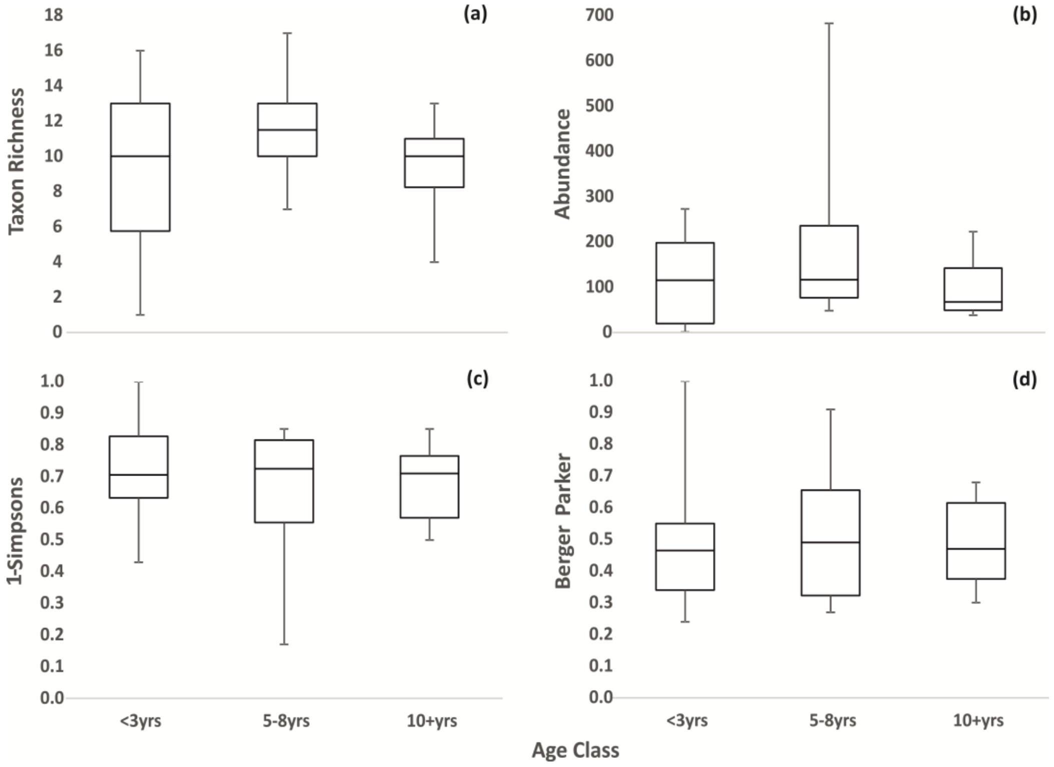

Figure 4.7. Biodiversity metrics (chronosequence pools) by age class; (a) Taxon richness, (b) Abundance, (c) Simpsons Diversity Index (λ-1) and (d) Berger-Parker Dominance Index (D).

4.3.3 Macroinvertebrate community composition

The Moor House pools displayed a significant difference in community similarity between pools ages (ANOSIM, Global R = 0.468, p = 0.001) (Figure 4.8). Pairwise comparisons showed that the community similarity was most similar for pool ages of 4 and 6 months (R = 0.174, p = 0.12). The community similarity was least similar for pool ages of 16 and 18 months (R = 0.796, p = 0.008), followed by pool ages of 10 and 18 months (R = 0.752, p = 0.008) then 4 and 8, and 4 and 18 months (both R = 0.716, p = 0.008).

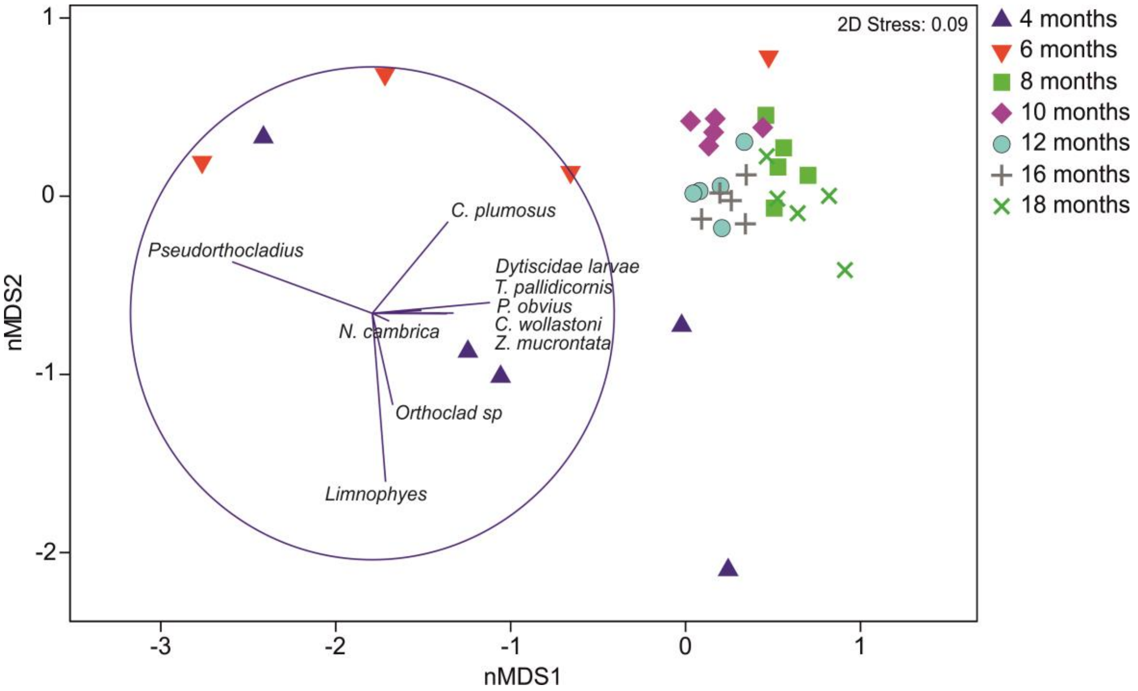

Figure 4.8. nMDS ordination (Moor House pools) showing the similarity between the pools of different ages, overlaid with taxa highlighted by the SIMPER analysis (see Table 4.6 & 4.7).

In the Moor House pools, macroinvertebrate communities generally became more similar with age (Table 4.6). The pools were least similar to each other at 6 months (9.70%) and most similar at 16 months (68.23%). At 4, 6 and 8 months, the defining taxa were all chironomids with the exception of *Nemoura* spp. in the 4 months pools. Chironomids continued to dominate until the 18 months pools, when the taxa contributing most to the overall community similarity were *C. wollastoni* and Dytiscidae larvae, followed by two chironomid taxa. The defining chironomid taxa changed over time at Moor House, with *Limnophyes* and *Pseudorthocladius* found only in the 4 and 6 months pools, then *C. plumosus* becoming prominent from 8 to 16 months before being replaced by *Z. mucronata* and *P. obvius* in the 18 month old pools. Average dissimilarity between the two June sampling periods (6 and 18 months) was high (86.25%), with the abundance of *C. wollastoni*, Dytiscidae larvae and three chironomid species increasing markedly in the older pools, whereas abundance the beetle *H. flavipes* reduced to zero (Table 4.7).

Table 4.6. SIMPER analysis (Moor House pools) – intra-pool age similarity. Defining taxa for each pool age (i.e. contributing up to 70% of the overall similarity); average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Age	Taxon	Av. Abund.	% Contrib.	% Cum.
4 months Average similarity: 18.45%	*Nemoura cambrica*	3.70	37.11	37.11
	Orthoclad sp	2.68	28.94	66.05
	Limnophyes	2.86	13.83	79.88
6 months Average similarity: 9.70%	*Pseudorthocladius*	3.17	76.79	76.79
8 months Average similarity: 62.52%	Chironomus plumosus	6.33	37.65	37.65
	Psectrocladius obvius	5.76	35.17	72.81
10 months Average similarity: 62.59%	*Chironomus plumosus*	8.51	62.47	62.47
	Dytiscidae larvae	2.36	12.3	74.76
12 months Average similarity: 61.68%	*Chironomus plumosus*	6.12	34.88	34.88
	Nemoura cambrica	3.71	19.01	53.89
	Psectrocladius obvius	3.63	13.16	67.05
	Zalutschia mucrontata	2.42	10.14	77.19
16 months Average similarity: 68.23%	*Chironomus plumosus*	5.46	24.68	24.68
	Tanytarsus pallidicornis	4.23	18.67	43.35
	Psectrocladius obvius	3.41	14.56	57.91
	Nemoura cambrica	2.81	10.61	68.51
	Zalutschia mucrontata	2.56	10.13	78.64
18 months Average similarity: 61.39%	*Callicorixa wollastoni*	5.1	24.67	24.67
	Dytiscidae larvae	3.45	18.91	43.58
	Psectrocladius obvius	3.98	16.33	59.91
	Zalutschia mucrontata	2.81	13.16	73.07

Table 4.7. SIMPER analysis (Moor House pools) – inter-age class dissimilarity. Taxa which contribute at last 5% to the overall difference between the two June sampling efforts (when the pools were aged 6 and 18 months). Average abundance (after square root transformation), % contribution and % cumulative contribution to overall dissimilarity.

Pool Ages	**Taxon**	**Av. Abund.**	**Av. Abund.**	**% Contrib.**	**% Cum.**
		6 months	**18 months**		
Groups 6 & 18 months Average dissimilarity = 86.25%	*Callicorixa wollastoni*	1.41	5.1	12.81	12.81
	Psectrocladius obvius	0	3.98	11.2	24.01
	Chironomus plumosus	2.23	3.66	9.59	33.6
	Dytiscidae larvae	0.82	3.45	8.52	42.12
	Pseudorthocladius	3.17	0	8.46	50.58
	Zalutschia mucrontata	0	2.81	7.93	58.51
	Helophorus flavipes	2	0	6.43	64.94
	Parametriocenmus	1.87	0	5.57	70.51

There was a significant difference in macroinvertebrate community similarity between the three chronosequence age classes (ANOSIM, Global R = 0.356, p = 0.001). Pairwise comparison revealed that community similarity for all three age classes was significantly different from each other, with the <3years and 10+years pools being the least similar (R=0.515, p = 0.001), followed by the 5-8years and 10+years pools (R=0.334, p = 0.001). The <3rs and 5-8years pools were the most similar (R=0.205, p = 0.001) (Figure 4.9). SIMPER analysis for the chronosequence pools showed that the pools became more similar to each other with time since blocking; the 10+ age class pools displayed the highest level of similarity (41.31%) then the 5-8 years (37.42%) with the <3 years pools the least similar (30.86%) (Table 4.8). In all three age classes Dytiscidae larvae were the biggest contributors to overall similarity. However, in the <3 years pools the remaining contributors consisted of two chironomid taxa and *C. wollastoni*, in the 5-8 years pools the stonefly *N. cambrica* was the second largest contributor, followed by two chironomid species, and the 10+ years pools were further defined by the adult beetles *H. tristis* and *H. gyllenhalii* (Table 4.8).

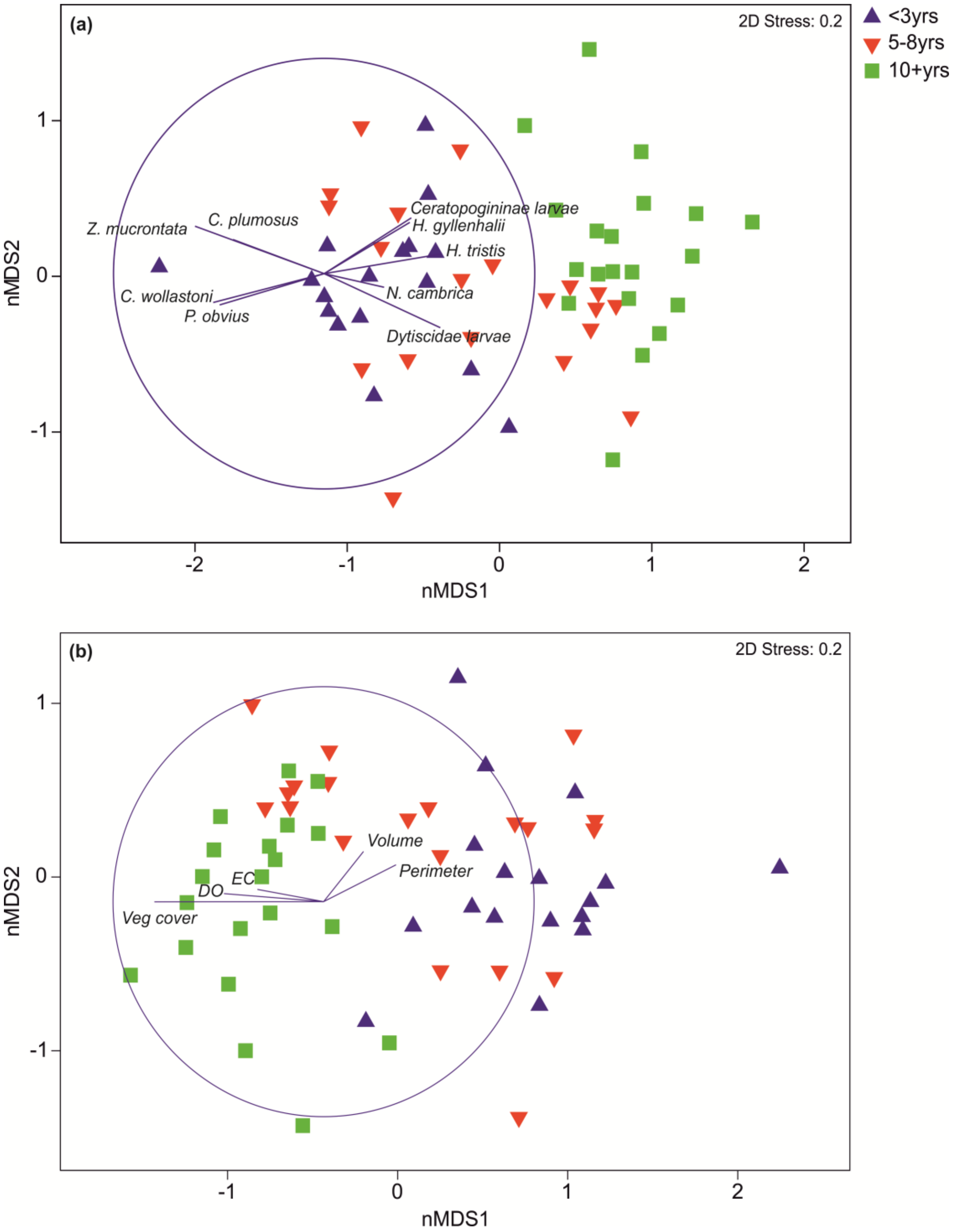

Figure 4.9. nMDS ordination (chronosequence pools) showing the similarity between the different age classes (a) overlaid with taxa highlighted by the SIMPER analysis (see Table 4.8 & 4.9) and (b) overlaid with environmental variables which resulted in Pearson's correlations of >0.3 with either nMDS ordination axis.

Dissimilarity analysis revealed that the youngest and oldest age classes were the least similar to each other (average dissimilarity = 81.81%), with Dytiscidae larvae, *H. tristis*, *H. gyllenhalii* and the biting midge larva Ceratopogininae all more abundant in the 10+

pools (Table 4.9). The hemipteran *C. wollastoni* was more abundant in the >3 years pools than either of the other age classes and the stonefly *N. cambrica* more abundant in the 5-8 years pools.

Table 4.8. SIMPER analysis (chronosequence pools) - intra-age class similarity. Defining taxa for each age class (i.e. contributing up to 70% of the overall similarity); average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Age	Taxon	Av. Abund.	% Contrib.	% Cum.
Group <3yrs Average similarity: 30.86	Dytiscidae larvae	3.46	28.90	28.90
	Chironomus plumosus	3.20	20.62	49.52
	Psectrocladius obvius	2.83	16.39	65.91
	Callicorixa wollastoni	2.11	8.30	74.21
Group 5-8yrs Average similarity: 37.42	Dytiscidae larvae	5.22	38.38	38.38
	Nemoura cambrica	2.46	15.85	54.23
	Psectrocladius obvius	1.93	8.25	62.49
	Zalutschia mucrontata	2.08	7.88	70.37
Group 10+yrs Average similarity: 41.31	Dytiscidae larvae	5.68	43.36	43.36
	Hydroporus gyllenhalii	2.20	14.02	57.38
	Hydroporus tristis	2.27	13.76	71.14

Table 4.9. SIMPER analysis (chronosequence pools) – inter-age class dissimilarity. Taxa which contribute at last 5% to the overall difference between age classes, average abundance (after square root transformation), % contribution and % cumulative contribution to overall dissimilarity.

Pool Ages	Taxon	Av. Abund	Av. Abund	% Contrib.	% Cum.
		Group <3yrs	**Group 5-8yrs**		
Groups <3yrs & 5-8yrs Average dissimilarity = 72.87%	Dytiscidae larvae	3.46	5.22	9.05	9.05
	Chironomus plumosus	3.20	1.69	8.46	17.51
	Psectrocladius obvius	2.83	1.93	6.95	24.47
	Nemoura cambrica	0.20	2.46	6.84	31.31
	Callicorixa wollastoni	2.11	1.05	6.53	37.84
	Zalutschia mucrontata	1.27	2.08	6.05	43.89
		Group <3yrs	**Group 10+yrs**		
Groups <3yrs & 10+yrs Average dissimilarity = 81.91%	Dytiscidae larvae	3.46	5.68	8.07	8.07
	Chironomus plumosus	3.20	0.00	8.02	16.08
	Psectrocladius obvius	2.83	0.34	6.48	22.56
	Hydroporus tristis	0.16	2.27	5.51	28.08
	Callicorixa wollastoni	2.11	0.34	5.51	33.59
	Ceratopogininae larvae	0.00	2.17	5.41	38.99
	Hydroporus gyllenhalii	0.22	2.20	5.13	44.12
		Group 5-8yrs	**Group 10+yrs**		
Groups 5-8yrs & 10+yrs Average dissimilarity = 69.16%	Dytiscidae larvae	5.22	5.68	7.68	7.68
	Nemoura cambrica	2.46	1.14	6.25	13.94
	Ceratopogininae larvae	0.00	2.17	6.04	19.97
	Zalutschia mucrontata	2.08	0.04	5.68	25.65
	Psectrocladius obvius	1.93	0.34	5.26	30.92
	Hydroporus tristis	0.80	2.27	5.02	35.93

4.3.4 Chironomidae biodiversity and community composition

The 10+ years pools hosted the least diverse chironomid communities, with the lowest richness, abundance and 1-Simpsons and the highest Berger Parker score (Table 4.10, Figure 4.10). There was a significant difference between age classes for taxon richness, abundance and Berger Parker, with the main differences between the 10+ pools and both of the younger age classes.

Table 4.10. Chironomidae biodiversity metrics (chronosequence pools). Means (st.dev) for the different age classes in the chronosequence pools, along with GLM results reporting the overall differences and those between the three age classes. Results at p<0.05 are highlighted in bold.

	Age Class			GLM Results			
Variable	**<3 years**	**5-8 years**	**10+ years**	**Overall**	**<3 v 5-8 yrs**	**<3 v 10+ yrs**	**5-8 v 10+ yrs**
Taxon Richness	4.85 (2.62)	4.20 (2.09)	1.90 (1.12)	**p < 0.001**	t = -0.89 p = 0.38	t = -5.29 **p < 0.001**	t = 4.44 **p < 0.001**
Abundance	73 (71)	96 (156)	14 (34)	**p = 0.004**	t = 0.51 p = 0.61	t = -2.93 **p = 0.005**	t = 3.43 **p = 0.001**
1-Simpsons	0.56 (0.16)	0.60 (0.19)	0.44 (0.33)	p = 0.13	t = 0.54 p = 0.60	t = -1.45 p = 0.15	t = 1.95 p = 0.06
Berger Parker	0.63 (0.18)	0.61 (0.21)	0.78 (0.22)	**p = 0.02**	t = -0.32 p = 0.75	t = 2.27 **p = 0.03**	t = -2.59 **p = 0.01**

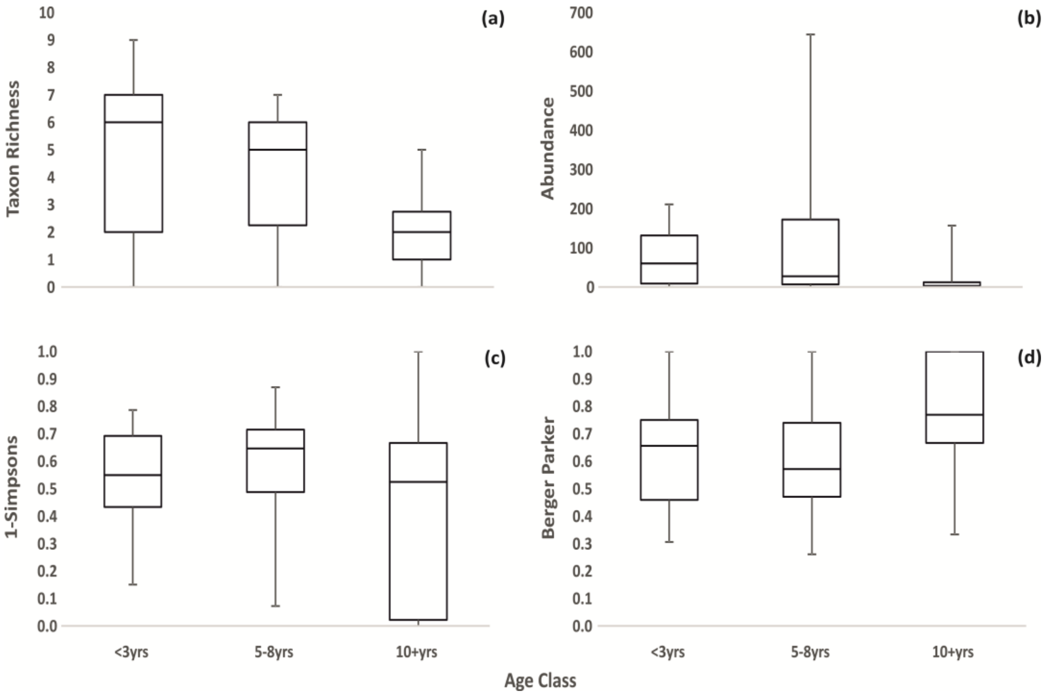

Figure 4.10. Chironomidae biodiversity metrics (chronosequence pools) by age class; (a) Taxon richness, (b) Abundance, (c) Simpsons Diversity Index (λ-1) and (d) Berger-Parker Dominance Index (D).

The nMDS ordination suggested overlap between all three of the age classes with regards to community composition, although the youngest and oldest pools appeared to be the least similar (Figure 4.11). This was reflected in the ANOSIM, which reported a significant difference in community composition between the three age classes, although the R statistic was low (ANOSIM, Global R = 0.196, p = 0.001). Pairwise comparison confirmed that the main difference lay between the youngest and oldest pools (R = 0.32, p = 0.001), followed by the 10+ and 5-8 years pool (R = 0.161, p = 0.001). The two youngest age classes were the most similar to each other (R = 0.085, p = 0.01).

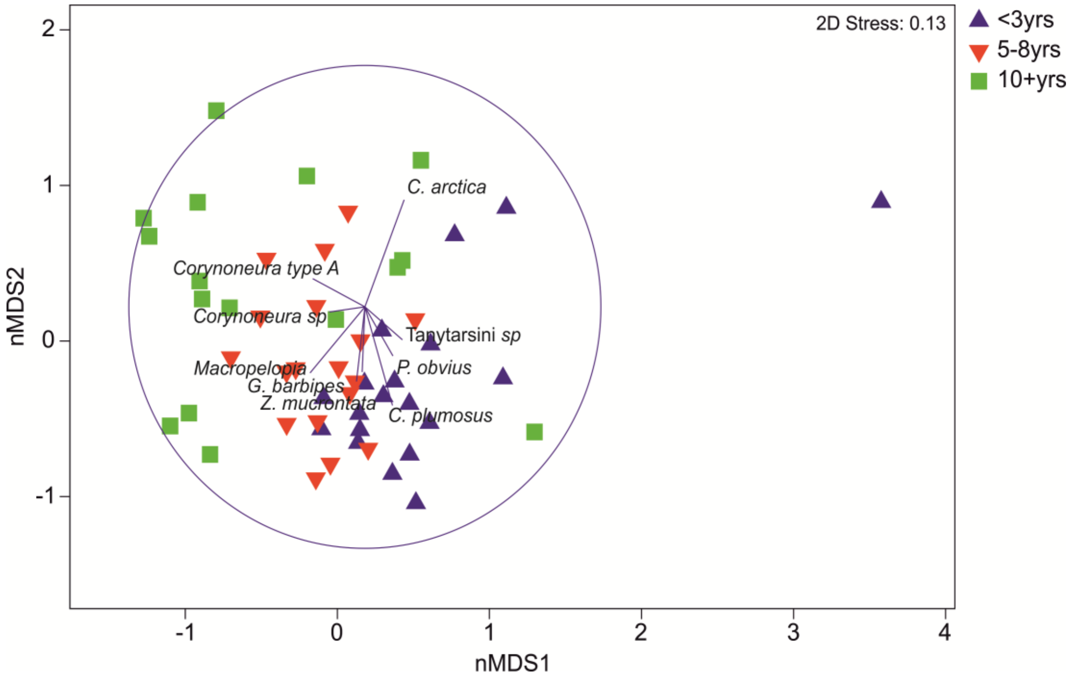

Figure 4.11. Chironomidae nMDS ordination (chronosequence pools) showing the similarity between the different age classes and overlaid with taxa highlighted by the SIMPER analysis (see Tables 4.11 & 4.12)

SIMPER analysis showed that intra-age class similarity decreased with pool age, dropping from 29.48% in the youngest pools to 15.52% in the oldest (Table 4.11). The same three chironomid taxa; *C. plumosus*, *P. obvius* and *Z. mucrontata*, defined the

Table 4.11. Chironomidae SIMPER analysis (chronosequence pools) - intra-age class similarity. Defining taxa for each age class (i.e. contributing up to 70% of the overall similarity); average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Age	Taxon	Av. Abund.	% Contrib.	% Cum.
Group <3yrs Average similarity: 29.48%	*Chironomus plumosus*	4.26	39.74	39.74
	Psectrocladius obvius	3.64	29.80	69.54
	Zalutschia mucrontata	1.65	6.84	76.38
Group 5-8yrs Average similarity: 24.84%	*Psectrocladius obvius*	3.36	32.62	32.62
	Zalutschia mucrontata	2.79	23.06	55.68
	Chironomus plumosus	2.41	16.99	72.67
Group 10+yrs Average similarity: 15.52%	Corynoneura type A	3.06	45.28	45.28
	Macropelopia	2.34	26.29	71.57

Table 4.12. Chironomidae SIMPER analysis (chronosequence pools) – inter-age class dissimilarity. Taxa which contribute at last 5% to the overall difference between age classes, average abundance (after square root transformation), % contribution and % cumulative contribution to overall dissimilarity.

Pool Ages	Taxon	Av. Abund.	Av. Abund.	% Contrib.	% Cum.
		Group <3yrs	**Group 5-8yrs**		
Groups <3yrs & 5-8yrs Average dissimilarity: 76.30%	*Psectrocladius obvius*	3.64	3.36	14.55	30.57
	Zalutschia mucrontata	1.65	2.79	11.11	41.68
	Corynoneura sp	0.61	1.48	6.88	48.55
	Glyptotendipes barbipes	1.35	0.91	6.26	54.81
	Macropelopia	0.12	1.65	6.10	60.92
	Corynoneura arctica	0.75	0.88	5.73	66.65
		Group <3yrs	**Group 10+yrs**		
Groups <3yrs & 10+yrs Average dissimilarity: 94.13%	*Chironomus plumosus*	4.26	0.00	15.54	15.54
	Psectrocladius obvius	3.64	1.01	12.37	27.91
	Corynoneura type A	0.00	3.06	11.19	39.10
	Macropelopia	0.12	2.34	9.15	48.25
	Corynoneura arctica	0.75	1.91	8.88	57.13
	Zalutschia mucrontata	1.65	0.20	5.52	62.65
	Tanytarsini *sp*	1.21	0.35	5.00	67.65
		Group 5-8yrs	**Group 10+yrs**		
Groups 5-8yrs & 10+yrs Average dissimilarity: 88.26%	*Psectrocladius obvius*	3.36	1.01	14.01	14.01
	Corynoneura type A	0.95	3.06	13.24	27.25
	Macropelopia	1.65	2.34	12.34	39.58
	Zalutschia mucrontata	2.79	0.20	10.22	49.80
	Corynoneura arctica	0.88	1.91	9.31	59.11
	Chironomus plumosus	2.41	0.00	8.91	68.02
	Corynoneura sp	1.48	0.81	7.62	75.64

<3years and the 5-8 years pools, but two different taxa, *Corynoneura* Type A and *Macropelopia*, were most abundant in the 10+ years pools. Dissimilarity analysis revealed that all three pools types were highly dissimilar to each other but the highest

average dissimilarity lay between the youngest and oldest pools (94.13%) (Table 4.12). The most abundant taxa in the <3 years pools, *C. plumosus*, was absent from the 10+ years pools, and the most abundant taxa in the 10+ years pools, *Corynoneura* Type A, was absent from the >3 years pools.

4.3.5 Coleopteran biodiversity and community composition

There were significant differences between the pool age classes for all four biodiversity metrics (Table 4.13, Figure 4.12). The 10+ years pools displayed the highest levels of taxon richness, and this was significantly higher than the >3 years pools. Both the 5-8 years and 10+ years pools had significantly higher beetle abundance than the >3 years pools. The diversity indices suggested that the 10+ pools were significantly more diverse than both of the younger age classes.

Table 4.13. Coleoptera biodiversity metrics (chronosequence pools). Means (st.dev) for the different age classes in the chronosequence pools, along with GLM results reporting the overall differences and those between the three age classes. Results at p<0.05 are highlighted in bold.

	Age Class			**GLM Results**			
Variable	**<3yrs**	**5-8yrs**	**10+yrs**	**Overall**	**<3 v 5-8yrs**	**<3 v 10+yrs**	**5-8 v 10+yrs**
Taxon Richness	2.90 (2.36)	3.85 (2.18)	4.50 (1.19)	**p = 0.04**	t = 1.52 p = 0.13	t = 2.56 **p = 0.01**	t = -1.04 p = 0.30
Abundance	26 (22)	51 (45)	58 (50)	**p = 0.009**	t = 2.51 **p = 0.02**	t = 3.01 **p = 0.004**	t = -0.50 p = 0.62
1-Simpsons	0.24 (0.18)	0.25 (0.23)	0.54 (0.19)	**p < 0.001**	t = 0.14 p = 0.89	t = 4.40 **p < 0.001**	t = -4.52 **p < 0.001**
Berger Parker	0.88 (0.12)	0.84 (0.18)	0.64 (0.19)	**p < 0.001**	t = 0.70 p = 0.49	t = -4.33 **p < 0.001**	t = 3.78 **p < 0.001**

The nMDS ordination suggested some overlap between the three age classes, with the youngest and oldest pools appearing the most distinct from each other (Figure 4.13). This was reflected in the ANOSIM tests; there was significant difference between all three age classes but with a low R statistic (ANOSIM, Global R = 0.199, p = 0.001). The largest differences lay between the >3 years and 10+ years pools (R =

0.324, p = 0.001) and the 5-8 years and 10+ years pools (R = 0.223, p = 0.001). The >3 years and 5-8 years pools were the most similar (R = 0.059, p = 0.02).

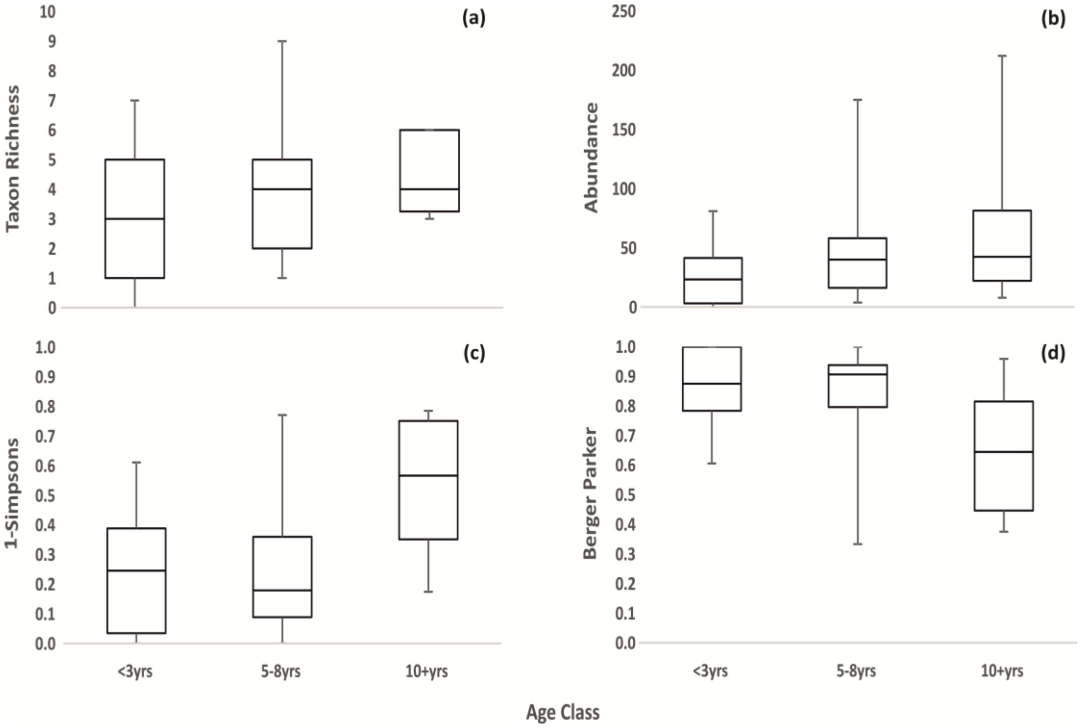

Figure 4.12. Coleoptera biodiversity metrics (chronosequence pools) by age class; (a) Taxon richness, (b) Abundance, (c) Simpsons Diversity Index (λ-1) and (d) Berger-Parker Dominance Index (D).

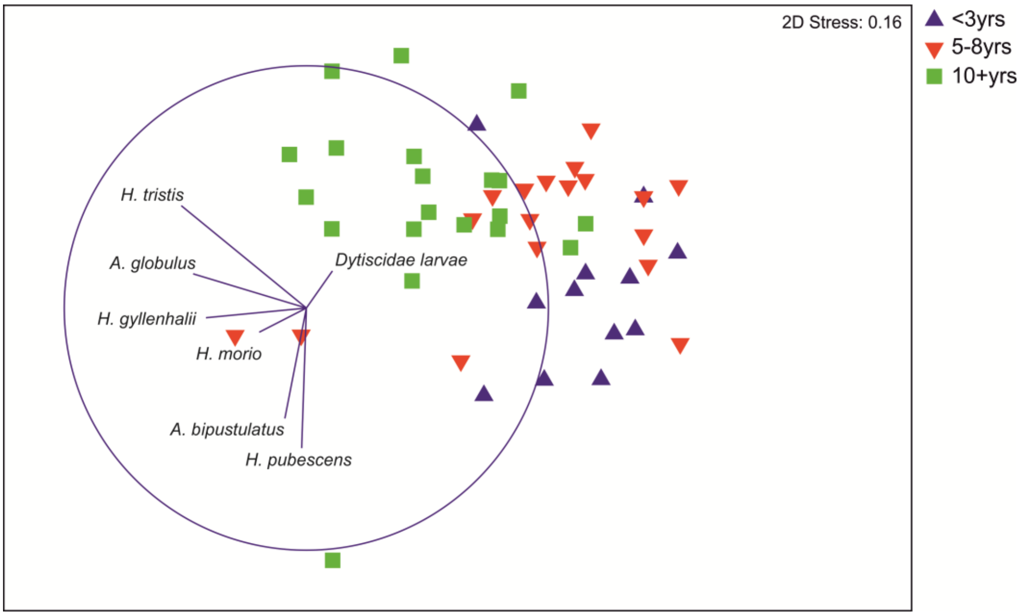

Figure 4.13. Coleoptera nMDS ordination (chronosequence pools) showing the similarity between the different age classes and overlaid with taxa highlighted by the SIMPER analysis as contributing >5% to overall similarity between age classes (see Tables 4.14 and 4.15).

SIMPER analysis showed that the <3 years pools were the least similar to each other, and that Dysticidae larvae were the most abundant and defining taxon in each age class (Table 4.14). The only other taxon listed in the intra-age class similarity analysis was *H. gyllenhalii* in the 10+ years age class. The youngest and oldest age classes were the least similar to each other, with all taxa being more abundant in the 10+ years pools (Table 4.15).

Table 4.14. Coleoptera SIMPER analysis (chronosequence pools) - intra-age class similarity. Defining taxa for each age class (i.e. contributing up to 70% of the overall similarity); average abundance (after square root transformation), % contribution and % cumulative contribution to the overall similarity.

Pool Age	Taxon	Av. Abund.	% Contrib.	% Cum.
Group <3yrs Average similarity: 45.98%	*Dytiscidae larvae*	7.45	88.47	88.47
Group 5-8yrs Average similarity: 66.76%	*Dytiscidae larvae*	8.96	86.89	86.89
Group 10+yrs Average similarity: 65.73%	Dytiscidae larvae	7.64	58.21	58.21
	Hydroporus gyllenhalii	2.96	18.05	76.26

Table 4.15. Coleoptera SIMPER analysis (chronosequence pools) – inter-age class dissimilarity. Taxa which contribute at last 5% to the overall difference between age classes, average abundance (after square root transformation), % contribution and % cumulative contribution to overall dissimilarity.

Pool Ages	Taxon	Av. Abund	Av. Abund	% Contrib.	% Cum.
		Group <3yrs	**Group 5-8yrs**		
Groups <3yrs & 5-8yrs Average dissimilarity: 45.75%	Dytiscidae larvae	7.45	8.96	30.80	30.80
	Hydroporus gyllenhalii	0.40	1.65	12.53	43.33
	Agabus bipustulatus	1.02	0.93	10.30	53.63
	Hydroporus pubescens	0.98	0.63	9.41	63.04
	Hydroporus tristis	0.27	1.11	9.25	72.29
		Group <3yrs	**Group 10+yrs**		
Groups <3yrs & 10+yrs Average dissimilarity: 54.61%	Dytiscidae larvae	7.45	7.64	23.03	23.03
	Hydroporus tristis	0.27	3.18	19.04	42.07
	Hydroporus gyllenhalii	0.40	2.96	17.21	59.28
	Hydroporus morio	0.58	1.32	8.96	68.24
	Anacaena globulus	0.19	1.22	7.70	75.95
		Group 5-8yrs	**Group 10+yrs**		
Groups 5-8yrs & 10+yrs Average dissimilarity: 39.34%	*Hydroporus tristis*	1.11	3.18	19.24	19.24
	Hydroporus gyllenhalii	1.65	2.96	18.44	37.68
	Dytiscidae larvae	8.96	7.64	15.01	52.69
	Anacaena globulus	0.58	1.22	10.15	62.83
	Hydroporus morio	0.12	1.32	10.08	72.92

4.4 Discussion

This study provides valuable insights into how the macroinvertebrate communities of drain-blocked pools assemble and change over time. Aspects of biodiversity and community composition both differed significantly with age, driven at least partially by an increase in vegetation cover with pool age which facilitates the colonisation of a wider range of taxa but might inhibit others. This section will now discuss and contextualise the significant results.

4.4.1 Environmental characteristics

One very apparent physical change which happens to the pools over time is the increase in vegetation cover, which is reflected in the 10+ years pools having significantly more vegetation cover than pools in either of the other age classes. Indeed, 17 out of the 20 pools in the 10+ age class had 100% vegetation cover. The only other study to look at the establishment of pool vegetation in recently-blocked drains found that mean pool vegetation cover was 76% after only eighteen months (Peacock et al., 2013); a much higher figure than the <3 years pools in my study, which had a median cover of only 13%. Vegetation is important for macroinvertebrates as it increases intra-pool structural complexity, providing different habitat niches and food sources for invertebrate taxa compared to open water pools. For example, members of the caddisfly genus *Limnephilus* are effective grazers of macrophytes (Dvorak and Imhof, 1998) and both the presence and composition of vegetation stands serves to facilitate odonate selection of suitable habitat (Buchwald, 1992). However, vegetation can also inhibit other taxa; for example, Hemiptera abundance decreased in older pools similar to findings of Mazerolle et al. (2006) who reported that the presence of low shrubs and moss negatively impacted their capture because they typically swim on or just under the surface of the water. The relative lack of vegetation in the youngest pools (<3 years) may also explain the significantly lower levels of DO found in them, due to reduced rates of photosynthesis. The significantly higher concentrations of EC in the oldest pools, underpinned by significantly higher concentrations of Mg, Na and Cl, remain unexplained, as concentrations of Na and Cl would usually increase with proximity to the coast (Hannigan and Kelly-Quinn, 2014), but no such geographical bias was present in this study. Also, there is nothing to suggest that the relatively higher ionic concentrations contributed to the lower biodiversity found in the older pools, as the background levels were so low.

4.4.2 Macroinvertebrate biodiversity

The Moor House pools were dominated by chironomids, providing support for H_1 which posited that chironomids would be early colonisers. This was also reflected in the longer-term chronosequence study, when the relative abundance of chironomids was high in the <3 years age class but had declined substantially for the pools that had reached ten years of age. The biodiversity metrics for the Chironomidae dataset also suggested that chironomid communities were more far diverse in younger pools, although the average abundance was in fact higher in 5-8 years pools. Diptera, and especially Chironomidae, are well known to be early colonisers of freshwater habitats from many studies, ranging from excavated clay-ball pits in Dorset (UK) (Barnes, 1983), to Arctic streams created by glacial retreat (Flory and Milner, 2000) to a shallow coastal lake near Barcelona (Spain) created as a mitigation measure against wetland habitat loss (Cañedo-Argüelles and Rieradevall, 2011). This ability to colonise new habitats quickly is partly a result of good dispersal ability (wind assisted during swarming events) along with a short life cycle, which allows members of this diverse group to establish and develop rapidly in different aquatic habitats (Armitage et al., 1995). Although voltinism varies greatly between chironomid taxa, Armitage et al. (1995) estimated that out of 125 chironomids taxa studied, 33% were univoltine (one generation per year), 44% were bivoltine (two generations per year) whilst 18% were multivoltine (three + generations per year). Orthocladiinae constituted over half of the chironomid taxa found in both the Moor House and the chronosequence pools, which agrees with the findings of Barnes (1983) and Dowling and Murray (1981) who both reported that orthoclads dominated in acidic pools. As Orthocladiinae were found to include more species with multivoltine life cycles than the Chironominae (Armitage et al., 1995), this could help them to establish quickly and to have better survival rates in the face of stochastic drought or freezing events (Chase, 2007).

Several results supported the first part of H_2, which theorised that taxonomic richness and abundance would rise most sharply within the first two years after pool creation. The Moor House dataset supplied clear evidence that pioneering communities assemble quickly, with the total abundance increasing massively between 6 and 8 months, and with 39 of the eventual 45 taxa found within the first ten months. Layton and Voshell (1991) also found that diversity and the number of taxa increased most rapidly in the first seven months of a study of experimental ponds. Cañedo-Argüelles and Rieradevall (2011) reported that all actively dispersing taxa (except one) found in a 15 month study of a newly created lake were recorded within the first nine months. Another study exhibited an even faster colonisation rate, in which ~ 50% of the species found in a one-year study of newly-created shallow ponds on the NE Iberian Peninsula were captured during the first two months after the ponds were flooded (Ruhí et al., 2009). Christman and Voshell (1993) also found no significant difference in biodiversity metrics (total density, taxonomic richness, Shannon diversity index, Bray-Curtis similarity index) in experimental ponds between the end of the first and second years after pond creation. The authors theorised that this was partly due to the close proximity of many sources of colonizing macroinvertebrates, meaning that most taxa able to disperse to the new habitat had done so within the first twelve months.

The 5-8 years pools displayed significantly higher taxonomic richness than the 3 years pools and also significantly higher abundance than the 10+ years pools. This contradicted the second part of H_2 which predicted no significant differences in biodiversity metrics between the oldest age classes. The higher taxonomic richness in the middle age class was because 17 new taxa were added between five and eight years. This was unexpected as most pond studies report a levelling out of new taxa by the fifth year. For example, Williams et al. (2008), monitored a set of newly-created ponds at Pinkhill Meadow in Oxfordshire (UK) and found that an initially rapid increase in species richness flattened out after three to four years. In a study of recently constructed wetlands in southern Sweden, Hansson et al. (2005) found that species richness of benthic invertebrates levelled out after about five years. My results therefore suggest that the species curve in drain-blocked pools does not stabilise as quickly as in other lotic habitats. The increased taxonomic richness and abundance seen in the 5-8 year pools may be due to physical factors, i.e. the increased depth and water volume of these pools compared to the other age classes, although no significant difference was found between pool depth and water volume and any of the biodiversity metrics in Chapter 3 of this thesis. Furthermore, the 5-8 years pools showed more inter-pool variation in vegetation cover compared to the other two age classes, perhaps encouraging colonisation of a wider range of taxa than if the pools had all been heavily vegetated (as with the 10+ years pools) or mainly sparsely vegetated (as with the <3 years pools).

It is notable that the species curve for the chronosequence pools continued to rise even in the very oldest pools, with three new taxa found for the first time in the 15 year old pools at Oughtershaw Beck. The chronosequence time series data also showed a slight upwards trend for taxonomic richness in the 15 years pools. This suggests that studies covering even longer time periods could be informative. Hassall et al. (2012) demonstrated that the macroinvertebrate communities of even very old ponds are still subject to temporal change. The authors studied a set of 51 ponds in northwest England, 44 of which were marl pit ponds excavated in the late 1700s, and analysed changes in both the macroinvertebrate and macrophyte communities between 1995/96 and 2006. The alpha-diversity of invertebrates increased markedly between the two surveys, although a corresponding decline in beta-diversity indicated that the ponds were becoming increasingly similar with time (Hassall et al., 2012).

Although no rare or endangered taxa were found in this study, several taxa which rely (to varying extents) on acid-mire habitat were identified. For example, the caddisfly *Limnephilus coenosus* is classed as an acid-mire obligate whilst the Brown Hawker dragonfly (*Aeshna juncea*) is an acid mire preferential (Boyce, 2004) (Appendix A). Four beetles species found are classified as acid mire specialists (*Agabus congener*, *Hydroporus gyllenhalii, Hydroporus morio* and *Hydroporus obscurus*) and three as acid mire preferentials (*Helophorus flavipes, Hydroporus melanarius* and *Hydroporus tristis*) (Boyce, 2004). The two hemipteran taxa identified were *Gerris costae* (an acid mire specialist) and *Callicorixa wollastoni* (an acid mire preferential) (Boyce, 2004). Although the majority of these taxa (five beetle species and the caddisfly) were more abundant in the 10+ years pools, the taxon richness of characteristic taxa was actually lowest (n=7) in this age class, compared to the < 3 years pools (n=8) and the 5 to 8 years pools (n=10). This appears to disagree with van Duinen et al. (2003) who found evidence that older pools are home to more rare and characteristic bog species than younger pools.

4.4.3 Macroinvertebrate community composition

The first part of H_3, which posited that macroinvertebrate community structure and the relative abundance of taxa would change over time, was supported by several results. Community similarity was significantly different between pools of different ages in both the Moor House and the chronosequence datasets. In the Moor House pools, there was a clear species turnover through the 18 months. Within the Chironomidae, two early-colonising orthoclad taxa, *Limnophyes* and *Pseudorthocladius*, were soon replaced by *Chironomus plumosus, Psectrocladius obvius, Tanytarsus pallidicornis* and *Zalutschia mucrontata.* By the end of the eighteen months, only *P. obvius* and *Z. mucronata* were dominant, and these two remained as defining taxa in both the <3 and 5-8 years chronosequence pools implying some element of tolerance as other taxa colonised. The overall prevalence of these two chironomid taxa agrees with a study of the Chironomidae of two Irish blanket bogs, which reported that the genera *Psectrocladius* and *Zalutschia* (along with *Limnophyes*) were dominant (Dowling and Murray, 1981). However, the Chironomidae SIMPER analysis showed that two different species; the tiny *Corynoneura* Type A and larger, carnivorous Macropelopia, were the defining taxa in the 10+ years pools, suggesting a distinct shift in community composition over time. However, the chironomid species turnover does not reflect that reported by Ruse (2002), in a study of excavated gravel pit lakes in a study near Windsor (UK), where Tanytarsini dominated the youngest lakes and Chironomini the oldest. This is most likely because of the dominance of Orthocladiinae in my study, so any succession from Tanytarsini to Chironomidae was far less discernible. Indeed, *Chironomus plumosus* was absent from pools older than 7 years.

Evidence of ecological succession was reflected in the substantial difference in relative abundance of taxa seen within the chronosequence pools, where less prevalence of Hemiptera, and especially of Chironomidae, was accompanied by greater relative abundance of other Diptera, Odonata and particularly of Coleoptera in older pools. The increase in predatory taxa such as dytiscid beetles and odonates could be seen as an example of the successional mechanism of facilitation, in this case the increased availability of prey in the form of chironomids (Malmqvist et al., 1991, Wellborn et al., 1996). For example, in a controlled laboratory experiment, the dytiscid beetle *Rhantus sikkimensis* was reported to consume between 10–90 small and 10–78 large *Chironomus* larvae per day (Aditya and Saha, 2006). Beetle larvae and odonate nymphs especially are known as voracious predators (Batzer and Wissinger, 1996), although there is some evidence that 100% vegetation cover can inhibit predation of chironomids by beetle larvae, by providing refuge for the chironomids and hampering beetle foraging activity (Batzer and Resh, 1991). The reduction in chironomid relative abundance could be viewed as an example of inhibition, caused by the increasing abundance of prey taxa. However, it is also possible that the sampling method (sweep-netting) was less effective at capturing chironomids in heavily-sphagnated pools, as the net was not always able to effectively sample the pool bottom. The decline in Hemiptera with increased vegetation cover, could also be seen as an example of inhibition, as their ability to move about on the surface becomes inhibited. Indeed, the decrease in Hemiptera mirrored the findings of Barnes (1983) who reported that the relative abundance of Hemiptera declined from 77% of (non-Dipteran) individuals to less than 15% after the second year of pool creation.

The increased importance of beetles in defining the community composition of the pools with age was illustrated firstly by the Coleoptera biodiversity metrics, which showed a clear increase in both biodiversity and abundance with pool age and secondly by the SIMPER analysis. Whilst Dytiscidae larvae were the most abundant taxa in all three chronosequence age classes, they were closely followed by other taxa, mainly chironomids. But, by the time the pools were ten years old, all three defining taxa were beetles; Dytiscidae larvae, *H. tristis* and *H. gyllenhalii*. However, unlike the findings of Fairchild et al. (2000), there was no evidence of predatory dytiscids being replaced by herbivorous taxa, even though vegetation cover in the 10+ years pools was almost always 100%.

One unexpected result was the abundance of the one stonefly species found in this study, *N. cambrica*, as stoneflies in general are known to prefer more oxygenated, lotic waters (Brittain, 1990). However, *N. cambrica* was also found in bog pools in the Pennines by Brown et al. (submitted) and Verberk et al. (2010a) reported the stonefly *Nemoura cinerea* from in the Korenburgerveen nature reserve in the Netherlands. These findings provide evidence that bog pools have the potential to act as a refuge for some taxa not usually associated with lentic waters, for example *N. cambrica* is usually associated with small, stony streams (Hynes, 1977). The large total and relative abundance of Plecoptera in the Moor House pools in December 2013 can perhaps be explained by the fact that some stonefly nymphs are known to enter diapause over dry periods in the summer and concentrate instead on winter development, when waters are generally colder and more permanent (Brittain, 1990). Overall, although the biodiversity metrics suggested that pools in the oldest age class were less diverse than the 5-8 years pools, the increased relative abundance of taxa such as Coleoptera, Odonata and other Diptera, along with the overall increase in acid-mire taxa abundance, indicates that they are vital habitats for some of the more charismatic taxa, and for those who depend on acid mire habitat to some extent for their persistence.

The second part of H_3, which suggested that inter-pool community similarity would increase with time since pool formation, was partially supported by the results. Increasing similarity was seen most strikingly in the Moor House pools, when the inter-pool similarity amongst the pools of different ages increased substantially throughout the study period. The large dissimilarity exhibited in the youngest pools (aged 4 and 6 months) was indicative of community assembly being driven by random rather than niche factors (Chase, 2007). In this case, the dissimilarity was most likely caused by small numbers of taxa arriving from nearby source populations and settling randomly in only one or two pools initially, then as more individuals arrived, their distribution spread out, thus generally homogenising the pool communities. Furthermore, it is also possible that any bi- or multi-voltine chironomid taxa would have emerged, mated and dispersed at least once during the eighteen months (Armitage et al., 1995), further increasing the dominance of those taxa in nearby pools and thus increasing inter-pool similarity. Increasing inter-pool similarity was also apparent, although to a lesser extent, over the longer term in the chronosequence pools. In this case, it is likely that the disturbance history will have contributed, e.g. dry summers would lead to periods of drought, and cold winters to freezing, which can both act as environmental filters, determining species persistence in small ponds (Wellborn et al., 1996, Chase, 2007). The UK experienced several periods of drought, unusually hot weather and unseasonal snowfall during the period 1999 (when the oldest pools in this study were blocked) to

2015 (Met Office, 2015). For example, 2010 to early 2012 saw a prolonged period of below average rainfall leading to drought in much of England and Wales, whilst significant snowfalls and unseasonably low temperatures were experienced by many parts of the UK from late March to early April 2013. However, it is also possible that disturbance events can result in community divergence. For example, in a study of small (1m^2) temporary pools in Northumberland (UK), Jeffries (2011) found that two years of high summer rainfall resulted in the introduction / expansion of taxa more associated with permanent ponds. The resumption of dry summers led to increased divergence between the pool communities with some retaining the taxa which had invaded during the wetter conditions and others being replaced by the original, pioneering colonisers (Jeffries, 2011). In the case of my study, dry summers would have led to low water levels and high water temperature which could have proved fatal to many of the pool occupants, thus allowing new (and potentially different) communities to colonise once the water levels had returned to normal. Thus, whilst the disturbance history of a site can be vital in explaining its current community composition, it can also act on the biodiversity of the habitat in question in different directions. One drawback of using chronosequence studies as opposed to long-term monitoring is that different sites may have different disturbance histories which remain unaccounted for (Johnson and Miyanishi, 2008).

4.4.4 Conclusions

Overall, it is clear from this study that the biodiversity and community composition of drain-blocked pools changes with time, with pools of different ages benefiting different taxa. New pools colonise very quickly and sustain high numbers of chironomids, which are a vital source of food for moorland birds such as Greenshank and Golden Plover (Downie et al., 1998b). Older pools house more diverse and abundant beetle communities. If macroinvertebrate biodiversity is important, then a gradient of vegetation cover and pool age appears to provide the maximum benefits for taxonomic richness and abundance. Although the oldest pools had fewer taxa classed as characteristic of acid-mires, this was mainly due to the absence of the two acid-mire Hemiptera, likely due to the increased vegetation cover. They did, however, host more individuals of taxa classed as acid-mire obligates, specialists or preferentials so may be important in sustaining larger communities, thus increasing the ability of these important taxa to persist in the face of stochastic extinction events. Therefore, this chapter provides evidence that drain-blocking, given time, helps to develop and maintain an aquatic macroinvertebrate assemblage characteristic of natural peatland pools.

Chapter 5: The metabolism of newly-created peatland pools

5.1 Introduction

Peatlands, although they cover only ~3% of the Earth's surface, are key components of the carbon cycle, with mid to high latitude peatlands in the northern hemisphere known to store ~15 to 30% of the world's soil carbon (Limpens et al., 2008). As such, studies looking at the carbon budget of peatlands and their potential response to climate change are widespread (e.g. Blodau et al., 2004, Drewer et al., 2010, Carter et al., 2012). Many peatlands are home to aquatic systems such as streams, lakes and pools, and recent evidence suggests that inland freshwater habitats play a more important role in carbon cycling than was previously thought (Battin et al., 2009, Raymond et al., 2013). For example, approximately twice as much carbon (1.9 Pg C y^{-1}) is thought to enter inland waters from surrounding terrestrial habitats than enters the sea from land (0.9 Pg C y^{-1}) (Cole et al., 2007). Furthermore, terrestrial carbon inputs to lentic waterbodies have been shown to be, on average, eight times more likely to be mineralised and emitted to the atmosphere than to be buried in sediment (Algesten et al., 2004). Therefore, understanding the carbon dynamics of aquatic systems which sit within carbon-rich peatlands is of vital importance.

The aquatic landscape of peatlands has recently been enhanced by the land management process of drain-blocking, which has created a vast array of small pools that form behind dams in drainage ditches (Armstrong et al., 2009, Parry et al., 2014). In the UK many hundreds of thousands of these pools have been created, often on areas of peatland which previously lacked substantial lentic habitat (e.g. the English Pennines). The extent of drain-blocking in the UK has increased massively in the 21st Century, with approximately £500m spent on the process in Northern England alone

(Ramchunder et al., 2012b). As the number of drain-blocked pools grows, so does the need to clarify their role in the carbon cycle. Because they are so small (usually <3m^2 – personal observation) their cumulative surface area (and therefore their potential for gaseous exchange with the atmosphere) may not be significant. Perhaps of more importance, however, is the cumulative area of water-sediment interface which provides a pathway for increased inputs of metabolically important substances (e.g. organic matter and nutrients) as well as a home for the bacterial communities which process them. For example, using a calculation based on the total length of drains blocked and the average spacing between dams, it is estimated that ~500,000 pools have been created in the North Pennines AONB since 1995 (pers. comm. Alistair Lockett, North Pennines AONB). Taking a very conservative estimate of their dimensions as 1 m^3, this would equate to a surface area of ~0.5 km^2; a fraction of the size of England's largest lake, Lake Windermere, at 14.8 km^2 (ECN, 2015). The cumulative water-sediment interface, however, would be five times the surface water area of the pools (2.5 km^2). However, drain-blocking is also widespread outside the North Pennines AONB and the total number of pools created throughout the UK is unknown, meaning that these estimates are very conservative.

There is already evidence that open-water pools on areas of peatland act as hotspots for methane (CH_4) release (Baird et al., 2009, Holden, 2009) and a study of CH_4 fluxes from tundra habitats in Alaska found that small lakes emitted substantially more CH_4 per unit area (77 mg m^{-2} d^{-1}) than larger lakes (3.8 mg m^{-2} d^{-1}) (Bartlett et al., 1992). There has been less research directed at fluxes of CO_2 from peatland pools, with studies tending to include pools as part of a wider peatland carbon budget approach (e.g. Waddington and Roulet, 2000). However, a synthesis by Hoellein et al. (2013) reported that the majority of freshwater systems, including wetlands and ponds, acted as carbon sources rather than carbon sinks. Therefore, the role of small pools, created through drain-blocking, as potential carbon sources or sinks needs further clarification, especially as one of the several drivers for their creation was to reduce carbon emissions from peatlands (Baird et al., 2009, Holden et al., in press).

The metabolic balance of an ecosystem is dictated by the ratio of photosynthesis to respiration (R). Systems which fix more carbon than they respire over the course of a year are net autotrophic (carbon sinks) and those which respire more carbon than they fix are net heterotrophic (carbon sources). However, photosynthesis and R are not strictly coupled because external (allochthonous) sources of organic carbon can supplement internal (autochthonous) supplies produced by photosynthesis. In aquatic systems, such allochthonous sources are often in the form of particulate and dissolved organic carbon (POC and DOC, respectively) which are released into the water from surrounding terrestrial habitats (Hanson et al., 2003). Bog pools in particular may receive large amounts of allochthonous carbon due to the high levels of DOC in the surrounding peat, part of which is made up of highly-coloured humic substances (Wallage et al., 2006). Such inputs not only have the potential to increase rates of R relative to photosynthesis, but also to subdue rates of photosynthesis by decreasing light availability (Karlsson et al., 2009). The trophic status (i.e. net autotrophic or heterotrophic) of a water body can be determined by calculating its Net Ecosystem Production (NEP). NEP represents the difference between the amount of carbon fixed by gross primary production (GPP) during photosynthesis and the amount released by both heterotrophic and autotrophic R (Lovett et al., 2006). Systems with a negative NEP are carbon sources and those with a positive NEP are carbon sinks.

There are many studies looking at the metabolic balance of lakes and large ponds (e.g. Cole et al., 2000, Gelda and Effler, 2002, Hanson et al., 2003, Lauster et al., 2006, Torgersen and Branco, 2008, Staehr et al., 2012a, Klotz, 2013) which generally report negative NEP values. For example, Hanson et al. (2003) studied 25 lakes in Wisconsin and Michigan, USA, of various sizes and with varying levels of DOC and total phosphorus (TP), and found that twenty had negative NEP figures compared to only five with positive NEP. Their study took place in the months of July and August 2000 so net trophic status (i.e. encompassing a whole year) cannot be inferred. However, it is pertinent that 80% of the lakes returned heterotrophic values in the summer months, when NEP can reasonably be expected to be at its highest levels due to the extended daylight hours and higher intensity solar input. The study found a positive relationship between TP and GPP, R and NEP, whereas DOC was positively correlated with R but negatively with NEP, suggesting that allochthonous sources of carbon were driving higher rates of R compared to GPP. The study also identified a threshold for levels of DOC > 10mg L^{-1}, over which most lakes displayed negative NEP.

Although higher concentrations of DOC are linked to increased heterotrophy, concentrations of DOC alone tell us little about its bioavailability. DOC can be aromatic / refractory (resistant to microbial decomposition) or labile (easily broken-down) or indeed lie anywhere on a spectrum between the two. The aromaticity of DOC may be characterised using the $SUVA_{254}$ method; the UV absorbance of a water sample at a 254nm wavelength normalized for dissolved organic carbon (DOC) concentration, with low $SUVA_{254}$ scores indicating higher bioavailability (Weishaar et al., 2003). Another measure of the bioavailability of DOC is the E4/E6 ratio; the ratio of UV absorbance at 465nm to that at 665nm, which is taken as a measure of the humification of peat (Thurman, 1985) with lower ratios considered to indicate increased humification and therefore more refractory DOC (Worrall et al., 2002, Hribljan et al., 2014). The E4/E6 ratio characterises the fulvic acid to humic acid content of the humic substances in a water sample, with fulvic acids being more labile with a lower molecular weight (Wallage et al., 2006). So, waters with high E4/E6 ratios and / or low $SUVA_{254}$ scores could be inferred to contain DOC which is more bioavailable, which could, in turn, fuel higher rates of respiration, although this theory apparently remains untested in the wider literature.

Recent evidence suggesting that the Earth's freshwater habitat cover is dominated by standing water bodies with a surface area of <1 km^2 (Downing et al., 2006) has prompted more research looking at the metabolic balance of smaller lakes and ponds (Torgersen and Branco, 2008, Christensen et al., 2013, Klotz, 2013). The metabolism of smaller waterbodies may be affected by relatively high inputs of terrestrially-derived DOC and nutrients per unit area compared to larger lakes, potentially driving higher rates of photosynthesis and, in particular, respiration (Staehr et al., 2012a). This may be especially pertinent when the drainage ratio (catchment area:lake area) is high resulting in an increase in the influence of benthic processes such as bacterial processing which can increase rates of respiration (Torgersen and Branco, 2007, Staehr et al., 2012a, Sand-Jensen and Staehr, 2009). Due to increased light availability, shallow lakes may also possess a larger extent of benthic plant cover than deeper lakes, thus potentially increasing rates of photosynthesis during daylight hours and autotrophic respiration at night (Christensen et al., 2013). Furthermore, shallower water is less prone to seasonal stratification, meaning that CO_2 produced by sediment respiration is spread throughout the water column on a daily basis rather than being restricted to the bottom layers (Holgerson, 2015). However, the ponds in studies such as those mentioned in this paragraph, although described as 'small', are large relative to the size of pools created by drain-blocking on blanket peatlands in the UK, which usually have a surface area of <3m^2 (personal observation.). For example, the seasonal pond studied by Christensen et al. (2013) varied in area from 700 to 3400 m^2 and the smallest pond studied by Staehr et al. (2012a) measured 1000m^2, although the depths (ranging from 0.3 to 0.8m and a mean of 0.5m respectively) are similar to those of drain-blocked pools. Thus, while the metabolism of larger lakes and ponds has been well-studied, the metabolism of very small waterbodies such as drain-blocked pools is unknown. However, the exclusion of small ponds, especially those with high terrestrial carbon loads, from global carbon budgets may lead to an underestimation of net carbon losses to the atmosphere (Holgerson, 2015).

The only studies known to this author which look at the metabolic balance of very small pools have taken place in controlled mesocosms (measuring 1 m^3) which were set up to analyse the response of metabolic processes to increased temperature (Yvon-Durocher et al., 2010b), using a theoretical framework based on the Metabolic Theory of Ecology (MTE) (Brown et al., 2004). The MTE describes how body size and temperature combine to influence the metabolic rates of cells, individual organisms, communities and ecosystems (Allen et al., 2005). For each individual organism, the carbon fluxes which occur during metabolic processing all have predictable mass and temperature dependencies, and each metabolic pathway has a different activation energy (i.e. the amount of energy needed for a given reaction to proceed). Photosynthesis has the smallest activation energy, followed by ecosystem respiration then methanogenesis; in practice this means that photosynthesis increases by ~four-fold over the temperature range 0-30°C, respiration by ~15-fold and methanogenesis by ~ 35-fold (Yvon-Durocher et al., 2010a). The experiments carried out by Yvon-Durocher et al. (2010b) produced results which agreed with the theory, concluding that although both respiration and photosynthesis scaled with temperature, the effects on respiration were greater. However, the mesocosm set-up precluded interaction with external terrestrial landscapes, thus preventing any allochthonous input of DOC (although they would have been open to leaf litter), and the study was not intended to inform the debate on the natural trophic status of small pools.

This chapter aims to establish the metabolism of a series of newly-created drain-blocked pools at Moor House NNR over a one year period, using the open-water dissolved oxygen (DO) change technique. It was hypothesised that:

H_1 - Pools would be net heterotrophic, with high levels of DOC derived from the surrounding peat resulting in a positive relationship between R and DOC and a corresponding negative relationship between NEP and DOC (Hanson et al., 2003). The bioavailability of the DOC would also influence metabolism, with rates of respiration being higher in pools with high E4/E6 ratios and / or low $SUVA_{254}$ values.

H_2 - Both R and GPP would scale with temperature but R would increase more due to the higher activation energy involved in the process (Yvon-Durocher et al., 2010b). There would also be a positive relationship between levels of nutrients and both GPP and R (Hanson et al., 2003), as both metabolic processes require these macronutrients to function but they are typically scarce in peatlands.

H_3 - Shallower pools would exhibit higher rates of R due to the greater influence of benthic processes (e.g. bacterial processing) on the water column (Torgersen and Branco, 2007, Staehr et al., 2012a).

5.2 Methodology

5.2.1 Study site

Burnt Hill is an expanse of upland blanket bog located within Moor House National Nature Reserve (NNR) in Cumbria, UK (54° 41' 27"N, 2° 22' 56"W). The area is ~575 m above sea level and lies within the Trout Beck catchment (11.4 km^2) which is used mainly for low density sheep grazing. The ombrotrophic peat deposits range from 0.4 to 5 metres in depth and the vegetation is dominated by ling heather (*Calluna vulgaris*), cotton grass (*Eriophorum spp*), *Sphagnum* and feather mosses (e.g. *Pleurozium schreberi*) (CEH, 2014). Mean annual precipitation from 2000 to 2012 was 2001 mm, with a corresponding mean monthly temperature of 6.28 °C (ECN, 2014). The ditches on Burnt Hill were dug, using the same techniques as were practiced widely at the time, in the early 1950s as part of a hydrological experiment (Conway and Millar, 1960, Holden et al., 2006). The drainage ditches on Burnt Hill were blocked in December 2012 using peat turves, and pools of water had formed behind the dams by January 2013 (Figure 5.1).

Figure 5.1. Photograph of pools in a blocked drainage ditch at Moor House NNR.

5.2.2 The DO change technique

There are several methods available for calculating rates of R, GPP and NEP in aquatic ecosystems, each with their own advantages and drawbacks (Table 5.1). Direct measurements using bottle or chamber incubations can be used for both pelagic zones (Navarro et al., 2004) and sediments (Fellows et al., 2006) and, when combined together, can provide estimates of whole ecosystem metabolism (Gazeau et al., 2005). Several methods involving the measurements of oxygen isotopes have been utilised in open waters (Russ et al., 2004, Sarma et al., 2005, Tobias et al., 2007). Estimates of net metabolism can be obtained from ecosystem budget studies which measure mass balances of physical inputs and outputs (Testa and Kemp, 2008). However, the method which has become perhaps most widely used for lacustrine systems is the open-water dissolved oxygen change technique (Odum, 1956). This technique uses the premise that changes in the levels of DO throughout a 24hr period (midnight to midnight) reflect the balance between GPP and R as well as the physical oxygen (O_2) flux between the air and surface waters, assuming no major advection of water with DO into the system (Staehr et al., 2010a). This method was chosen for this study for several reasons; it allows estimates of ecosystem metabolism, the data collection equipment can be left *in situ* and unattended which is beneficial for remote study sites such as Moor House, and the method is widely used so allows for easier comparison with other studies.

Table 5.1. A comparison of the most common methods of estimating the metabolic rates in aquatic ecosystems. For isotope methods, comments specific to the triple oxygen approach (TI) and the ^{18}O approach (^{18}O) are noted. Each approach has been used in estuaries, lakes, rivers and oceans. For a more in-depth analysis of the methods see Staehr et al. (2012b). Adapted from Staehr et al. (2012b).

Method	Temporal Scale	Advantages	Disadvantages
Diel O_2, TCO_2	Daily, seasonal, annual	Measures all system components Remote data collection Straightforward computation Precise measurements High frequency rates Multi-variable sensors	Air-water flux difficult to quantify O_2:C conversion problems Physics may obscure biology O_2 method misses anaerobic R Horizontal and vertical heterogeneity Stratification causes problems Import of water with gas super- or sub-saturated
Oxygen isotopes	Daily, seasonal	Measures all system components Rates can be long- and short-term Sensitive method	Air-water flux needed (TI) O_2:C conversion problems (TO, ^{18}O) Sampling is work-intensive (TI, ^{18}O) Traces diurnal GPP and R (^{18}O) Known fractionations limited (TI)
Ecosystem Budgets	Seasonal, annual	Measures all system components Straightforward computation Data widely available Formal error estimates	Air-water flux difficult to quantify O_2:C:DIP conversion problems Abiotic effects on PO_4^{3-} Large aggregation error Net rates (NEP) only
Incubations	Hourly, daily	Direct process measurement Highly controlled Precise measurements Can separate ecosystem components	O_2:C conversion problems Containment artefacts Labour intensive Difficult to upscale to ecosystem

The governing equation for estimating the metabolic balance of aquatic systems using changes in levels of DO was first proposed by Odum (1956):

$\Delta O_2/\Delta t = GPP-R-F-A$ (Table 5.2, eq. 1)

where $\Delta O_2/\Delta t$ is the change in levels of DO over time, GPP is gross primary production, R is ecosystem respiration (i.e. both autotrophic and heterotrophic), F is the exchange of O_2 between the atmosphere and surface waters and A is a combination of all other processes which might affect DO levels at the location of the DO sensor (Figure 5.2). The processes that make up A include, for example, turbulent mixing by wind, vertical or horizontal movement of pockets of DO within the water body or the photochemical oxidation of organic matter (which consumes O_2), but are often assumed to be negligible.

5.2.3 Sampling strategy

Five pools, MHM01 to MHM05 (from here on referred to as the ‘monthly pools’), located in different drains, were sampled from May 2013 to May 2014 inclusive on nine occasions (see Appendix B for a full list of sampling dates). The five pools were all of similar size (~2m^2) and located at the top of the hillslope. Each pool was situated at the top of its respective drain to minimise inflow (i.e. water input from pools higher up in the drainage system). No metabolism data were collected from MHM01 in June 2013 due to equipment failure. In August 2013, metabolism data were collected for MHM04 but no corresponding water chemistry data were obtained due to the water sample being damaged. Data were collected in only one winter month (December) due to inclement weather which hindered access to the study site and / or to the pools themselves, which were frozen.

In addition to the monthly pools, a further ten pools (MHM06 to MHM15 - from here on referred to as the ‘summer pools’), all located on flatter ground at the bottom of the hillslope were sampled on various dates during July and August 2013. This was done for three main reasons (1) to take advantage of the more clement weather conditions in summer, (2) to increase the spatial variability of the dataset and (3) to allow better comparison with the many lake metabolism studies which have been carried out in summer months. Altogether, 54 independent metabolism estimates and associated datasets were collected (Appendix B).

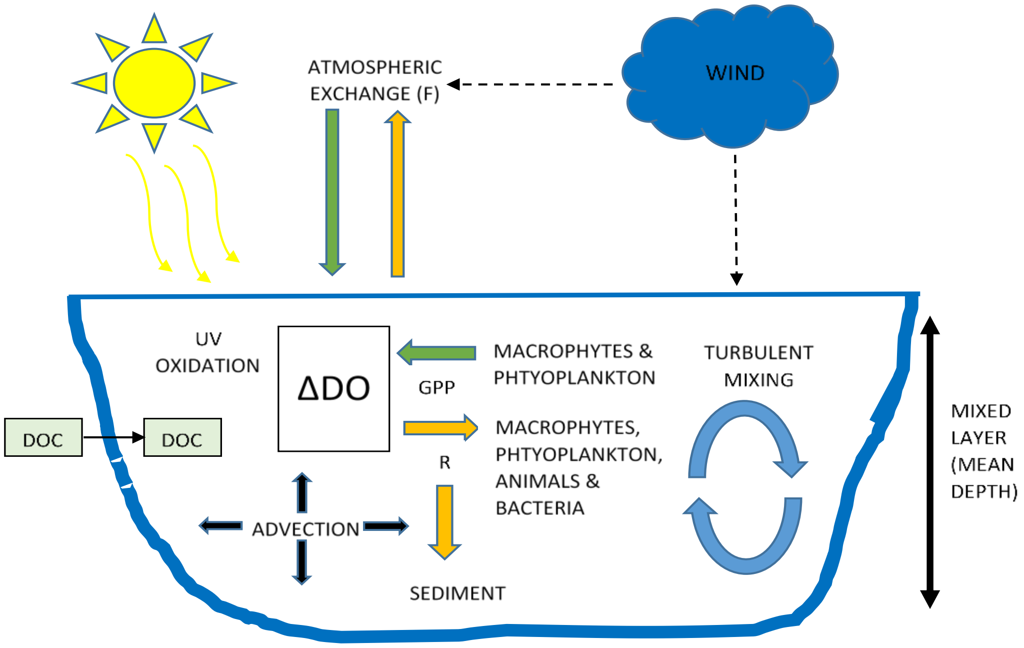

Figure 5.2. Conceptual model of the biological and physical mechanisms which contribute to levels of dissolved oxygen (DO) in a shallow pool. Green arrows represent O_2 gains via photosynthesis and atmospheric exchange (F) and orange arrows represent O_2 consumption by respiration (R) and O_2 loss by F. Further changes in DO levels can be caused by photochemical UV oxidation and photoinhibition in surface waters and physical mixing driven by wind. In larger, deeper lakes, advective mixing across a thermal stratification layer (metalimnion) during summer and horizontal exchange of oxygen with shallow littoral zones may cause significant noise in DO patterns during a diel cycle, but the prevalence of these processes in small pools is less clear. The mixed layer in shallow lakes (<3m deep) is taken as the mean depth. Adapted from Staehr et al. (2010a).

5.2.4 Data collection

DO (mg L^{-1}), water temperature (°C) and barometric pressure (kPa) were recorded using a YSI ProODO optical probe, which was deployed for a minimum of one diel period (midnight to midnight) in each pool, at 10 - 20 cm below the surface, depending on the pool depth. Probes were deployed in the deepest parts of each pool to ensure they were surrounded by water and to avoid contact with benthic sediment. The probe was calibrated using the ‘DO% in water saturated air 1-point calibration’ method outlined in the manufacturer's user manual before each deployment. This briefly involved placing the sensor in a plastic sleeve with a moistened sponge for five minutes allowing the sleeve to become saturated and the sensor to stabilize before using the built-in calibration menu. Readings were set to record every 15 minutes. Wind speed (m s^{-1}) and PAR (µmols m^{-2} s^{-1}) were recorded using a Vector Instruments Type A100R switching anemometer and Skye Instruments Quantum sensor, respectively, attached to a Campbell CR800 datalogger; readings were taken every 15 minutes to coincide with the DO, water temperature and pressure readings.

Mean depth was calculated from seven depth measurements taken in a transect across the pool, making sure to incorporate the deepest section. Approximate surface area (to the nearest 0.5 m^2) was estimated from axis measurements and pool shape. EC and pH were measured once per sampling period using a Hach HQ30d handheld probe. A 50 mL water sample was collected, passed through a 0.45-µm filter and subsequently analysed for concentrations of DOC, using an analytikjena multi N/C® 2100, TP and total nitrogen (TN), using a San^{++} Automated Continuous Flow Analyzer (CFA), and water colour, which was measured using a Jasco V-630 UV/VIS spectrophotometer set at the following wavelengths; 254nm, 400nm, 440nm, 465nm and 665 nm. The ratio of absorbance at 465nm to that at 665nm was also calculated and is expressed as E4/E6 for each pool. The specific UV absorbance ($SUVA_{254}$) was calculated as abs at 254nm (m^{-1})/DOC (mg L^{-1}).

5.2.5 Calculations

The equations used to calculate pool metabolism were based on those in Staehr et al. (2010a) and are provided in Table 5.2. In order to calculate F (atmospheric exchange of O_2) (Table 5.2; Eq. 8), the following steps were required:

Calculate O2sat:

(O_{2sat}) is the oxygen concentration in water in equilibrium with the atmosphere at ambient temperature, taking salinity into account and corrected for barometric pressure (BP) (Table 5.2; Eq. 2 & 3).

Calculate Schmidt number (Sc):

Sc represents the ratio of two molecular transport properties of a gas; $Sc = v/D$, where v = kinematic viscosity and *D* = the diffusion coefficient. *Sc* is calculated as a function of water temperature because D is temperature dependent (Table 5.2; Eq. 4).

Calculate wind speed (m s^{-1}):

Wind speed was measured using a portable weather station with the anemometer blades placed at ~80 cm above the surface of the pond. However, the piston velocity k_{600} (Table 5.2; Eq. 6) is usually estimated as a function of wind speed at 10 m above the waterbody's surface. Therefore, an empirically-derived equation to relate wind speed at the height measured (U_Z) and that at 10 m above the pool surface (U_{10}) was applied (Table 5.2; Eq. 5).

Calculate piston velocity (k):

k was calculated for each time step from the estimate of k_{600} and the ratio of Schmidt numbers (Table 2; Eq. 6 & 7). k_{600} is the piston velocity of gas exchange in cm h^{-1} for a gas with a Schmidt number of 600 (Hall Jnr et al., 2007).

Once F was calculated, the following steps were used to calculate rates of ER, GPP and NEP:

Calculate dayfraction:

Dayfraction represents the light proportion of the diel period, when irradiance is above 0 µmol photons m^{-2} s^{-1} (Table 5.2; Eq. 9). It is required to calculate $NEP_{daytime}$ (Table 2; Eq. 11) and $R_{daytime}$ (Table 2; Eq. 14). In this study, light availability was measured *in situ* by using a Photosynthetically Active Radiation (PAR) meter.

Calculate Z_{mix}:

In lake studies, Z_{mix} represents the depth of the mixed layer, where temperature remains relatively constant. In shallow water bodies (i.e. 2-3m deep lakes), Z_{mix} can be assumed to equal average lake depth (Staehr et al., 2010a). As the Moor House pools all average <50cm deep, mean depth was used as a proxy for Z_{mix}.

Calculate NEP for each time step (NEP_{hr}):

During daylight hours, changes in levels of DO may be caused by both photosynthesis (O_2 production) and respiration (O_2 consumption). In effect, this equates to NEP, which is the balance between the two, so day-time NEP can be directly measured by recording changes in levels of DO. Therefore, NEP for each time step is calculated directly from observed changes in DO after F has been taken into consideration, with F being divided by Z_{mix} to turn it from an areal (g O_2 m^{-2} d^{-1}) to a volumetric (g O_2 m^{-3} d^{-1}) rate; the same unit of measurement as ΔDO (Table 5.2; Eq. 10).

Calculate daytime NEP ($NEP_{daytime}$):

$NEP_{daytime}$ is the mean hourly NEP rate occurring whilst PAR is present extrapolated out over the number of daylight hours (Table 5.2; Eq. 11).

Table 5.2. Equations used to calculate pool metabolism. Adapted from Staehr et al. (2010a).

Parameter	Equation	Reference	Eq.
The governing equation	$\Delta O_2/\Delta t = GPP - R - F - A$	Odum 1956	1
Schmidt coefficient (*Sc*), from water temperature (T, Celsius)	$Sc = 0.0476\ T^3 + 3.7818\ T^2 - 120.1\ T + 1800.6$	Wanninkhof 1992	2
Wind speed, at 10 m height (U_{10}) from wind speed at height z (U_z, m/s)	U_{10} (m s^{-1}) = $U_Z \times \alpha$ $\alpha = 1.4125\ z^{-0.15}$	Smith 1985	3
Piston velocity (*k*)	k_{600} (m h^{-1}) = $(2.07 + 0.215\ U_{10}{}^{1.7})/100$ k (m h^{-1}) = k_{600}(m h^{-1}) x $([Sc/600]^{-0.5})$	Cole and Caraco 1998 Jähne et al. 1987	4 5
Oxygen saturation (O_{2sat}) as a function of temperature (T, kelvin) and salinity (S, ppt). *e* (a mathematical constant) is ~ 2.71828	O_{2sat} (mg L^{-1}) = (e^{C}) x 1.423 mg O_2 mL^{-1} C (ml O_2 L^{-1}) = $(-173.4292 + 249.6339 \times (100 / T) + 143.3483 \times \ln(T / 100) - 21.8492 \times (T / 100) + S \times [-0.033096 + 0.014259 \times (T / 100) - 0.0017000 \times (T / 100)^2]$	Weiss 1970	6
Correction of O_{2sat} for barometric pressure (BP, millibars)	O_{2sat} (mg L^{-1}) corrected for pressure = O_{2sat} (mg L^{-1}) x correction factor correction factor = (BP x 0.0987 - 0.0112)/100	USGS memo #81.11 1981 USGS memo #81.15 1981	7
Physical gas flux (*F*)	F (g O_2 m^{-2} h^{-1}) = $k\ (O_{2meas} - O_{2sat})$		8
Dayfraction light_hours determination	dayfraction = light_hours/24 h Light hours measured directly using a PAR meter		9
$NEP_{daytime}$	NEP_{hr} (g O_2 m^{-3} hr^{-1}) = ΔO_2 (g m^{-3} hr^{-1}) – F/Z_{mix} $NEP_{daytime}$ (g O_2 m^{-3} daylight period^{-1}) = mean NEP_{hr} during daylight x dayfraction x 24	Cole et al. 2000	10 11
R	R_{hr} (g O_2 m^{-3} h^{-1}) = mean NEP_{hr} during darkness $R_{daytime}$ (g O2 m_{-3} daylight period^{-1}) = R_{hr} x 24 h x dayfraction R_{day} (g O_2 m^{-3} d^{-1}) = R_{hr} x 24 h		12 13 14
GPP	GPP (g O_2 m^{-3} d^{-1}) = $NEP_{daytime} + R_{daytime}$		15
NEP	NEP (g O_2 m^{-3} d^{-1}) = GPP - R_{day}		16

Calculate respiration (R)

Respiration is assumed to be the only metabolic process operating during the hours of darkness, when GPP is assumed to be zero as it requires PAR. Therefore, night-time R can be measured directly and the hourly respiration rate (R_{hr}) equates to the mean changes in DO at night (Table 5.2; Eq. 12). R will almost always be negative (as levels of DO decrease overnight). However, since R is defined as a positive quantity, R_{hr} was transformed from a negative to a positive number for use in subsequent equations (Caffrey, 2003). Assuming that rates of R during the day are the same as night, then R_{hr} can be multiplied by 24 to provide R for the entire diel period (R_{day}) (Table 5.2; Eq. 13). R in the period when PAR is available (i.e. between sunrise and sunset) ($R_{daytime}$) is calculated from R_{hr} extrapolated over day length (Table 5.2; Eq 14).

Calculate GPP

GPP is calculated by adding together $NEP_{daytime}$ and $R_{daytime}$, to give the total amount of O_2 that would have been produced in daylight hours in the absence of R (Table 5.2; Eq 15).

Calculate NEP

Finally, overall NEP is calculated by deducting R_{day} from GPP (Table 5.2; Eq. 16).

Initial data analysis showed that using 15-minute time steps often resulted in negative GPP values, due to noisy diel DO signals. The number of negative GPP values decreased substantially when 1hr time steps were applied, so these were used for the metabolism calculations (Staehr et al., 2010a). However, even with 1hr time steps, thirteen datasets still produced negative GPP figures. Moving averages were applied (Gelda and Effler, 2002, Coloso et al., 2008) to try and smooth the data but this was unsuccessful, probably because too few consecutive days’ worth of data were available. For example in Gelda and Effler (2002) it took an average of seven days data to remove all such anomalies. Therefore, negative GPP values in this study were assumed to be zero (Coloso et al., 2008, Tuttle et al., 2008).

Different studies report R, GPP and NEP in different units of measurement. So, for the purposes of comparison in the discussion section, the MH results were converted from g O_2 m^{-3} d^{-1} to g O_2 m^{-2} d^{-1} (e.g. from volumetric to areal rates) by multiplying by Z_{mix} (m), which, in theory, represents the average metabolic rates per square meter of the entire waterbody (Staehr et al., 2010a). For other studies which reported volumetric rates, conversion was done using the relevant depth parameter provided (e.g. epilimnion depth). For studies which reported values in mmol O_2 m^{-2} d^{-1}, values were converted into g O_2 m^{-2} d^{-1} as follows: (value/1000) x 32, where 1000 is the number of millimoles in a mole and 32 is the molecular weight of O_2. In order to compare my results with those from terrestrial peatland carbon budget studies, units of O_2 production were converted to units of CO_2 consumption assuming respiratory and photosynthetic quotients of 1; for both photosynthesis and respiration;

$$\text{g C} = \text{g } O_2 \times (12/32)$$

where 12 = atomic weight of C and 32 = molecular weight of O_2. Volumetric rates were then converted to areal rates by multiplying by Z_{mix} (m).

5.2.5 Statistical analysis

Analysis was undertaken to establish the presence of any relationships between the metabolism estimates (R, GPP and NEP) and the predictor variables of DOC, mean water temperature, mean water depth, TN, TP, E4/E6 and $SUVA_{254}$. The two datasets (monthly pools and summer pools) were analysed separately and then all 53 independent datasets were combined together for further analysis. As the monthly and combined datasets included repeated sampling of the monthly pools, generalised linear mixed models (GLMMs) with pool as a random factor were applied (Bolker et al., 2009). For the summer pools, which were sampled only once each, generalised linear models (GLMs) were used. In both cases, maximum likelihood estimates (MLEs) were run to ascertain the most appropriate error distribution. When plotting the relationships between the independent and predictor variables for all pools combined, datasets were delineated by season; spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January and February). The summer pools were further split into the monthly pools sampled in summer (summer M) and the pools sampled as part of the one-off summer sampling (summer S).

5.3 Results

5.3.1 Environmental characteristics

The pools were small, shallow and characterised by low pH, low levels of nutrients and EC and high levels of DOC (Table 5.3). Individual variables will be discussed in the sections below.

5.3.2 Diel patterns of DO

Patterns of DO sometimes conformed to a standard diel curve (i.e. one which reflects levels of PAR) as on 24th July (Figures 5.3a & b). However, a more common DO pattern showed fairly flat or sometimes reducing levels throughout the day, followed by a spike in the early evening, with particularly pronounced evening DO spikes often led to negative GPP values as with MHM01 on 20th August (Figures 5.3 c & d). PAR was often patchy, but, even on days with a practically perfect PAR curve (Figure 5.3e) this was not always reflected in a corresponding DO curve (Figure 5.3f).

Table 5.3. Environmental variables (descriptive statistics) for the monthly pools (MHM01 and MHM04, n=8, MHM02, MHM03 and MHM05, n=9) showing median (+ interquartile range) values, and for the summer pools (MHM06 to MHM15) each sampled on one occasion.

Variable	**MHM01**	**MHM02**	**MHM03**	**MHM04**	**MHM05**	**MHM06**	**MHM07**	**MHM08**	**MHM09**	**MHM10**	**MHM11**	**MHM12**	**MHM13**	**MHM14**	**MHM15**
Date	Various	Various	Various	Various	Various	13-Jul	13-Jul	24-Jul	24-Jul	14-Aug	14-Aug	16-Aug	20-Aug	22-Aug	22-Aug
Area (m^2)	2.0	2.0	2.0	2.0	2.0	1.5	1.5	2.5	3.5	2.5	3	2	1.5	1.5	1.5
Mean Depth (cm)	35 (10)	33 (9)	44 (5)	38 (5)	36 (1)	18	12	39	33	24	26	35	24	26	21
Mean Temp (°C)	6.96 (4.70)	6.79 (5.64)	6.84 (5.71)	6.43 (5.03)	6.81 (5.41)	20.12	20.71	18.80	19.18	13.69	14.42	14.78	13.10	15.40	15.96
EC ($\mu S\ cm^{-1}$)	30.25 (4.82)	30.07 (9.45)	31.20 (8.75)	31.63 (12.92)	32.60 (12.30)	49.2	50.4	61.5	60.5	41.6	41.3	44.9	38.3	33.3	34.7
pH	4.29 (0.54)	4.63 (0.65)	4.36 (0.50)	4.25 (0.58)	4.55 (0.88)	3.98	3.93	6.34	3.7	4.33	4.40	4.42	4.53	5.2	4.32
TN ($mg\ L^{-1}$)	0.85 (0.76)	0.63 (0.66)	0.82 (0.69)	0.86 (0.58)	1.19 (0.78)	1.78	2.17	3.79	2.93	1.40	1.10	2.48	1.05	1.96	1.11
TP ($mg\ L^{-1}$)	0.021 (0.023)	0.014 (0.017)	0.015 (0.019)	0.012 (0.018)	0.010 (0.015)	0.028	0.040	0.084	0.056	0.016	0.023	0.032	0.023	0.042	0.010
DOC ($mg\ L^{-1}$)	26.34 (23.31)	32.77 (23.10)	33.33 (22.63)	30.68 (27.36)	35.60 (29.92)	42.48	63.93	89.85	72.90	47.15	46.06	52.58	40.70	51.55	26.95
E4/E6	8.40 (4.38)	7.90 (1.20)	8.35 (2.14)	6.84 (2.81)	7.97 (1.91)	5.92	6.07	5.47	5.24	7.19	8.01	6.61	6.44	5.63	8.59
SUVA	3.61 (0.44)	3.68 (0.45)	3.81 (0.68)	3.76 (0.69)	3.64 (0.80)	3.26	2.95	2.86	3.62	3.86	3.72	3.50	4.46	4.24	4.25
R ($g\ O2\ m^{-3}\ d^{-1}$)	12.26 (14.10)	13.23 (14.62)	9.02 (7.17)	10.41 (13.29)	10.15 (9.6)	28.81	37.82	17.00	15.48	28.23	25.22	15.73	23.93	8.98	28.30
GPP ($g\ O2\ m^{-3}\ d^{-1}$)	1.65 (2.79)	0.72 (3.28)	0.78 (2.18)	1.98 (2.73)	0.77 (3.05)	4.59	9.82	11.65	7.19	8.48	12.12	8.15	5.76	5.92	16.42
NEP ($g\ O2\ m^{-3}\ d^{-1}$)	-11.51 (12.74)	-13.63 (13.31)	-6.60 (7.85)	-6.92 (9.06)	-7.56 (6.44)	-24.23	-28.00	-5.35	-8.29	-19.76	-13.10	-7.58	-18.17	-3.07	-11.88

5.3.3 Oxygen saturation

The pools were almost always under-saturated with O_2, with measured levels of O_2 exceeding the calculated O_{2sat} value on only four occasions: MHM01 (9th April), MHM08 (24th July), MHM14 and MHM15 (both 22nd August) (Figures 5.4a & b).

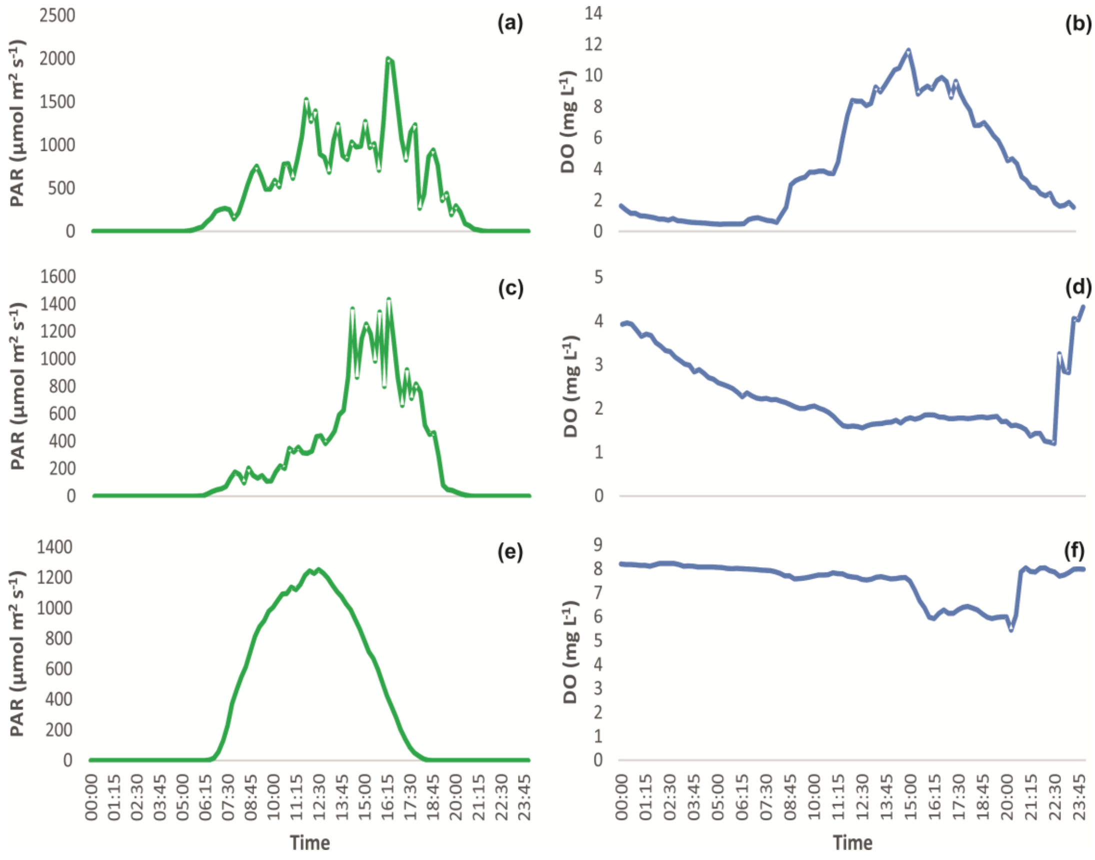

Figure 5.3. Examples of the different diel DO patterns observed in the Moor House pools, along with corresponding PAR readings; (a) and (b) show a fairly well-defined DO curve on a day with patchy but high PAR levels (MHM08 on 24th July); (c) and (d) show DO patterns for a typical day with negative GPP; note the sharp increase in DO after sunset (MHM01 on 20th August); (e) and (f) represent a day with an almost perfect PAR curve but no corresponding DO curve (MHM01 on 11th March) - note the early evening rise in DO levels.

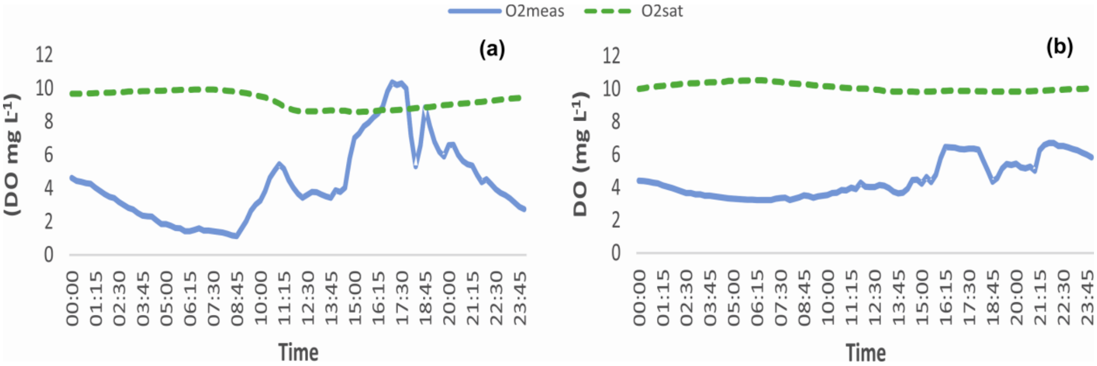

Figure 5.4. Levels of O_{2sat} and O_{2meas} in (a) MHM15 (24th July), one of only four occasions on which O_{2meas} rose above O_{2sat} and (b) MHM04 (11th June); an example of the prevalent O_{2meas} / O_{2sat} patterns.

5.3.4 R, GPP and NEP

Of the 53 independent diel datasets, all returned negative NEP values (heterotrophic).

5.3.4.1 Monthly pools

R was highest in December 2013 for four of the five monthly pools; MHM01 = 26.66, MHM03 = 26.60, MHM04 = 18.94 and MHM05 = 15.18 (all g O_2 m^{-3} d^{-1}). Only MHM02 did not follow this pattern, with R being marginally highest in June 2013 (21.01g O_2 m^{-3} d^{-1}). Rates of R were lowest for all pools in March 2014; MHM01 = 0.98, MHM02 = 0.98, MHM03 = 1.88, MHM04 = 2.06 and MHM05 = 2.93 (all g O_2 m^{-3} d^{-1}) (Figures 5.5a to e). GPP was low or zero (i.e. negative GPP estimates assumed to be zero) all year round in all of the pools, although there was an upwards trend towards the end of the study period, with the highest GPP values in all pools coming in May 2014; MHM01 = 6.96, MHM02 = 5.50, MHM03 = 3.30, MHM04 = 4.30, MHM05 = 4.13 (all g O_2 m^{-3} d^{-1}) (Figures 5.5a to e). These highest GPP values corresponded to the lowest maximum PAR values recorded throughout the study period (Figure 5.5g). NEP was highest in either March or April 2014 for all pools; MHM01 = -2.76 (April), MHM02

= -2.96 (March), MHM03 = -2.61 (April), MHM04 = -1.28 (April) and MHM05 = -2.17 (March) (all g O_2 m^{-3} d^{-1}). NEP was lowest for all pools in December; MHM01 = -26.1, MHM02 = -21.19, MHM03 = -25.82, MHM04 = -17.69, MHM05 = -16.99 (all g O_2 m^{-3} d^{-1}) (Figures 5.5a to e).

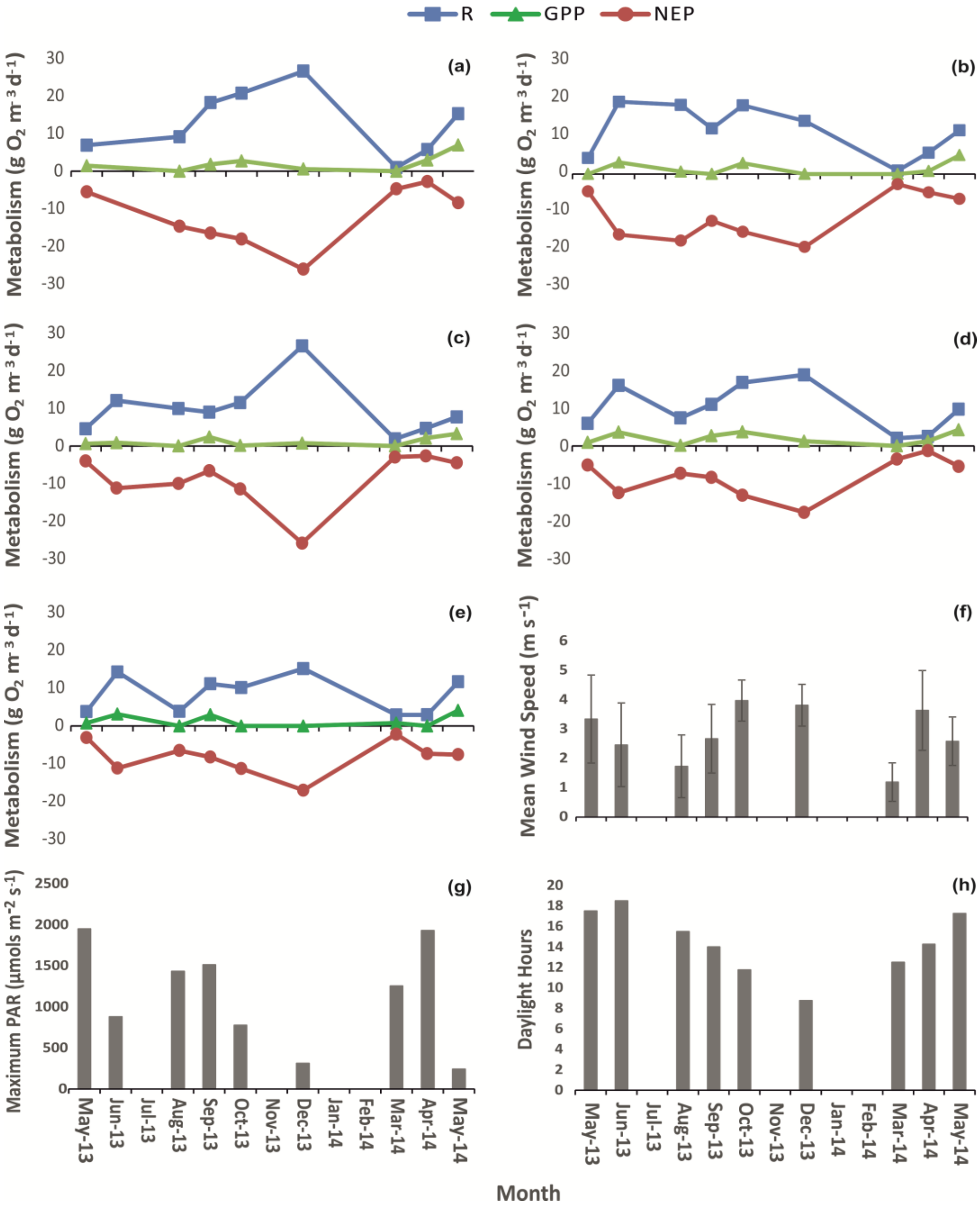

Figure 5.5. Metabolism estimates (R, GPP and NEP) for the monthly pools; (a) MHM01, (b) MHM02, (c) MHM03, (d) MHM04 and (e) MHM05. No values were obtained for MHM01 in June 2013 due to equipment failure. Corresponding meteorological data; (f) mean wind speed (+ st. dev), (g) maximum PAR and (h) number of daylight hours.

5.3.4.2 Summer pools

Rates of R in the summer pools ranged from 8.98g O_2 m^{-3} d^{-1} (MHM14) to 37.82g O_2 m^{-3} d^{-1} (MHM07). There were no negative GPP values with estimates ranging from 4.59g O_2 m^{-3} d^{-1} (MHM06) to 16.42g O_2 m^{-3} d^{-1} (MHM15). The summer pools all returned negative NEP figures ranging from -3.07g O_2 m^{-3} d^{-1} (MHM14) to -28.00g O_2 m^{-3} d^{-1} (MHM07) (Figure 5.6).

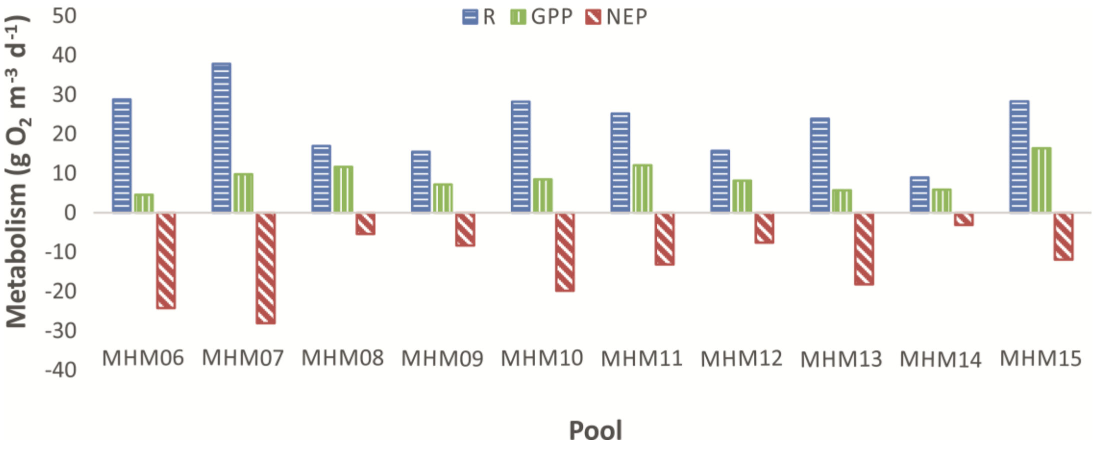

Figure 5.6. Metabolism estimates (R, GPP and NEP) for the summer pools.

5.3.5 Metabolism and DOC

Concentrations of DOC in the individual pools ranged from 12.87 mg L^{-1} (MHM03 on 11th March) to 89.85 mg L^{-1} (MHM08 on 24th July). Mean DOC concentration for all the pools combined were highest in July (mean = 67.29, +/- 19.73 mg L^{-1}) and lowest in March (mean = 13.85, +/- 1.20 mg L^{-1}) and suggested a tendency to be higher between May and October (Figure 5.7a). For all the pools combined, there was a significant positive relationship between R and DOC and also between GPP and DOC but no relationship between NEP and DOC (Table 5.5, Figures 5.7b, 5.7c 5.7d). The relationships in the monthly dataset were similar but with lower significance levels and the summer data exhibited no significant relationships (Table 5.5).

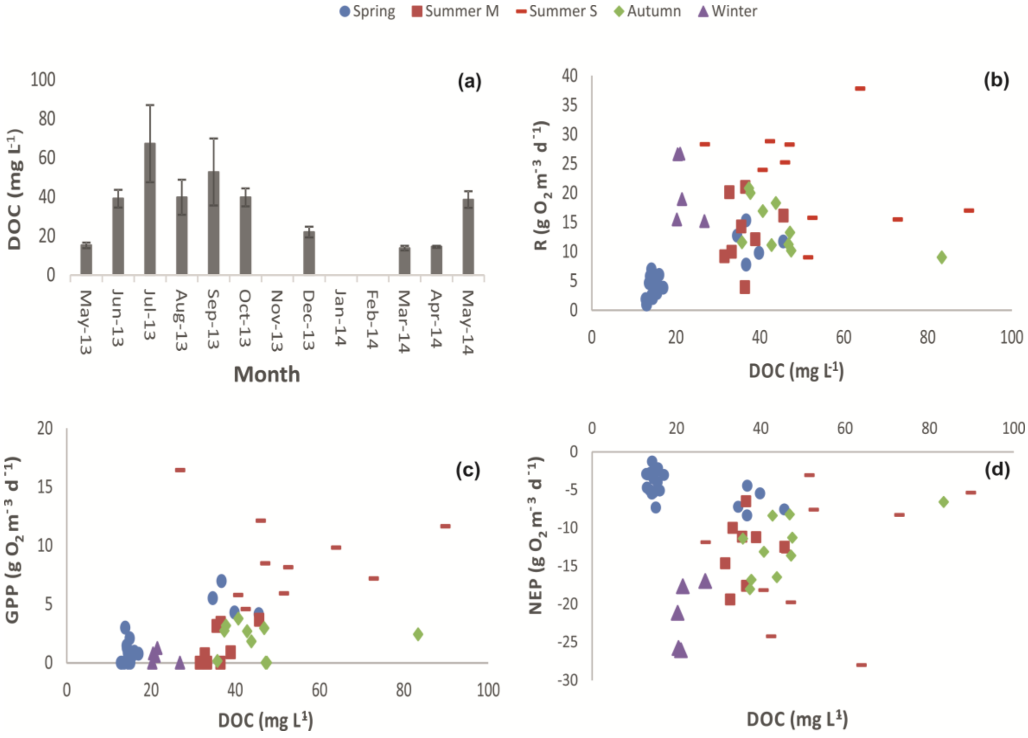

Figure 5.7. DOC concentrations and relationships with metabolism estimates (a) Mean DOC concentrations (+/- 1 st.dev) for all pools at Moor House throughout the sampling period, with the relationship between DOC and (b) R, (c) GPP and (d) NEP, delineated by season. Spring n=20, summer M n=8, summer S n=10, autumn n=10, winter n=5.

5.3.6 Metabolism and E4/E6 and SUVA$_{254}$

The highest individual E4/E6 ratio was 14.56 (MHM03 on 14th May, 2013) and the lowest was 5.24 (MHM09 on 24th July). The mean values per month ranged from 5.68 (+/- 0.38) in July to 9.52 (+/- 1.88) in April, with no clear seasonal pattern (Figure 5.8a). There were no significant relationships between R, GPP or NEP and E4/E6 for either all pools combined or for the monthly pools (Table 5.5, Figures 5.8b, c, d). However, when analysing the summer pools there was a significantly positive relationship between GPP and E4/E6 (Table 5.5). The highest individual SUVA$_{254}$ value was 4.55 L mg^{-1} m^{-1} (MHM05 on 14th May, 2013) and the lowest 2.10 L mg^{-1} m^{-1} (MHM03 on 10th September). The monthly mean values ranged from 3.11 L mg^{-1} m^{-1} (+/- 0.19) (April) to 4.46 L mg^{-1} m^{-1} (+/- 0.09) (May, 2013), with no clear seasonal pattern (Figure 5.9a). There were no significant relationships between R, GPP or NEP and SUVA in any of the datasets (Table 5.5, Figures 5.9b, c, d).

Table 5.5. GLMM and GLM results for relationships between environmental variables and metabolism estimates for the combined, monthly and summer datasets.

		All Pools (GLMM)		**Monthly Pools (GLMM)**		**Summer Pools (GLM)**	
Dependent Variable	**Predictor Variable**	**t-value**	**p-value**	**t-value**	**p-value**	**t-value**	**p-value**
R	DOC	3.22	**0.003**	2.76	**0.009**	-0.96	0.367
R	Temp	4.13	**<0.001**	0.60	0.553	0.70	0.503
R	TN	2.81	**0.008**	2.96	**0.005**	-1.38	0.206
R	TP	3.30	**0.002**	4.28	**<0.001**	-1.46	0.183
R	Depth	-5.74	**<0.001**	-1.84	0.073	-3.54	**0.008**
R	E4/E6	-1.39	0.172	-0.98	0.335	1.29	0.234
R	SUVA	0.88	0.383	1.28	0.209	-0.67	0.524
GPP	DOC	3.59	**0.001**	3.00	**0.005**	-0.25	0.812
GPP	Temp	3.77	**0.001**	2.59	**0.014**	-0.14	0.893
GPP	TN	3.28	**0.002**	2.51	**0.017**	-0.21	0.837
GPP	TP	3.20	**0.003**	3.07	**0.004**	-0.27	0.795
GPP	Depth	-0.59	0.557	0.01	0.995	0.14	0.889
GPP	E4/E6	-0.35	0.729	-0.33	0.747	2.63	**0.030**
GPP	SUVA	-0.01	0.991	0.12	0.906	0.86	0.414
NEP	DOC	-1.56	0.128	-1.64	0.110	0.86	0.414
NEP	Temp	-1.46	0.154	0.19	0.850	-0.79	0.454
NEP	TN	-1.06	0.298	-1.93	0.061	1.30	0.231
NEP	TP	-1.44	0.159	-2.85	**0.007**	1.34	0.216
NEP	Depth	3.87	**<0.001**	1.98	0.055	4.10	**0.003**
NEP	E4/E6	1.16	0.254	0.85	0.400	-0.37	0.718
NEP	SUVA	-0.40	0.689	-0.94	0.351	0.64	0.543

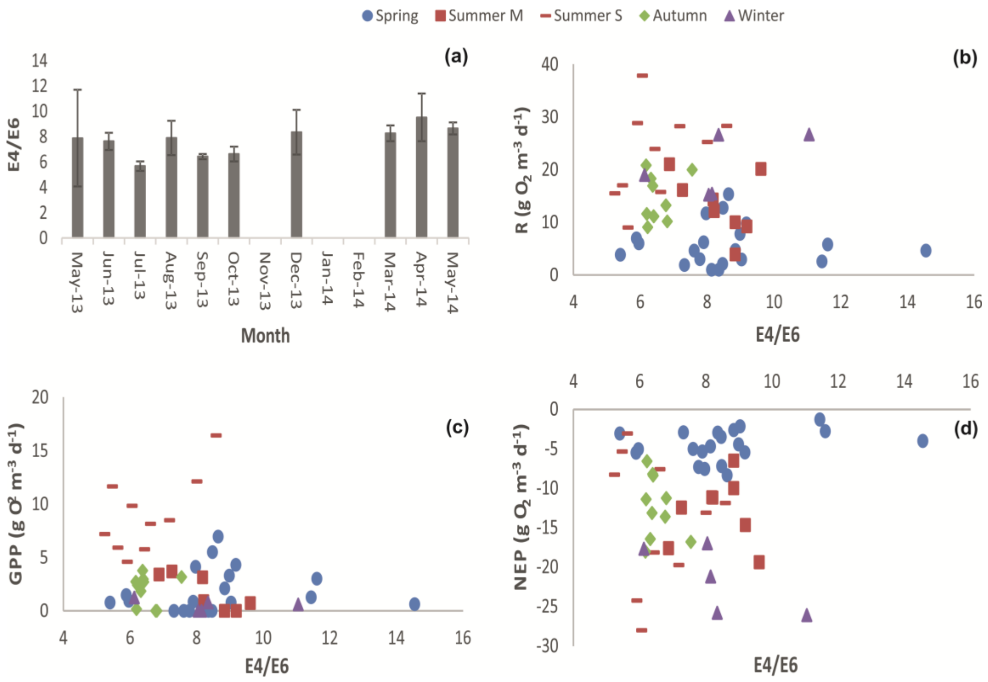

Figure 5.8. E4/E6 ratios and relationships with metabolism estimates (a) Mean E4/E6 ratios (+/- 1 st.dev) for all pools at Moor House throughout the sampling period with the relationship between E4/E6 and (b) R, (c) GPP and (d) NEP, delineated by season. Spring n= 20, summer M n=8, summer S n=10, autumn n=10, winter n=5

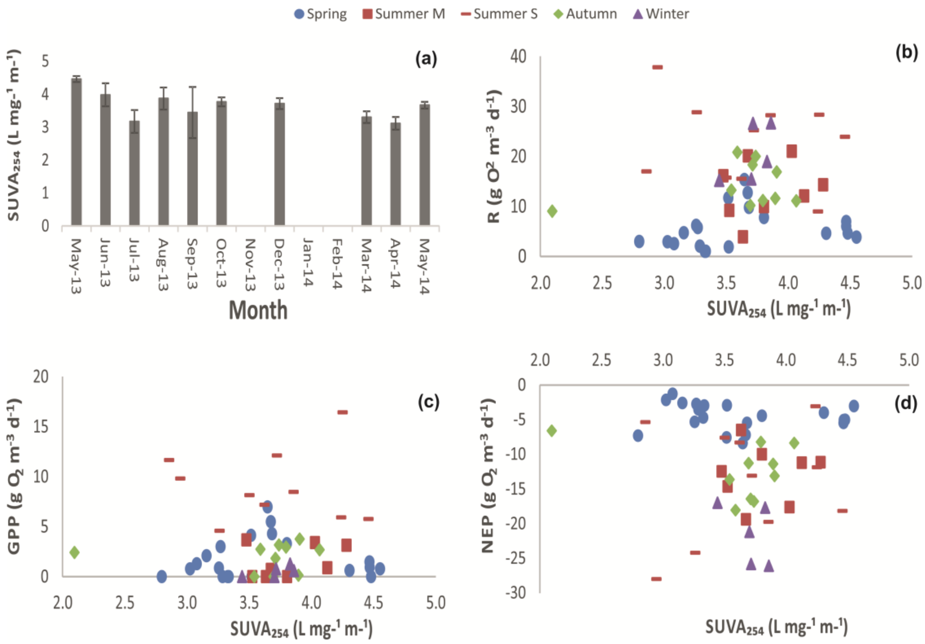

Figure 5.9. SUVA$_{254}$ values ratios and relationships with metabolism estimates (a) Mean SUVA$_{254}$ values (+/- 1 st.dev) for all pools at Moor House throughout the sampling period with the relationship between SUVA$_{254}$ and (b) R, (c) GPP and (d) NEP, delineated by season. Spring n= 20, summer M n=8, Summer S n=10, autumn n=10, winter n=5

5.3.7 Metabolism and water temperature

Mean temperature for all of the pools combined was lowest in December (mean = 4.33, +/- 0.14°C) and highest in July (mean = 19.70, +/- 0.17°C) (Figure 5.10a). There was a highly significant positive relationship between R and water temperature although the scatterplot highlighted two fairly high R values at low temperatures in winter (Table 5.5, Figure 5.10b). There was also a significantly positive relationship between GPP and water temperature but no relationship between NEP and water temperature (Table 5.5, Figures 5.10c, 5.10d). For the monthly pools, the relationship between temperature and GPP was also positively significant but there was no significant relationship between either R or NEP and temperature. The summer pools exhibited no significant relationships (Table 5.5).

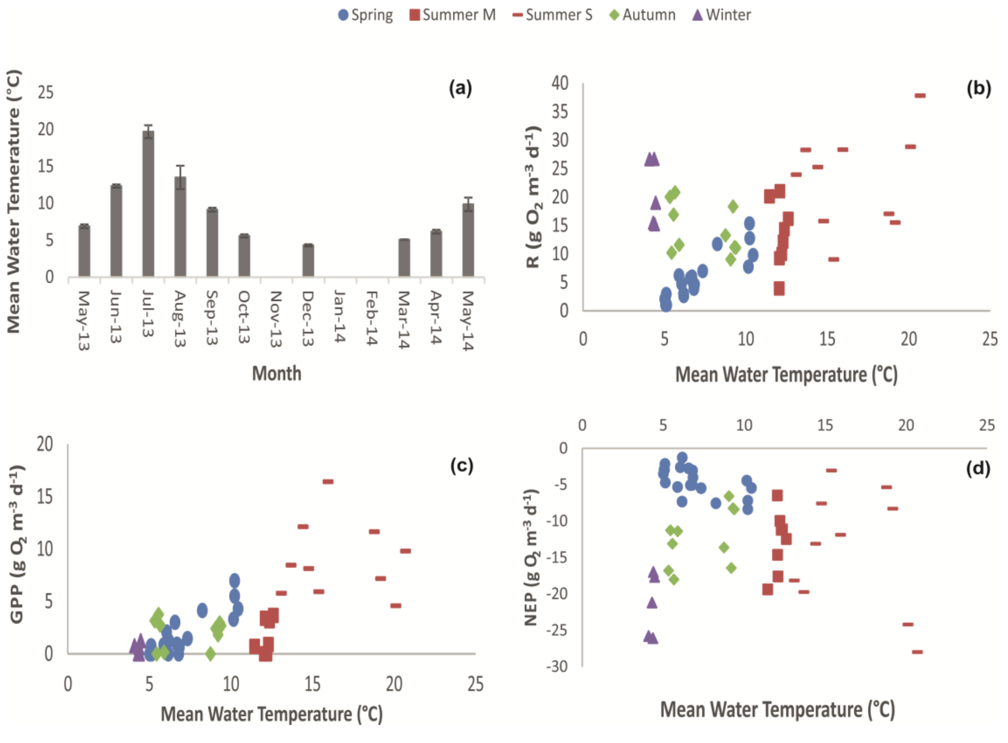

Figure 5.10. Water temperature and relationships with metabolism estimates (a) Mean water temperature (+/- 1 st.dev) for all pools at MH throughout the sampling period with the relationship between water temperature and (b) R, (c) GPP and (d) NEP, delineated by season. Spring n=20, summer M n=8, summer S n=10, autumn n=10, winter n=5.

5.3.8 Metabolism and TN

Concentrations of TN were low in all pools, ranging from 0.11 mg L^{-1} (MHM03 on 14th May, 2013) to 3.78 mg L^{-1} (MHM08 on 24th July). Taking the mean values per calendar month, concentrations of TN were highest in July (2.67, +/- 0.89 mg L^{-1}) and lowest in May 2013 (0.39, +/- 0.18 mg L^{-1}). For all pools combined there were highly significant positive relationships between R and TN, and GPP and TN but no relationship between NEP and TN (Table 5.5, Figures 5.11b, c, d). Similar results were found for the monthly pools, with positive relationships between R and TN and GPP and TN and, whilst the relationship between NEP and temperature for the monthly pools was still not significant, it was much closer to being so (Table 5.5). The summer pools exhibited no significant relationships (Table 5.5).

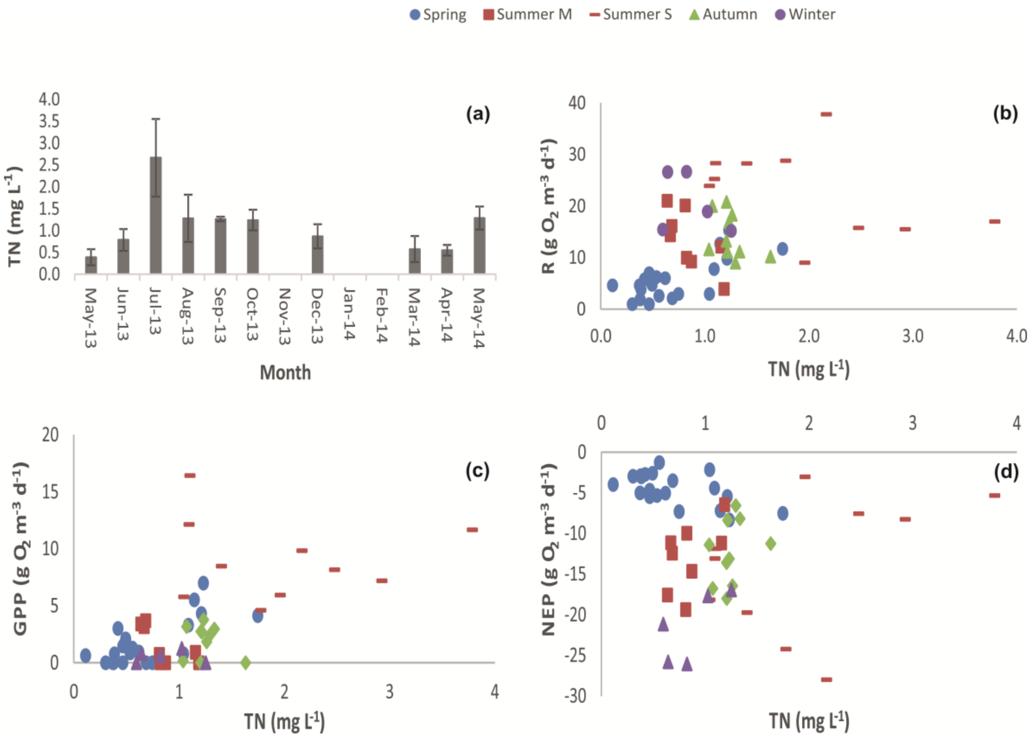

Figure 5.11. TN concentrations and relationships with metabolism estimates (a) Mean TN concentrations (+/- 1 st.dev) for all pools throughout the sampling period relationship with relationships between TN and (b) R, (c) GPP and (d) NEP, delineated by season. Spring n= 20, summer M n=8, summer S n=10, autumn n=10, winter n=5.

5.3.9 Metabolism and TP

Concentrations of TP were very low in all the pools. Individual pool readings of TP ranged from 0.003 mg L^{-1} in MHM04 on 11th March to 0.084 mg L^{-1} in MHM08 on 24th July. Mean concentrations of TP were highest in July (0.052, +/- 0.024 mg L^{-1}) and lowest in March (0.005, +/- 0.001 mg L^{-1}) (Figure 5.12a). For all pools combined there was a highly significant positive relationship between R and TP, and GPP and TP but no relationship between NEP and TP (Table 5.5, Figures 5.12b, c, d). For the monthly pools, the relationships between R and TP and GPP and TP were both still significantly positive although the relationship between NEP and TP was now significantly negative (Table 5.5). The summer pools exhibited no significant relationships (Table 5.5).

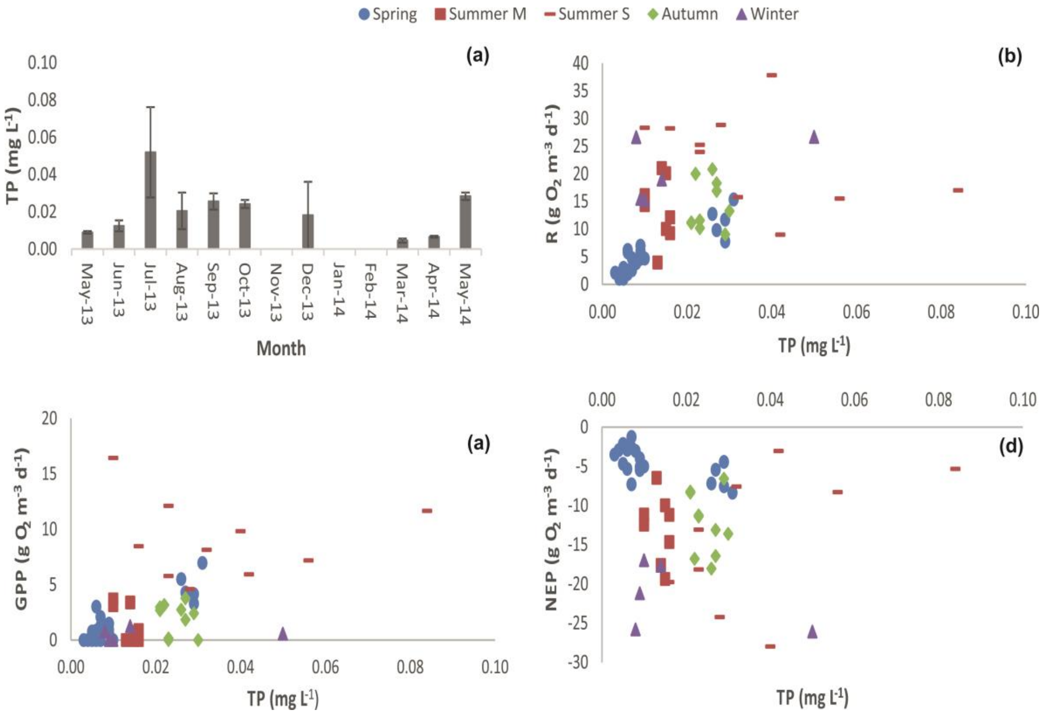

Figure 5.12. TP concentrations and relationships with metabolism estimates (a) Mean TP concentrations (+/- 1 st.dev) for all pools at Moor House throughout the sampling period with the relationship between TP and (b) R, (c) GPP and (d) NEP, delineated by season. Spring n= 20, summer M n=8, summer S n=10, autumn n=10, winter n=5

5.3.10 Metabolism and water depth

Mean water depth was lowest in July (25.89, +/- 12.40cm) and highest in March (42.46, +/- 4.71) (Figure 5.13a). R and water depth were significantly negatively related for all pools combined and for the summer pools, but for the monthly pools the relationship became weaker and non-significant (Table 5.5, Figure 13b). The relationship between GPP and water depth was not significant for any of the three datasets (Table 5.5, Figure 5.13c). NEP and water depth were significantly positively related for all pools combined and for the summer pools, with the relationship for the monthly pools on the cusp of significance (Table 5.5, Figure 5.13d).

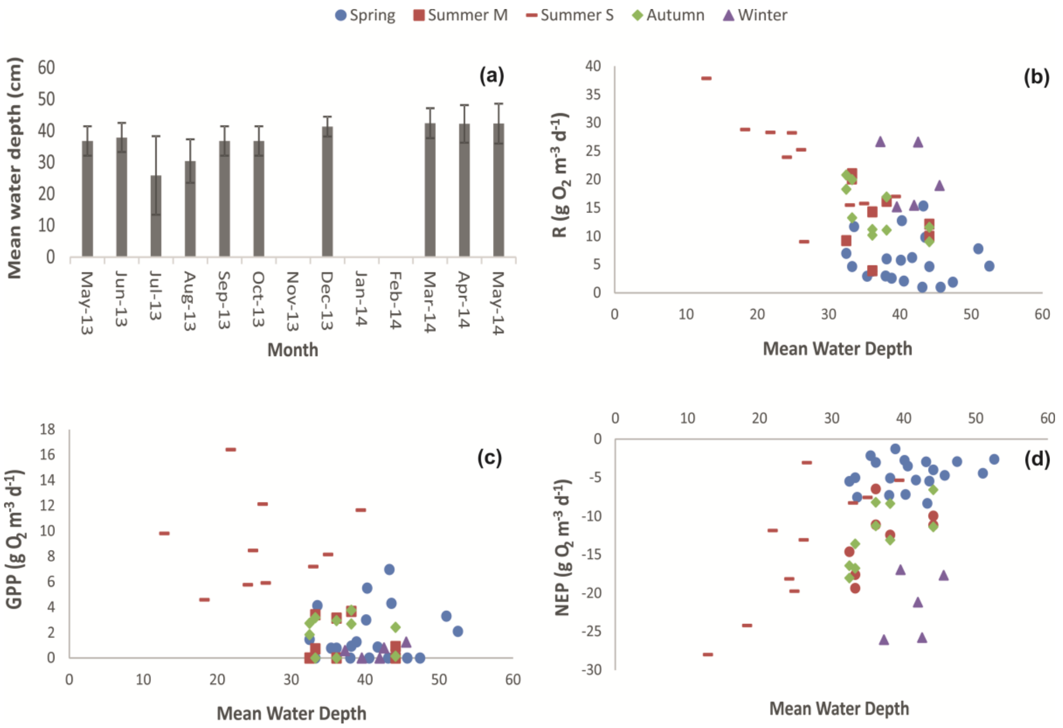

Figure 5.13. Water depth and relationships with metabolism estimates (a) Mean water depth (+/- 1 st.dev) for all pools at Moor House throughout the sampling period with the relationship between depth and (b) R, (c) GPP and (d) NEP, delineated by season. Spring n= 20, summer M n=8, summer S n=10, autumn n=10, winter n=5

5.4 Discussion

This study provides strong evidence that pools in newly-blocked drains on areas of blanket bog act as bioreactors, emitting more CO_2 to the atmosphere than they fix via photosynthesis. This section will now discuss these findings in the context of other studies looking at the metabolism of lentic waters, and will conclude by assessing the suitability of the DO diel change technique when studying small, peatland pools and providing recommendations for its use in future studies.

5.4.1 Prevalence of heterotrophy

Every pool returned a negative NEP value which is indicative of heterotrophy and thus the first part of H_1 was accepted. This finding agrees with those of most other studies looking at the metabolism of dystrophic lakes and ponds (Table 5.6). Indeed, heterotrophy in lakes has been found to be so strong in some cases that it persists even after experimental nutrient enrichment (Cole et al., 2000). However, a study of two shallow beaver ponds in central New York State found that the pond with greater nutrient enrichment due to agricultural run-off had a positive mean NEP value during the sampling period (Klotz, 2013). This section will now discuss the metabolism estimates obtained from Moor House compared to those listed in Table 5.6.

Mean NEP in the Moor House pools ranged from -3.00 (MHM05) to -4.50 g O_2 m^{-2} d^{-1} (MHM02) and these values were similar to Northgate Bog and Crystal Bog (both dystrophic lakes in Wisconsin, USA) where mean NEP was recorded at -3.38g and -1.33 g O_2 m^{-2} d^{-1}, respectively (Hanson et al., 2003, Lauster et al., 2006) (Table 5.6). Reddington Bog returned a slightly lower mean NEP value than any of the MH pools (-4.64g O_2 m^{-2} d^{-1}) and, although the trophic state of this lake was not specified in the original study (Hanson et al., 2003), the high levels of DOC (23.10 mg L^{-1}) are suggestive

Table 5.6. Comparison of metabolism estimates with studies of other lentic habitats. Average rates of R, GPP and NEP, along with selected environmental characteristics, taken from studies looking at metabolism in lentic waters using the diel DO change technique. All metabolism values converted into g O_2 m^{-2} d^{-1} to allow for direct comparison.

								g $O_2 m^{-2} d^{-1}$		
Reference	**Waterbody**	**Location**	**Trophic Status**	**Study Months**	**Surface Area**	**Depth Parameter (m)**	**DOC (mg L^{-1})**	**R**	**GPP**	**NEP**
This study	MHM06 to MHM15	Cumbria, UK	Dystrophic	Jul & Aug	2m^2	0.26 (mean depth)	53.42	5.54	2.37	-3.16
This study	MHM01	Cumbria, UK	Dystrophic	May to May	2m^2	0.37 (mean depth)	26.49	4.84	0.77	-4.50
This study	MHM02	Cumbria, UK	Dystrophic	May to May	2m^2	0.37 (mean depth)	27.85	4.51	0.55	-4.35
This study	MHM03	Cumbria, UK	Dystrophic	May to May	2m^2	0.46 (mean depth)	32.46	4.39	0.55	-3.90
This study	MHM04	Cumbria, UK	Dystrophic	May to May	2m^2	0.40 (mean depth	29.44	4.18	0.90	-3.36
This study	MHM05	Cumbria, UK	Dystrophic	May to May	2m^2	0.36 (mean depth)	31.86	3.07	0.48	-3.00
Hanson et al., 2003	Northgate Bog	Wisconsin, USA	Dystrophic	Jul & Aug	0.3ha	1.5 (thermocline)	24.60	3.72	0.34	-3.38
Hanson et al., 2003	Cranberry Bog	Wisconsin, USA	Mesotrophic	Jul & Aug	1.4ha	1.8 (thermocline)	11.50	2.85	1.98	-0.86
Hanson et al., 2003	Trout Bog*	Wisconsin, USA	Dystrophic	Jul & Aug	1.1ha	1.5 (thermocline)	17.00	1.69	2.36	0.67
Hanson et al., 2003	Reddington Bog	Wisconsin, USA	n/a	Jul & Aug	1.2ha	1.5 (thermocline)	23.10	5.28	0.64	-4.64
Hanson et al., 2003	Little Arbor Vitae	Wisconsin, USA	Eutrophic	Jul & Aug	216.1ha	5 (thermocline)	3.20	17.95	23.09	5.15
Lauster et al (2006)	Crystal Bog	Wisconsin, USA	Dystrophic	Summer	0.5ha	0.5 (thermocline)	n/a	2.17	0.85	-1.33
Lauster et al (2006)	Muskellunge	Wisconsin, USA	Eutrophic	Summer	107.7ha	4.7 (thermocline)	n/a	32.13	35.19	-0.33
Lauster et al (2006)	Big Muskellunge	Wisconsin, USA	Mesotrophic	Summer	396.3ha	8 (thermocline)	n/a	3.57	2.66	0.67
Lauster et al (2006)	Sparkling	Wisconsin, USA	Oligotrophic	Summer	64ha	3 (thermocline)	n/a	0.12	0.32	1.67
Klotz (2013)	Timmerman Pond (beaver pond)	New York State, USA	Eutrophic	Jul to Nov May to Jul	8690m^2	0.44 (mean depth)	n/a	12.40	16.10	3.70
Hagerthey et al (2010)	Shallow water Everglades	Florida, US	Various	All year	various	0.43 (mean depth)	19.8	7.04	3.30	-3.74
Cornell and Klarer	Old Woman Creek (Low water levels)	Ohio, USA	n/a	Apr to Oct	n/a	0.62 (mean depth)	n/a	1.61	1.33	-0.28
Christensen et al (2013)	Limestone quarry (highest rates)	Öland, Sweden	Oligotrophic	May to Sep	700 to 3400 m$_2$	0.3 to 0.8 (max depth)	n/a	10.18	10.11	1.41

of dystrophy. Conversely, NEP for the dystrophic Trout Bog was positive at 0.67 g O_2 m^{-2} d^{-1}, although there were unusually high levels of Chlorophyll a in this lake (Hanson et al., 2003). Overall, the MH pools fell at the lower (i.e. more heterotrophic) end of the spectrum of NEP values returned by dystrophic lakes (Table 5.6). Furthermore, dystrophic lakes (characterised by low nutrients and pH but with high levels of organic matter which typically stain the water brown) returned lower (more negative) NEP values compared to waterbodies of other trophic states. For example, the mesotrophic Cranberry Bog returned a mean NEP value of -0.86 g O_2 m^{-2} d^{-1}, whilst the eutrophic Little Arbor Vitae Lake had a positive NEP value of 5.15 g O_2 m^{-2} d^{-1} (Table 5.6). Staehr et al. (2010b) attributed low levels of NEP in a dystrophic lake in Denmark to the high levels of coloured dissolved organic matter present, which was suppressing primary production by attenuating an average of 82% of the available light. Furthermore, a comparative study of 25 lakes in Denmark found that that brown-coloured (i.e. dystrophic) lakes had significantly less irradiance available for photosynthesis in the mixed layer compared to clearer lakes (Staehr et al., 2012a).The dystrophic lakes studied by Lauster et al. (2006) had littoral vegetation comprised of emergent macrophytes and *Sphagnum* mats and the authors theorised that this contributed to the low NEP values as follows; the O_2 produced by emergent macrophytes during photosynthesis was lost to the atmosphere (so its presence was not captured by the probe in the water) and the *Sphagnum* mats, which have been shown to host large colonies of bacteria (Fisher et al., 1998), were potentially fuelling increased rates of respiration in the lake as a whole.

Overall, the MH pools returned some of the lowest NEP values of all the waterbodies listed in Table 5.6 and were therefore greater carbon sources to the atmosphere per unit area. The heterotrophic nature of the MH pools was also reflected in the near-constant sub-saturation of O_2, suggesting that rates of respiration were nearly always in excess of production, thus not allowing concentrations of O_2 to reach equilibrium. This link between O_2 sub-saturation and net heterotrophy (increased R and decreased NEP) has also been noted in other studies (Hanson et al., 2003, Hagerthey et al., 2010, Staehr et al., 2010a).

Studies of terrestrial peatland carbon budgets provide mixed results. For example, a study by Green et al. (Unpublished) undertaken on the Migneint, North Wales, used gas flux chambers to measure fluxes of CH_4 and CO_2 both in and between drainage ditches. Results from two chambers placed 1 m away from the drainage ditches showed that annual net ecosystem exchange (NEE) switched between negative (CO_2 uptake) and positive (CO_2 source) from one year to the next. For the two chambers over three years, four annual figures reported a net CO_2 uptake (the largest uptake was -2164.2 g CO_2 m^{-2} y^{-1}) and two a net CO_2 loss (the largest loss was 253.2 g CO_2 m^{-2} y^{-1}). In contrast, Roulet et al. (2007) undertook a six year study based at Mer Bleue peatland near Ottawa (Canada) and reported that, whilst there was a large inter-annual variation in NEE, every year reported a net carbon uptake, with a mean NEE value of -40.2 (+40.5) g CO_2 m^{-2} y^{-1}. In my study, the NEP values were consistently negative (in this case indicating carbon losses). For example, the monthly pools median NEP values ranged from -0.99 to -1.69 g CO_2 m^{-2} d^{-1} and the summer pools single NEP values from -0.30 to -1.78 g CO_2 m^{-2} d^{-1}. Scaling up the lowest and highest of these figures by 365 to represent an annual budget provides carbon losses of between 109.5 and 649.7 g CO_2 m^{-2} y^{-1}. Although this is a very rough calculation lacking any consideration of seasonal dynamics, it suggests that pools may release more CO_2 to the atmosphere per unit area than the surrounding peat soils/vegetation.

As the DO change technique does not account for CO_2 or methane (CH_4) release due to anaerobic respiration or oxidation of organic matter by, for example, nitrate (neither of which consume O_2), it is probable that overall R rates have been underestimated (Torgersen and Branco, 2007, Staehr et al., 2010a). Furthermore, using this technique, R is assumed to be constant through the diel period when, in reality, it is likely that day-time R exceeds night-time R due mainly to increased temperatures but also possibly driven by the more labile DOC exuded during photosynthesis (Tobias et al., 2007). However, although this would under-estimate the magnitude of R and GPP, the value of NEP would remain unchanged as estimates of R and GPP would both change in proportion (Cole et al., 2000, Staehr et al., 2010a). Conversely, R might be overestimated due to the increased chemical oxygen demand caused by bacterial processing of organic matter; this produces reduced chemical species (e.g. Fe^{+2}, Mn^{+2} etc.) which are subsequently oxidised using O_2 (Torgersen and Branco, 2007).

5.4.2 Low GPP

The trend towards heterotrophy in the MH pools is partly attributable to the very low rates of GPP. This could be due to the young age of the pools; at the time of the first sampling effort in May 2013 the pools had been in existence for only five months, and would have been potentially frozen for much of the first three of those. Thus, there was limited time for submerged vegetation / algal communities to become established, whereas bacterial communities would already have been present in the sediments. Indeed, the trend towards higher GPP levels at the end of the study period in the monthly pools, even though PAR levels were very low, suggests that GPP might have been increasing with pool age. Another contributing factor to the low rates of GPP would have been the brown staining of the pool waters, caused by inputs of dissolved organic matter (DOM) from the surrounding peat. Coloured DOM (CDOM) was shown to attenuate an average of 82% of the light entering dystrophic Gribsø Lake in Sweden (Staehr et al., 2010b), thus severely limiting the potential for photosynthesis in the lower water column and leading to net heterotrophy. Indeed, the impact of CDOM on light attenuation has recently been mooted as being a more important limiting factor on autotrophic production than lack of nutrients (Karlsson et al., 2009).

5.4.3 DOC

Rates of R were strongly positively related to concentrations of DOC for all pools combined and the monthly pools, which supports the second part of H_1 and is in agreement with findings from other studies (Hanson et al., 2003, Staehr et al., 2010b, Staehr et al., 2012a). All the MH pools displayed DOC >10 mg L^{-1}, which Hanson et al. (2003) identified as a threshold above which most lakes were heterotrophic. Indeed, the MH pools displayed considerably higher levels of DOC than all the other lakes listed in Table 5.6 and returned some of the lowest NEP values. However, the third part of H_1 (that there would be a significant negative relationship between NEP and DOC) was not supported by the analysis. This was probably because the relationship between GPP and DOC was more strongly positive than that between R and DOC, whereas Hanson et al. (2003), who found a negative correlation between NEP and DOC, found no relationship between GPP and DOC. Although photosynthesis does not require DOC as an input, it may be that primary producers are exuding DOC, thus increased GPP could be driving increased concentrations of DOC. Indeed, a positive relationship between GPP and DOC was also reported by Staehr et al. (2010b) and Staehr et al. (2012a). However in both of these cases, unlike the MH pools, the relationship was stronger for R and DOC, leading to a significantly negative relationship between NEP and DOC. In contrast, Hagerthey et al. (2010) found that DOC in the Florida Everglades was negatively related to R, GPP and NAP (net aquatic production). The authors inferred from their results, along with other unpublished data, that DOC was unlikely to be an important driver of R which they theorised was associated mainly with the bottom sediments rather than the water column. In this case, the authors believed that bacteria in the sediments mainly remineralised detrital-flocculent organic matter (floc), an unconsolidated layer of decomposing plant matter and periphyton overlying the peaty bottom, in preference to DOC. Floc has been shown to decompose more quickly than the underlying peat and to exhibit C turnover in the order of days rather than the years seen for peat soils. The presence or absence of such a layer was not established for the MH pools, although large amounts of suspended detritus have been found in sieved water samples from the site (pers.comm Lee Brown) and future studies might consider investigating this as a possible driver of R.

Freshwater metabolism studies which attempt to characterise DOC using $SUVA_{254}$ and E4/E6 values are rare. One study which looked at DOC quality in a Quebec (Canada) peatland restored ten years previously, reported that $SUVA_{254}$ was significantly lower (more bioavailable) at sites with higher rates of photosynthesis (Strack et al., 2015). However, in this case, the authors were not suggesting that low $SUVA_{254}$ was driving photosynthesis; rather that photosynthesis was lowering $SUVA_{254}$ by augmenting the supply of fresh leaf litter which decomposed quickly and resulted in a more labile carbon source. This may help to explain the only significant relationship found in the analysis of the potential aromaticity of the DOC at Moor House (the E4/E6 and $SUVA_{254}$ datasets); a positive relationship between GPP in the summer pools and E4/E6 (Table 5.5). Although there is no apparent reason why GPP should increase as DOC becomes less aromatic (more bioavailable), perhaps the increased GPP leads to more bioavailable DOC. Overall, however, there was no evidence to support the final part of H_1, namely that lower $SUVA_{254}$ or higher E4/E6 values resulted in increased rates of R. Indeed, the relationship between E4/E6 and R, whilst not significant or linear, suggested that R was actually lowest at high E4/E6 values.

5.4.4 Temperature

As hypothesised in H_2, rates of R and GPP were both positively related to increased temperatures, at least for the whole dataset combined. However, the relationship between R and temperature was not significant for the monthly pools alone and this was probably due to the removal of the high rates found in the summer pools at high temperatures, along with some unexpectedly high rates of R found at low temperatures in winter. A study of stream metabolism at Moor House also found some high values of R at low temperatures (Aspray, 2012). One potential driver of high R at low temperatures could be the relatively high ratios of E4/E6 seen in December, even though there was no significant relationship between E4/E6 and R overall (Table 5.5). Indeed, the E4/E6 data suggest a trend towards the DOC being more bioavailable in winter and spring, even though it is present in lower concentrations. It is unclear why this would be the case, as any fresh organic input from surrounding vegetation (e.g. autumnal leaf-fall) would have been around for at least a couple of months, giving the microbes plenty of time to use up the bioavailable fraction. However, the high rates of R in winter and the potential link to more bioavailable DOC merits further investigation.

Another finding was that the significant relationship between R and water temperature was weaker than that for GPP and temperature for all pools combined, and was not significant for the monthly or summer pools. Therefore, R did not scale more with temperature and there was not a corresponding decrease in NEP, thus not supporting the second part of H_2. This pattern was also found by Staehr et al. (2010b) when reporting Pearson correlation coefficients for a dystrophic lake in Sweden. Furthermore, at all four sites sampled by Cornell and Klarer (2008) at Lake Eerie, USA, temperature had no effect on the GPP:R ratio, even though at two of the sites both R and GPP were positively correlated with temperature. One possible reason for this departure from metabolic theory of ecology predictions could be the low levels of nutrients found in dystrophic waterbodies which may act as a limiting factor on both metabolic processes. However, marine studies have reported that bacterial production in warm, oligotrophic conditions is more strongly nutrient-limited than bacterial respiration (López-Urrutia and Morán, 2007), leading Yvon-Durocher et al. (2010b) to theorise that freshwater R would be less impacted by nutrient limitation than freshwater GPP. Another reason for the departure from the metabolic theory of ecology predictions could be that, unlike in the mesocosms set up by Yvon-Durocher et al. (2010b), the Moor House sampling was not designed with warmed and control pools sampled at the same time of year, so other elements related to seasonality (e.g. water chemistry, water levels, microbial communities, etc.) might act as confounding factors. Future field-based work to further inform the relationship between metabolism and temperature could include experimental manipulation of nutrient levels and also artificial warming of pools to allow for comparisons between control and warmed treatments.

5.4.5 Nutrients

Both TN and TP displayed significant, positive relationships with R and GPP, for all pools combined and for the monthly pools, thus supporting the final part of H_2.

However, the very low levels probably contributed to the low GPP rates and overall heterotrophy. The positive relationship between the two metabolic rates and TP reflects the findings of Hanson et al. (2003), but these authors also reported a positive correlation between TP and NEP which was absent in this study. In fact, for the monthly pools there was a significant negative relationship between NEP and TP, because the positive relationship between R and TP was stronger than that for GPP and TP. Staehr et al. (2012a) also found that volumetric rates of GPP and R significantly increased along with concentrations of TP whereas NEP decreased. In contrast, Hagerthey et al. (2010) found that Total Kjeldahl Nitrogen (TKN) and TP were negatively related to R, GPP and NAP (net aquatic production) in the Florida Everglades, although the relationships were poor (low r values).

5.4.6 Water depth

All the Moor House pools were shallow, with mean depths < 50cm. However, the relationships between mean R and NEP and water depth were significant and strong, supporting H_3. As the summer pools also tended to be shallower, it is possible that the higher water temperatures in summer confounded the depth analysis, although this theory is negated somewhat by the strong relationship between R and water depth found for the summer pools alone. Also, the relationships for the monthly pools alone were verging on statistical significance, especially for NEP and depth. It seems likely, therefore, that heterotrophy in the Moor House pools could have been partly driven by the shallow water levels which increased the amount of substrate available for microbial processing and respiration relative to the volume of water (Torgersen and Branco, 2008). Furthermore, shallower waters are less prone to seasonal stratification, meaning that diurnal mixing events can facilitate the transport of oxygen-depleted waters / sediment-derived CO_2 from the pool bottom into the upper reaches (Holgerson, 2015). The shallow depth effectively turns the whole waterbody into a littoral rather than pelagic environment and studies looking at larger lakes have reported that littoral (i.e. shallower) areas of the lake contribute to metabolism more than do pelagic zones (Cole et al., 2000, Lauster et al., 2006). Lauster et al. (2006) also found that the *Sphagnum* mats surrounding dystrophic lakes decreased NEP by the presence of increased microbial activity. Staehr et al. (2012a) reported that volumetric rates of R and GPP both decreased significantly along with increasing lake depth, although at Moor House the relationship between GPP and water depth was not significant for any of the three datasets.

High R and low NEP values, comparable to those at Moor House, were found in the shallow peatland everglades in Florida, USA (Hagerthey et al., 2010). The everglade pools were similar to the MH pools in that they were shallow, with a mean depth of 0.43m, and exhibited relatively high levels of DOC, although at 19.8 mg L^{-1} levels were still substantially lower than those at MH (Table 5.6). The shallow water levels could have been helping to fuel high rates of R although it is also likely that the high mean water temperature (all readings >20°C) was a contributing factor. The authors, however, believed the prevalent heterotrophy found in their study was caused mainly by the vegetation present; the waters were dominated by emergent and floating-leaved macrophytes which vented the majority of oxygen produced during photosynthesis into the atmosphere, whilst underwater respiration, especially from the layer of floc on the pool bottoms, depleted the O_2 concentrations in the water column. As the vegetation communities in the Moor House pools were, as yet, not well established, this is an unlikely driver of heterotrophy there.

One apparent anomaly in the dataset occurred when comparing the monthly and summer pools sampled in August 2013. For example, of the four monthly pools, three returned negative GPP values even at the 1hr sampling frequency, and were assumed to be zero for the purposes of statistical analysis. These three pools were sampled on the same date as MHM13 (20th August, 2013) which reported a much higher GPP value of 5.76 g O_2 m^{-3} d^{-1}, and the two summer pools sampled on 22nd August (MHM14 and 15) were even higher (5.92 and 16.42 g O_2 m^{-3} d^{-1} respectively). The rates of R in MHM13 and 15 were also high compared to three of the monthly August pools. The pools all displayed similar water chemistry and were also mainly open-water; the main difference was the slightly smaller dimensions of MHM13, 14 and 15 and their location (at the bottom of the hillslope as opposed to the top). It is therefore possible that the increased metabolism estimates in the summer pools sampled in late August was due to their smaller size. Also, their location at the bottom of the hillslope might have allowed the peat there to remain ‘wetter’ in dry conditions, as water from upslope pooled at the bottom, which may have resulted in more stable water levels and thus more permanent and / or diverse microbial communities, driving rates of both R and GPP.

5.4.7 Diel DO Patterns and negative GPP values

The heterotrophic nature of the Moor House pools was reflected in the majority of diel DO patterns, which rarely produced a diel curve to mirror PAR. Instead, the more common pattern of minimal DO change throughout the day suggested that photosynthesis was rarely reaching a rate which exceeded that of respiration. One of the dystrophic lakes studied by Hanson et al. (2003), the dystrophic and heterotrophic Northgate Lake (Table 5.6) also seemed to exhibit relatively constant DO levels throughout daylight hours. Similarly, the oligotrophic Sparkling Lake sampled by Lauster et al. (2006) showed little variation in DO levels with diel DO excursions of <1 mg L^{-1}, even though this lake was autotrophic.

One interesting feature of many of the diel DO patterns was the existence of an evening ‘spike’ in DO levels. Often the spike occurred close to sunset, with no obvious biological reason (i.e. no correspondence with increased PAR). Other studies have also reported night-time rises in levels of DO and attributed them to physical rather than biological processes. For example, Hanson et al. (2008) found night-time increases in DO in Crystal Bog and hypothesised that they were caused by a pocket of DO rich water moving past the sensor, either vertically or horizontally. In larger lakes, water with higher levels of DO might originate in the more metabolically active littoral zone before moving out (e.g. via advection) to the pelagic area (Lauster et al., 2006). The horizontal movement theory was also posited by Gelda and Effler (2002) to account for the several sudden instances of increased DO concentrations during dark hours in their study of the eutrophic Onondaga Lake, New York (USA). It therefore seems likely that the late evening / night-time rises in DO levels seen in the MH pools might be caused by mixing or advective events which cause pockets of more oxygenated water to pass the sensor.

One consequence of the evening spikes in DO was the ‘warping’ of estimations of R (and therefore also GPP), as some NEP_{hr} values during dark hours were positive when they should have been negative (photosynthesis does not happen in the dark so O_2 levels should fall, not rise), leading to negative R estimations. For systems to be suitable for the open-water DO technique rates of both R and GPP should be greater than zero and GPP should be greater than NEP. These conditions may not be met when physical processes override biological oxygen dynamics, for example when pockets of water moving past the sensor are heterogeneous with regards to O_2 concentrations (Caffrey, 2003), and this outcome is not rare in lake metabolism studies. For example, Cornell and Klarer (2008) found that on average, only 46% to 75% of the data met their screening criteria (HRR>0, GPP>NP). Gelda and Effler (2002) found that community respiration estimates were negative on ten days due to night-time DO increases, and on six of these days this resulted in corresponding anomalous negative GPP estimates. Hanson et al. (2005) reported that, in dystrophic and eutrophic lakes, 50-80% of metabolism estimates were classified as atypical, suggesting that physicochemical processes were often confusing the biologically-controlled diel DO signals. As the Moor House pools are so small, it seems unlikely that horizontal movement of water would be responsible for the evening spikes in DO. More likely would be a vertical mixing event, as daytime microstratification in the mixed layer breaks down at night (Coloso et al., 2011).

5.4.8 Conclusions

The drain-blocked pools at Moor House were consistently heterotrophic, due in part to the very low rates of GPP. When compared to other studies, the NEP estimates were at the low end of the spectrum, indicating that the MH pools are stronger sources of CO_2 to the atmosphere per unit area than other freshwater systems. Also, comparisons to studies of the carbon budgets of terrestrial peatlands suggest that pools act as hotspots for CO_2 release in the wider peatland landscape. Furthermore, the actual level of heterotrophy may be even greater than reported due to methodological constraints which precluded the estimation of anaerobic R.

The main drivers of increased R in the pools appeared to be concentrations of DOC (a positive relationship) and water depth (a negative relationship; shallow pools displayed higher levels of R). As high concentrations of DOC are inherent to peatland settings and therefore difficult to control, it is suggested that the creation of deeper pools (as opposed to shallower ones) may help to reduce any extra carbon fluxes to the atmosphere caused by drain-blocking. Increased concentrations of TN and TP fuelled both R and GPP, but levels were so low that they were probably, ultimately, limiting factors to metabolism. GPP was linked strongly to water temperature and rates may also increase with time as vegetation and algal communities become better established in the pools. The instance of high rates of R at low temperatures in December was an unexpected finding which warrants further research, especially in relation to the possible increased bioavailability of DOC as suggested by high E4/E6 ratios. Also worthy of further investigation is the occurrence of evening DO spikes which, in many cases, disrupted the biological signals and contributed to negative R and GPP values and also, possibly, to the underestimation of daytime R. For future studies of the metabolism of small, peatland pools it is recommended that trials be carried out prior to sampling to establish the DO diel patterns. A large number of evening DO spikes may mean that the pools are not suitable for the open-water DO technique and that other methods should be considered.

Chapter 6: The thermal stratification of peatland pools and its implications for biogeochemical processes

6.1 Introduction

The seasonal thermal stratification of lentic waterbodies is a well-established phenomenon (Hutchinson and Löffler, 1956). Stratification is driven by changes in water temperature at different depths which causes corresponding changes in the water density; as water cools it becomes denser until it reaches a density maximum at 4°C. The three layers in a stratified lake are (1) the epilimnion (or mixed layer), where temperatures are highest and the water is less dense so it 'floats', (2) the metalimnion (or theromocline), a middle layer, usually thin, in which the temperature changes rapidly, and (3) the hypolimnion, the dense, bottom layer. The usual pattern for a temperate lake is to fully mix twice a year (a dimictic lake) in spring and autumn, when the lake is approximately the same temperature throughout the water column. In summer and winter temperate lakes are usually stratified. In summer, the warmer mixed layer is separated from the bottom cooler layer, although extreme weather events such as heavy rainfall or high winds may lead to isolated mixing events. In winter the reverse may be true; the surface may be covered by ice and the waters immediately below can be colder than the denser water (4°C) which sinks to the lake bottom.

Lake stratification has consequences for the biogeochemistry (e.g. concentrations of dissolved gases and nutrients) of the waterbody. For example, during summer stratification, any DO produced by photosynthesis in the epilimnion cannot diffuse down into the hypolimnion, where the existing oxygen supply is gradually consumed by bacteria feeding on the organic matter which continues to sink down from the surface waters (Macan, 1974). In productive lakes with a shallow hypolimnion this leads to anoxia in the hypolimnion which can cause fish fatalities, and the chemistry of the bottom sediments is altered, leading to the release of phosphorous into the hypolimnion (Nurnberg and Peters, 1984, Søndergaard et al., 2003). When this build-up of phosphorus is released into the upper layers, by storms or autumn mixing, it can lead to algal blooms. Diurnal stratification has also been shown to restrict the diffusion of methane (CH_4) through the water column (Ford et al., 2002) and to impact the dynamics of chromophoric dissolved organic matter (CDOM) fluorescence, which can be used a proxy for the quantity or quality of DOM / DOC (Watras et al., 2015).

Shallow lakes and ponds, however, have previously been assumed to be vertically well-mixed, and facilities such as stormwater and aquaculture ponds have been purposefully designed as shallow systems to avoid the problems, such as oxygen depletion, caused by stratification (Persson, 2000, McEnroe et al., 2013). However, although shallow systems avoid seasonal stratification, they have been shown to experience a diurnal, rather than an annual, thermal stratification cycle (Ganf, 1974, Van Buren et al., 2000, Condie and Webster, 2002). This diurnal cycle happens because a very shallow surface layer is heated during the day but is cooled at night to the point where it overturns and mixes with the cooler water below. This diurnal pattern has important implications for both the biota and the biogeochemistry of the pond. Indeed Macan (1973) noted that such diurnal stratification '…may be one of the most important phenomena affecting life in the pond.' It has also been reported that deeper, thermally stratified lakes experience microstratification in the mixed layer over the course of a day and that this has implications for metabolism estimates (Coloso et al., 2011).

The diel oxygen change technique is used in many lake studies to estimate rates of respiration (R) and gross primary production (GPP) and thereby the net ecosystem production (NEP) value of a waterbody (see Chapter 5 of this thesis for more details). DO probes are typically deployed in the surface waters (0.5 to 1 m) and are assumed to measure levels of DO throughout the stable, upper mixed layer. The depth of the mixed layer (Z_{mix}) is usually obtained from regular (e.g. bi-weekly) temperature profiles and is defined by most studies as the depth at which temperature changes by at least 1°C over a given unit of depth (e.g. 0.5 m) (Staehr et al., 2010a, Coloso et al., 2011). In lakes with microstratification, however, Z_{mix} may change throughout the course of a day and temporary thermal boundaries may prevent the probe from detecting oxygen changes throughout the mixed layer. Microstratification may also impact on other processes, such as light, nutrient levels and atmospheric gas exchange, which help to drive metabolism (Coloso et al., 2011). Furthermore, the depth of the mixed layer (Z_{mix}) is used in metabolism calculations to convert the volumetric rate of DO change into an areal rate so that atmospheric gas exchange (which is essentially an areal process) can be accounted for. However, if temporary stratification prevents atmospheric O_2 from reaching the probe (i.e. it is located below the stratified surface layer), but gas exchange is still being accounted for, then this will lead to errors in the metabolism estimates. Therefore, Z_{mix} is a vital parameter in metabolism calculations (Coloso et al., 2011).

Chapter 5 of this thesis calculated the metabolism of a set of drain-blocked pools at Moor House in northern England, and assumed that Z_{mix} equalled the average depth of the pools, which is standard practice for shallow lakes and pools (Staehr et al., 2010a). However, the evening ‘spike’ in DO levels found in many of the pools suggested that a pocket of oxygen-rich water was regularly moving past the sensor in the evening. One cause of this could be a vertical mixing event caused by changes in thermal stratification during the diurnal cycle. In some cases the DO spikes heavily influenced the metabolism estimates for the pool because DO levels after dark increased, rather than decreased, which led to negative R values (see Chapter 5 for more details). Furthermore, if diurnal thermal stratification is found to be severe in the pools, then using the average pool depth as the value of Z_{mix} might not be a valid assumption (i.e. the vertical temperature profile might change by >1 °C over the measured mean depth). If this is the case, it is possible that temperature gradients would need to be integrated into the metabolism calculations to provide more realistic and fluid values of Z_{mix}, rather than one static value based on depth measurements alone (Coloso et al., 2011).

The overall aims of this chapter were three-fold; (1) to further investigate the evening DO spike in the Moor House pools by obtaining vertical temperature and DO profiles, and to compare these to profiles from other peatland pools, (2) to ascertain how any diurnal thermal stratification impacted upon metabolism estimates, and (3) to consider the wider implications of diurnal thermal stratification for peatland biogeochemistry. It was hypothesised that:

H_1 – pools would stratify thermally, at least on warmer days, and experience vertical mixing when temperatures cooled (usually in the evenings).

H_2 – thermal stratification would result in different metabolism estimates from DO probes placed at different depths as thermal boundaries restrict the movement of gases throughout the water column.

6.2 Methodology

6.2.1 *Study sites*

Pools at three sites were sampled (Table 6.1). These were i) Moor House, northern England; ii) Forsinard, northern Scotland and iii) Abisko, northern Sweden. The Moor House site is described in Chapter 5 and is the location of the original metabolism study where the DO spikes were first observed. The Cross Lochs pool complex in Forsinard is situated in the Flow Country of northern Scotland which is the largest blanket peatland in Europe (c. 4000 km^2) and lies within the RSPB Forsinard reserve. The pool vegetation is broadly limited to aquatic *Sphagna* (*S. cuspidatum* and *S. denticulatum*), *Eriophorum angustifollium*, and bog bean (*Menyanthes trifoliata*). Local terrestrial vegetation comprises a mosaic of typical blanket bog species, including *Sphagnum* mosses, (*S. papillosum, S. tenellum S. capillifolium*) sedges (*E. angustifollium, Eriophorum. vaginatum, Trichophorum cespitosum*), ericacous shrubs (*Calluna vulgaris*, *Erica tetralix*), sundews (*Drosera rotundifolia, Drosera intermedia and Drosera anglica*), bog asphodel (*Narthecium ossifragum*) and the locally common liverwort (*Pluerozia purpurea*). Railway bog, near the town of Abisko, lies within the Arctic Circle in northern Sweden and is a palsa mire surrounded by poor arctic fen. The vegetation of the fen is dominated by *E. angustifolium*. The palsa itself is relatively dry and cracked but contains pools, some deep enough to remain open-water all year round, except during winter freezing. The palsa vegetation is comprised mainly of *Rubus chamaemorus*, Labrador tea (genus *Ledum*), *Betula nana*, *Sphagnum fuscum*, *Andromeda polifolia* and *Vaccinium* spp.; also present are some very dry hummocks with peat surfaces covered by lichen. Pool vegetation is dominated by the aquatic *Sphagna S. cuspidatum* and *S. linbergii* and *E. angustifolium*. Peat cores taken during the sampling period showed the peat depth to range between 20 and >130cm, with an underlying strata that varied between lake sediment, rock, permafrost and grey silt with clay.

Table 6.1. Study site descriptions. The weather data for Moor House cover 2000 to 2012 and for Forsinard and Abisko 2000 to 2014. The 2015 Forsinard dataset was used for depth profiles only, not metabolism estimates, due to the datasets not covering a complete diel period.

Site Name	Country	Lat Long	Pool Type	Sampling Dates	Altitude (m)	Mean Annual Precipitation (mm)	Mean monthly temp (°C)
Moor House	UK (England)	54° 41' 27"N 2° 22' 56"W	1 x Blocked	28th May to 1st June, 2014	572	2001	6.28
Forsinard	UK (Scotland)	58° 22' 21"N 3° 57' 32"W	2 x Natural	26th June, 2014	211	940	7.01
Forsinard	UK (Scotland)	58° 22' 21"N 3° 57' 32"W	2 x Natural 2 x Blocked	23rd to 26th June, 2015	211	940	7.01
Abisko	Sweden	68° 5' 12"N 19° 49' 50"E	3 x Natural	June, 2015	490	339	0.44

6.2.2 Sampling methodology

The sampling methods (probe deployment and water sample collection and analysis) were as outlined in Chapter 5, apart from the vertical positioning of the probes. At Moor House and Forsinard (2014), five probes were established at 10 cm increments (10 to 50 cm) and at Abisko, three probes were left at 10, 30 and 50 cm depths. At Moor House, five consecutive diel datasets (28th May to 1st June, 2014) were obtained from one drain-blocked pool (MHM01). At Forsinard one diel dataset (26th June, 2014) was obtained from two natural pools (FORS01 and FORS02) and at Abisko, two diel datasets (5th and 6th August, 2014) were obtained for each of three natural pools (ABSK01, ABSK02 and ABSK03). Furthermore, in 2015, temperature and depth profiles were obtained from four pools at Forsinard; again from FORS01 and FORS02, where the probes were again positioned at 10 cm increments from 10 to 50 cm, and also from two drain-blocked pools (FORS03 and FORS04) which were instrumented only at 10, 20 and 30 cm due to their shallow depth. However, this 2015 dataset did not cover one full diel period (i.e. midnight to midnight) but was instead collected from midday to midday. Thus, although the 2015 depth profiles are included for comparative purposes, the data could not be subjected to metabolism calculations using the diel DO change technique.

6.2.3 Data analysis

Metabolism at the different depths was calculated using the methodology outlined in Chapter 5. A further set of analysis was then carried out for MHM01, when metabolism was estimated at depths of 10 and 20 cm using both the fixed Z_{mix} value (mean depth) and a fluid Z_{mix} value, when Z_{mix} was defined as the depth at which water temperature increased by >1 °C per increment (10 cm). As sensors were not placed at 0 cm, the temperature differential between 0 and 10 cm could not be calculated, therefore the shallowest possible Z_{mix} value was 20 cm. However, it is likely that Z_{mix} would have been shallower than 20 cm for at least some of the study period.

6.3 Results

6.3.1 Environmental characteristics

FORS01 had by far the largest surface area of all the pools (850 m^2) and the drain-blocked pools (MHM01, FORS03 and FORS04) were the smallest (2 to 4 m^2). The remaining pools ranged from 13 m^2 to 32 m^2 (Table 6.2). Mean depth was similar for all pools except ABSK01, which had a mean depth of only 18 cm (although there was a deep section at one end which allowed instrumentation of the pool to 50 cm). Water chemistry was most variable in the Abisko pools where, for example, DOC ranged from 35.6 mg L^{-1} (ABSK03) to 114.4 mg L^{-1} (ABSK01) and EC from 40.1 µs cm^{-1} (ABSK03) to

129.0 µs cm^{-1} (ABSK02). Nutrient levels were very low across all the pools, although TN was slightly elevated in ABSK01 and ABSK02 (Table 6.2). The DOC concentrations in the two Forsinard blocked pools (FORS03 and FORS04) were substantially higher than for the natural pools (FORS01 and FORS02).

Table 6.2. Environmental variables (descriptive statistics) for the sampled pools. Data for FORS01 and FORS02 are from the 2014 sampling effort and those for FORS03 and FORS04 are from 2015.

Pool	MHM01	FORS01	FORS02	FORS03	FORS04	ABSK01	ABSK02	ABSK03
Surface Area (m^2)	2	850	32	4	4	16	31	13
Mean Depth (cm)	43	50	40	30	30	18	49	35
Vegetation cover (%)	10%	<5%	<5%	80	60	<5%	100	20
EC (µs cm^{-1})	30.30	65.02	68.08	84.27	79.58	92.20	129.00	40.10
pH	4.18	4.62	4.57	4.26	4.41	3.85	3.93	5.86
TN (mg L^{-1})	1.23	0.41	0.40	n/a	n/a	3.90	3.46	1.28
TP (mg L^{-1})	0.031	0.003	0.004	n/a	n/a	0.224	0.095	0.034
DOC (mg L^{-1})	36.77	8.73	10.25	24.4	25.5	114.35	94.04	35.62
Abs 254.0 (nm m^{-1})	134.12	22.69	22.52	n/a	n/a	343.50	424.00	152.03
$SUVA_{254}$ (L mg^{-1} m^{-1})	3.65	2.60	2.20	n/a	n/a	3.00	4.51	4.27
E4/E6	8.65	7.00	3.97	n/a	n/a	6.10	5.31	4.60

6.3.2 Temperature and DO profiles

The longest consecutive time series dataset was collected at Moor House and allowed for comparison between warm and cooler days (Figure 6.1). On cooler days the temperature variation both in and between different strata was much less marked. For example, on 29th May the temperature at 10 cm ranged from 7.6 to 8.6 °C, and the biggest temperature difference between 10 cm and 50 cm at any point during the day was 0.4 °C (between 17:00 and 18:00). Indeed, for most of 29th May (up to 12:00 and from 21:30 onwards), the temperature at 50 cm depth was recorded as being up to 0.2

°C warmer than at 10 cm depth (although it must be noted that the probes are accurate to ± 0.3° C). However, on warmer days, the temperature at 10 cm depth varied widely; on 1st June the temperature at 10 cm depth ranged from 9.2 to 18.5 ° C and the maximum difference between temperature at 10 and 50 cm depths was also much larger, i.e. at 16:30 the difference was 9.1 °C, ranging from 9.4 °C at 50 cm to 18.5 °C at 10 cm (Figure 6.1a).

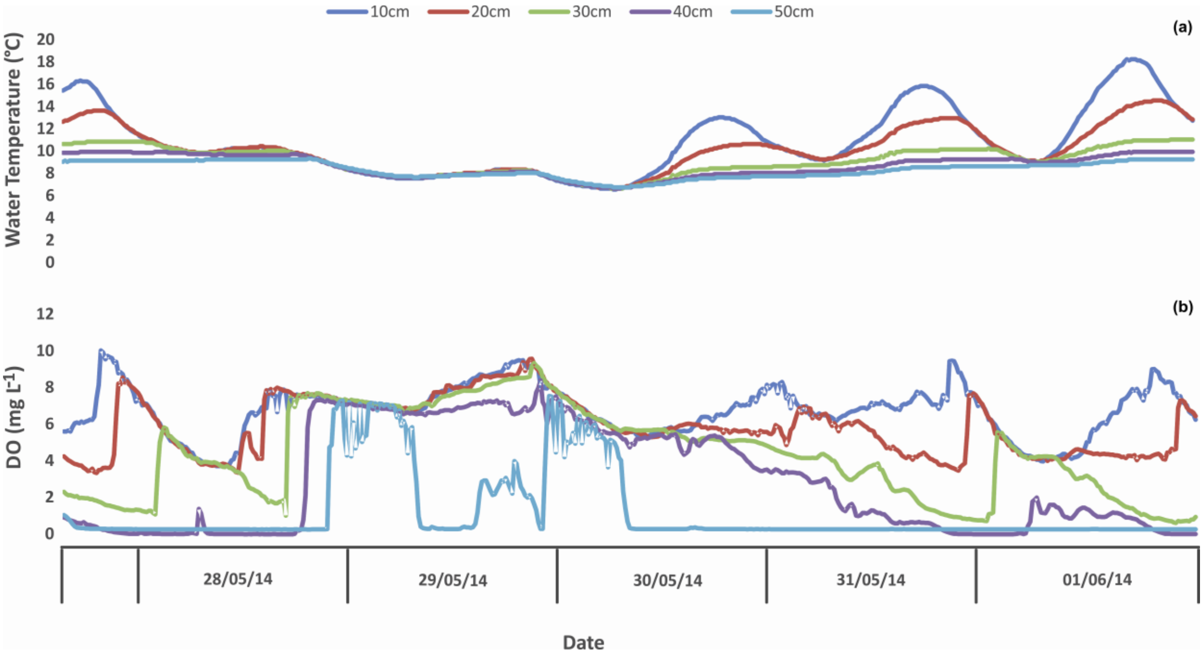

Figure 6.1. Water temperature and DO profiles for Moor House 2014 (a) water temperature and (b) DO for MHM01. Data obtained from 27th May to 1st June, 2014.

The corresponding DO profile at Moor House showed that on days with little thermal stratification (e.g. 28th and 29th May), there was much more mixing of DO throughout the water column whereas, on warmer days, levels of DO were more stratified along with water temperature (Figure 6.1b). For example, concentrations of DO at 50 cm depth remained consistently very low (0.33 mg L^{-1}) throughout most of the sampling period when the surface and bottom temperatures failed to mix at night (e.g. overnight 30th – 31st May). In contrast, DO concentrations at 50 cm depth rose sharply when temperatures in the upper layers merged towards the end of the day on both 28th and 29th May. The early evening spike in DO reported in chapter five was present most notably on the evenings of 27th and 31st May and 1st June, when diurnal thermal stratification had been most marked, and corresponded to a cooling of the surface waters. The spike appeared first in the upper layer (10 cm depth) and was then replicated throughout the strata at 20, 30 and 40 cm depths. The time intervals between the spikes at different depths were: on the evening of 27th May - 10 cm (19:00), 20 cm (21:00), 30 cm (02:00) and 40 cm (06:30); then on the evening on 31st May - 10 cm (21:00), 20 cm (23:00), 30 cm (02:00) and 40 cm (06:00). A similar pattern, but with much smaller spikes in the upper layers and a large spike at 50 cm depth, was apparent on the evening of 29th June when diurnal thermal stratification had not taken place. The pattern of spikes was not present on the evening on 30th May, when diurnal thermal stratification had occurred, with the only spike occurring at 20 cm (Figure 6.1b).

The temperature and depth profiles at Forsinard in 2014 showed much less variation than those at Moor House (Figure 6.2). On 26th June the temperature at 10 cm depth in FORS01 ranged from 14.6 to 17.2 °C and there was very little variation with depth, with temperatures at 50 cm depth nearly always within 0.1 °C of those at 10 cm depth (Figure 6.2a). There was however, evidence of a little more variation both at and between depths on the previous day (25th June) with the temperature at 10 cm depth reaching a peak of 20.5 °C at 17:30, when the corresponding temperature at 50 cm depth was 19 °C. On 26th June the temperature in FORS02 at 10 cm depth ranged from 13.2 to 17.1 °C and, as with FORS01, temperatures at 50 cm depth were very similar although with slightly more variation between the two depths (Figure 6.2b). For example, the temperature differential between 10 and 50 cm depths reached 1.9 °C at 15:20, when it was 17.1 °C at 10 cm and 15.2 °C at 50cm. Again, there was evidence of more differentiation on the previous afternoon and evening, with the temperature at 10 cm depth reaching a high of 22.2 °C when the temperature at 50 cm depth was 17.8 °C (Figure 6.2b).

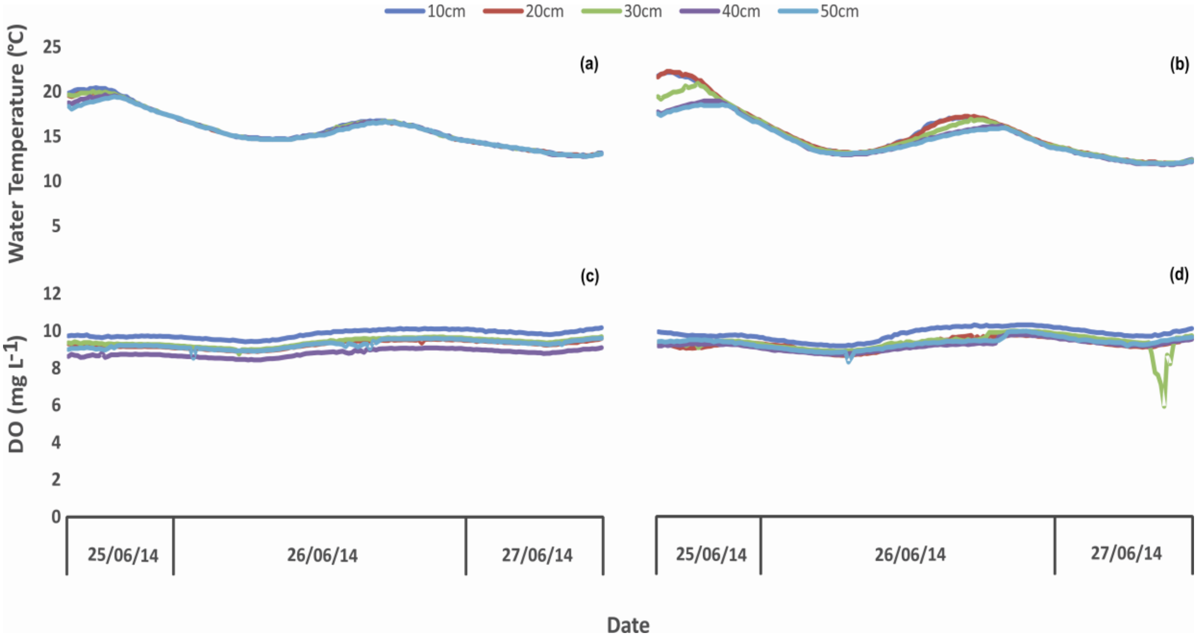

Figure 6.2. Water temperature and DO profiles for Forsinard 2014 (a) water temperature and (c) DO for FORS01, and (b) water temperature and (d) DO for FORS02. Data obtained from 25th June to 27th June, 2014.

The corresponding DO profiles at Forsinard showed very little variation both in and between strata. In FORS01 the DO concentrations at 10 cm depth never dropped below 9.4 mg L^{-1} and reached a maximum of 10.19 mg L^{-1} (Figure 6.2c). The DO readings in FORS01 at 50 cm depth were almost always < 1 mg L^{-1} lower than those at 10 cm depth and, whilst the DO concentrations at 40 cm depth were slightly lower than those at 50 cm depth, they were still always ~ 1 mg L^{-1} lower than those at 10 cm depth. The DO profile in FORS02 was very similar, with concentrations at 10 cm depth ranging from 9.21 to 10.35 mg L^{-1} (Figure 6.2d). The DO concentrations at 40 and 50 cm depth were very similar to each other and always <1 mg L^{-1} lower than those at 10 cm depth. The only anomaly in what were otherwise very smooth DO concentrations, was found in FORS02 at 30 cm depth on the morning of 27th June 2014, when concentrations dropped from 9.40 mg L^{-1} at 07:35 to 5.96 mg L^{-1} by 08:50, and had risen back to 9.27 mg L^{-1} by 09:30 (Figure 6.2d). No DO evening spikes were present at any depth in either FORS01 or FORS02 (Figures 6.2c, 2d).

The Forsinard 2015 data showed very similar results to 2014 for the two natural pools (FORS01 and FORS02) with water temperature virtually identical at all depths (Figures 6.3a, 3b). Levels of DO were also similar to 2014, with very little variation either at or between the depths, although this time the concentrations at 10 cm depth were approximately 1.5 to 2.5 mg L^{-1} higher than at any of the other depths, which in turn were almost identical to each other (Figures 6.3c, 3d). In contrast, the profiles obtained from two drain-blocked pools (FORS03 and FORS04) showed more marked variation in temperature and, especially, in concentrations of DO (Figures 6.3e to 3h). For example, in FORS03, the maximum temperature difference between 10 and 30 cm depth was 3.5 °C at 17:45 on 25th June, when the temperature at 10 cm depth was 14.7 °C and that at 50 cm depth was 11.2 °C (Figure 6.3e). Concentrations of DO at 50 cm depth in FORS03 were very low and bottomed out at 0.55 mg L^{-1} for most of the sampling period (Figure 6.3g). However, concentrations at 10 cm depth increased from ~4 to over 11 mg L^{-1} in the course of the later afternoon and evening of 25th June before steadily falling again. Concentrations of DO at 20 cm depth were low (< 4 mg L^{-1}) until ~ midnight on 25th June, when they rose markedly to > 8 mg L^{-1} in the space of 45 minutes. This rise coincided approximately with the water temperatures at 10 and 20 cm depths becoming similar (Figures 6.3e, 3g). Unlike FORS03, the concentrations of DO in FORS04 did not rise steadily throughout the afternoon of 25th June 2015 but instead displayed a sharp evening peak, more like those seen at Moor House (Figure 6.3h). However, unlike at Moor House, this peak was not replicated in the lower strata, as concentrations of DO at both 20 and 30 cm depths were consistently very low, flat-lining at 0.35 and 0.14 mg L^{-1} respectively for most of the sampling period (Figure 6.3h).

Water temperature in the three Abisko pools all followed a similar patter and varied most at 10 cm depth, i.e. in ABSK03 on 6th August 2014, temperatures at 10 cm depth ranged from 16.1 to 23.8 °C (Figure 6.4e). The temperature differential between 10 and 50 cm depth was also marked; for example, it reached 10.3 °C in ABSK02 on 6th August at 15:30 (Figure 6.4b). Temperatures at 30 cm depth were less variable while those at 50 cm depth, whilst being relatively high, hardly varied at all. For example, the temperature at 50 cm depth in ABSK01 varied by 1 °C over the course of 2+ days, from 14.0 to 15.0 °C (Figure 6.4a). Concentrations of DO at 10 cm depth were highly variable in all three Abisko pools and, especially in ABSK01 and ABSK03, displayed 'standard' diel curves (i.e. that would be expected in response to levels of PAR) (Figures 6.4b, 4c, 4f). In both ABSK01 and ABSK03, there was evidence of thermal mixing leading to evening spikes in DO at depths of 30 cm (Figures 6.4b, 4f). However, in ABSK02, concentrations of DO at both 30 and 50 cm depths were consistently <1 mg L^{-1}, as were concentrations at 50 cm depth in the other two pools.

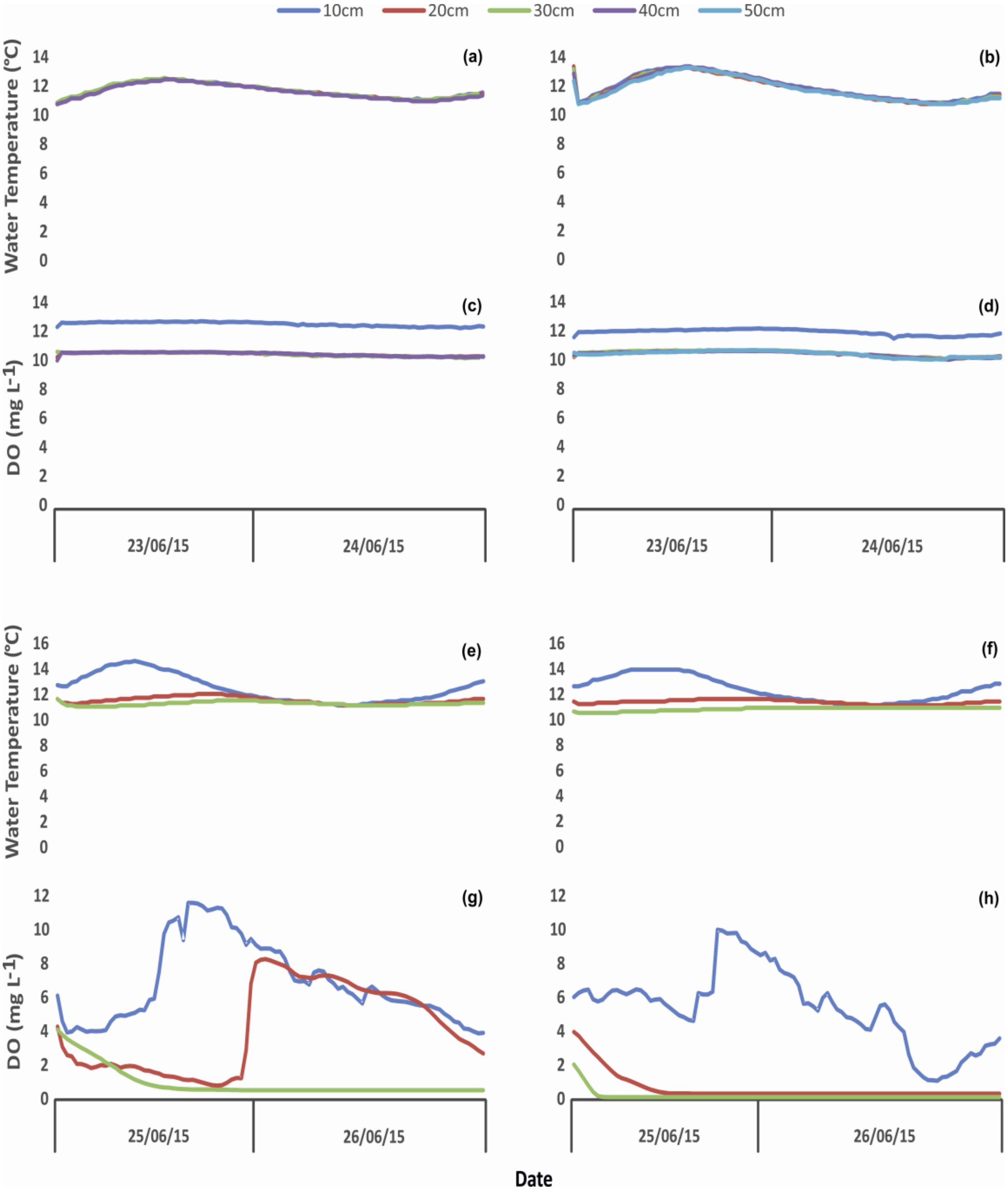

Figure 6.3. Water temperature and DO profiles for Forsinard 2015 (a) water temperature and (c) DO for FORS01, (b) water temperature and (d) DO for FORS02, (e) water temperature and (g) DO for FORS03 and (f) water temperature and (h) DO for FORS04. Data obtained from 23rd to 26th June, 2015.

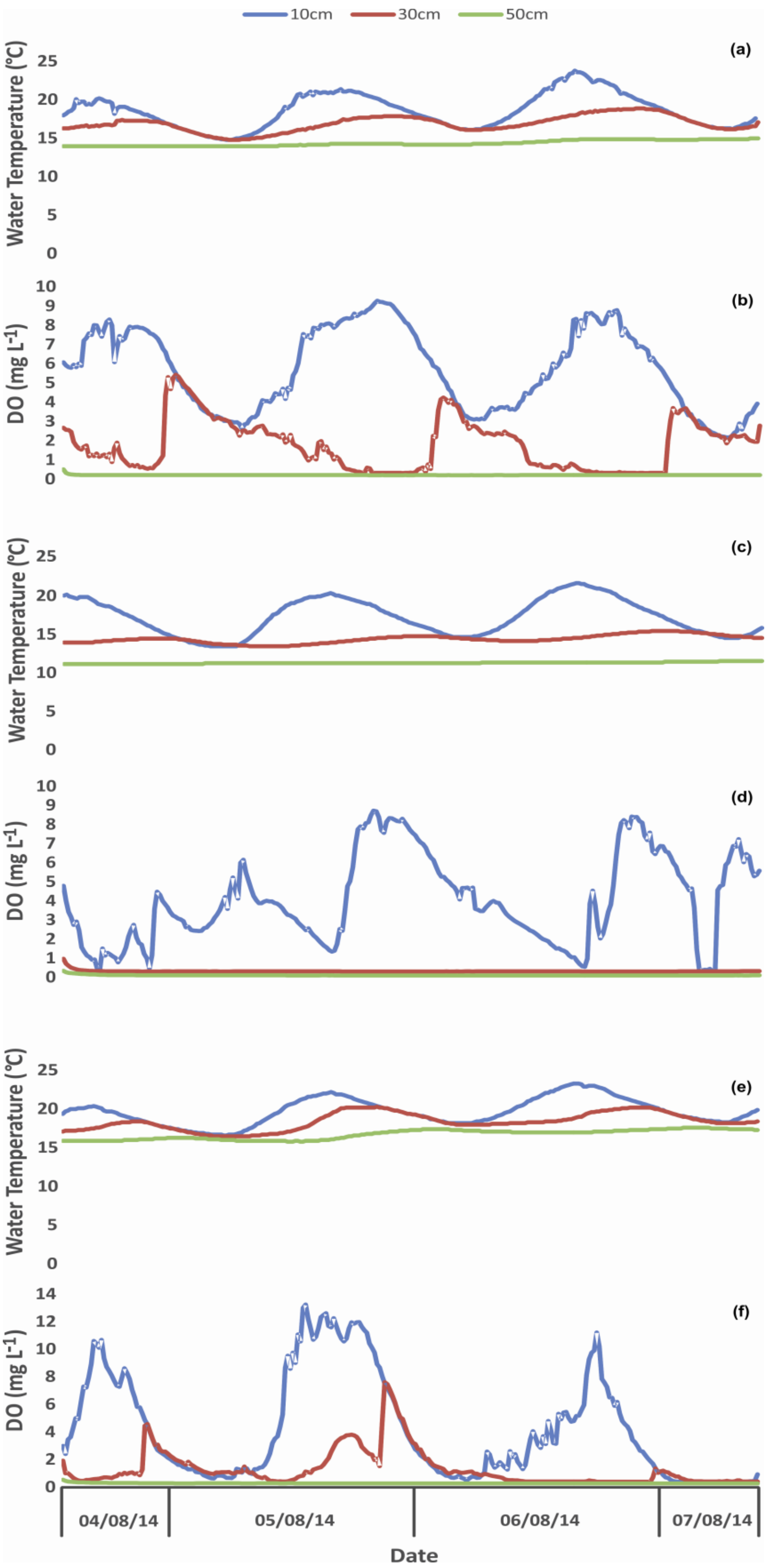

Figure 6.4. Water temperature and DO profiles for Abisko 2014 (a) water temperature and (b) DO for ABSK01, (c) water temperature and (d) DO for ABSK02 and (e) water temperature and (f) DO for ABSK03. Data obtained from 4th to 7th August, 2014.

6.3.3 Metabolism estimates

At Moor House, the metabolism estimates varied with probe depth and this was more marked on days with thermal stratification (Figure 6.5). For example, on 1st June, rates of R varied from -5.90 g m^{-3} d^{-1} at 30 cm depth to 18.66 g m^{-3} d^{-1} at 10 cm depth and rates of GPP from -18.88 g m^{-3} d^{-1} at 30 cm depth to 13.00 g m^{-3} d^{-1} at 10 cm depth (Figure 6.5e). Rates of NEP on 1st June varied in magnitude from -5.66 to -15.63 g m^{-3} d^{-1}. On the day with the least thermal stratification (29th May) the rates of R, GPP and NEP were much more even along the vertical profile, apart from at 50 cm depth when both R and GPP returned strongly negative values (Figure 6.5b). In particular, rates of NEP between 10 and 40 cm depth were almost identical on 29th May, ranging from -5.09 g m^{-3} d^{-1}at 10 cm depth to -7.12 g m^{-3} d^{-1} at 40 cm depth. Generally, the most reliable estimates (i.e. when the rates of GPP and R were always positive) were obtained at 10 cm depth whereas the least reliable estimates (i.e. either R or GPP or both returning negative values) were obtained at 50 cm depth (Figures 6.5a to 5e). The strongly negative GPP and R figures on 31st May at 20 cm depth were due to a sudden and large increase in DO levels after dark, caused by a thermal mixing event (Figure 6.5d).

The vertical positioning of the probes at Forsinard made the difference between NEP being either positive or negative for the day (Figures 6.5f, 5g). For example, in FORS01 at 10 cm depth, rates of GPP were greater than R, leading to a positive NEP value of 0.83 g m^{-3} d^{-1}, whereas at 20 cm depth R was greater than GPP, with a resulting NEP value of -0.22 g m^{-3} d^{-1} (Figure 6.5f). However, both of the Forsinard pools were much less metabolically active than the Moor House pool; the highest rates of R (2.66 g m^{-3} d^{-1}) were found at 50 cm depth in FORS01, whilst the highest rates of GPP were in FORS02 at 10 cm depth (3.11 g m^{-3} d^{-1}). Unlike the estimates obtained at Moor House, rates of R and GPP at Forsinard were positive at all depths in both pools (Figures 6.5f, 5g).

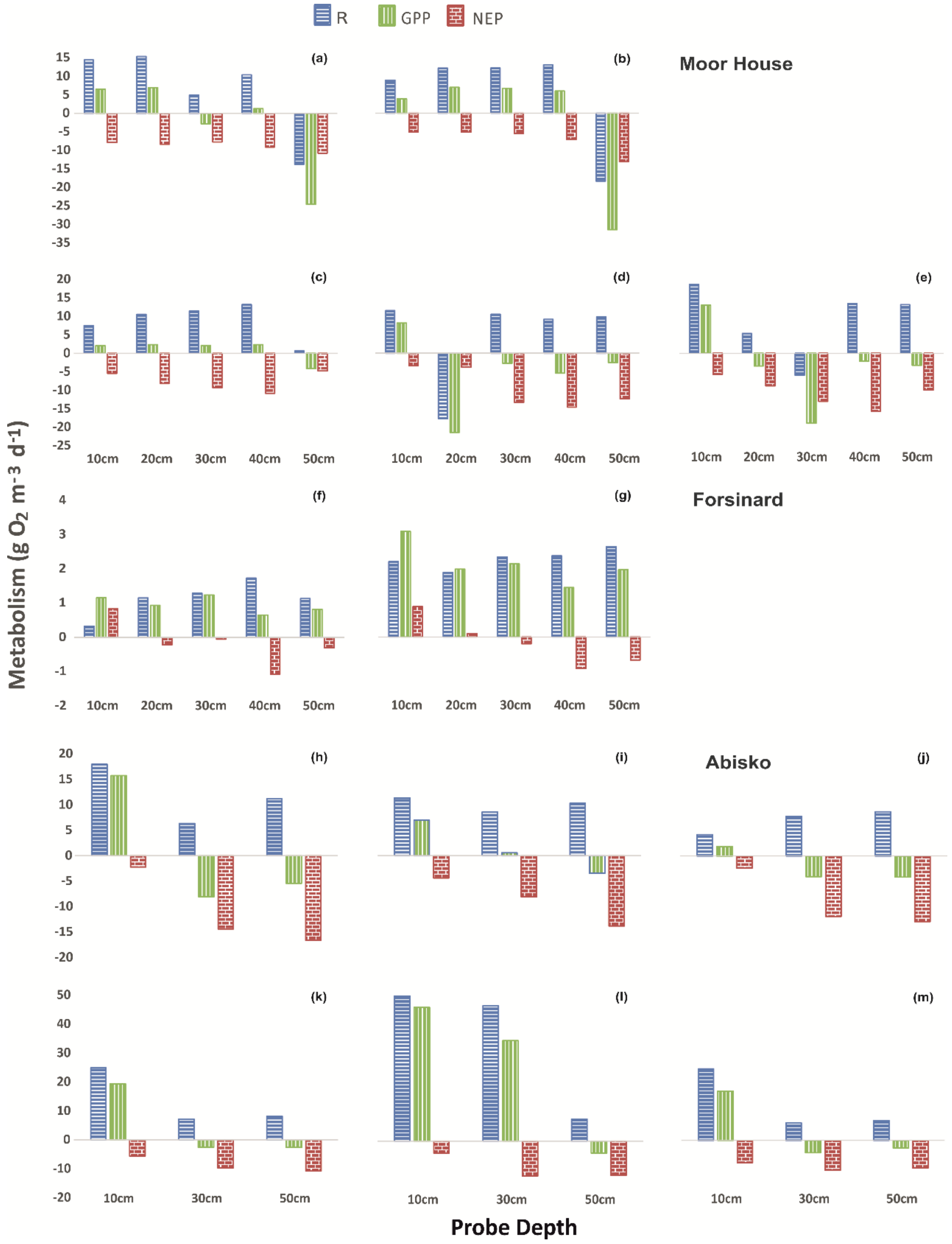

Figure 6.5. Metabolism estimates obtained from probes at different depths (a - e) MHM01 on 28th May to 1st June, 2014, (f) FORS01 and (g) FORS02 on 26th June, 2014, and (h and i) ABSK01, (j and k) ABSK02 and (l and m) ABSK03 on 5th and 6th August, 2014.

The positioning of the probes at Abisko resulted in very different metabolism estimations (Figures 6.5h to 5m). For example, in ABSK01 on 5th August, rates of R were much higher at 10 cm depth (17.98 g m^{-3} d^{-1}) than at 30 cm depth (6.35 g m^{-3} d^{-1}), and GPP was positive at 10 cm depth (15.78 g m^{-3} d^{-1}) but negative at 30 cm depth (-8.04 g m^{-3} d^{-1}) (Figure 6.5h). Even when both R and GPP readings were positive at 10 and 30 cm depths (ABSK03 on 5th August) there was a difference in NEP which was -7.66 g m^{-3} d^{-1} at 10 cm depth and -10.27 g m^{-3} d^{-1} at 30 cm depth (Figure 6.5l).

In Chapter 5 of this thesis, the mean depth (and therefore the Z_{mix} value used in the calculations) of MHM01 was found to be 43 cm. In the current chapter, on days with little or no thermal stratification, this value was still valid for most of the time-step calculations because it fell within the depth of the mixed layer (Z_{mix}). For example, on 28th May, MHM01 stratified from 00:00 to 01:15 at a depth of 40 cm but for the rest of the day the temperature differential between 0 cm and 40 cm depth was < 1 °C. On 29th May, MHM01 exhibited no thermal stratification at all so there was no reason to use a fluid Z_{mix} value. However, on 30th May, the pool was stratified to various depths between 10:45 and 00:00 and for the majority of that time (12:30 to 22:00) it was stratified to 20 cm depth. On 31st May, MHM01 was stratified to some extent for the entire diel period, whilst on 1st June it was stratified between 00:00 and 01:30, then again between 08:45 and 00:00, again mostly at 20 cm depth on both days. On days with little (28th May) or no (29th May) stratification, the fluid Z_{mix} values made correspondingly little or no difference to the metabolism estimates (Table 6.3). However, as diurnal stratification became more severe (30th May to 1st June) the fluid Z_{mix} value caused NEP to reduce (become more negative) due to the increase in R and the correspondingly larger decrease in GPP. For example, on 1st June at 10 cm depth, rates of R and GPP calculated using the fixed Z_{mix} value of 43 cm depth were estimated at 18.66 and 13.00 g O_2 m^{-3} d^{-1} respectively, giving a NEP value of -5.66 g O_2 m^{-3} d^{-1}. However, using the fluid Z_{mix} values, the estimates changed to 19.29 (R), 10.42 (GPP) and -8.87 (NEP) g O_2 m^{-3} d^{-1} (Table 6.3.)

Table 6.3. R, GPP and NEP values at 10 and 20 cm depths in MHM01 comparing the fixed and fluid zmix values. Estimates in g O_2 m^{-3} d^{-1} using both the fixed Z_{mix} value (mean depth) of 43 cm and a fluid Z_{mix} value equating to the depth at which water temperature increased by >1°C per depth increment of 10 cm, and differences between the two. Values in red show negative GPP and R values (energetic impossibilities). Values on 29th May are the same for both methods as stratification to the specified level did not occur. Values for 31st May at 20 cm depth are included for completeness but are not discussed (a sharp increase in DO levels after dark led to a negative rate of R and correspondingly warped the GPP figures).

	Fixed Z_{mix}			**Fluid Z_{mix}**			**Difference (fixed - fluid Z_{mix})**		
	Probe depth = 10 cm								
Date	**R**	**GPP**	**NEP**	**R**	**GPP**	**NEP**	**R**	**GPP**	**NEP**
28/05/14	14.40	6.50	-7.90	14.43	6.52	-7.91	-0.04	-0.03	0.01
29/05/14	8.95	3.86	-5.09	8.95	3.86	-5.09	n/a	n/a	n/a
30/05/14	7.49	2.06	-5.44	7.87	-0.07	-7.94	-0.37	2.13	2.50
31/05/14	11.58	8.20	-3.38	12.47	7.00	-5.47	-0.89	1.21	2.10
01/06/14	18.66	13.00	-5.66	19.29	10.42	-8.87	-0.63	2.58	3.21
	Probe depth = 20 cm								
Date	**R**	**GPP**	**NEP**	**R**	**GPP**	**NEP**	**R**	**GPP**	**NEP**
28/05/14	15.32	6.96	-8.36	15.36	6.99	-8.37	-0.04	-0.03	0.01
29/05/14	12.19	7.02	-5.17	12.19	7.02	-5.17	n/a	n/a	n/a
30/05/14	10.54	2.39	-8.16	11.17	-0.03	-11.20	-0.63	2.41	3.04
31/05/14	-17.67	-21.45	-3.78	-16.04	-24.13	-8.09	-1.63	2.68	4.31
01/06/14	5.38	-3.42	-8.80	6.30	-8.64	-14.95	-0.92	5.22	6.15

6.4 Discussion

This study provides clear evidence that small peatland pools can experience a complete cycle of thermal stratification during the course of a single diel period, with a high vertical temperature gradient during the day followed by mixing at night, which does not always reach down to the pool bottom. In the smallest pool (MHM01), the temperature differential between the surface waters (10 cm) and the pool bottom (50 cm) reached a maximum of 9.1°C. This high degree of variability, both within and between strata, had clear consequences for DO concentrations throughout the water column. The sections below will discuss these findings in relation to other studies of shallow lentic waterbodies, concluding by outlining the impact that diurnal stratification may have on metabolism estimates in small or shallow pools and other aspects of their biogeochemistry, along with recommendations for future metabolism studies of peatland pools.

6.4.1 Temperature profiles

Other studies have reported vertical temperature gradients for shallow waterbodies, but mainly to a much lower degree than those found at Moor House. For example, MacIntyre (1993) found that the upper meter of a shallow (max depth 2.6 m), eutrophic lake near Perth (Australia) displayed a temperature gradient of between 2°C and 4°C. However, unlike some of the pools in my study, the lake in MacIntyre (1993) always mixed completely at night to a depth of at least 2 m. Van Buren et al. (2000) studied an on-stream stormwater pond in Ontario (mean depth ~1 m) and reported a temperature gradient of up to 3.67 °C, although the authors also reported that even moderate winds resulted in enough mixing potential to completely reverse the stratification. The wind speed at Moor House during the sampling period was generally < 2 m s^{-1} and never rose above 4 m s^{-1}, so it is unclear if stronger winds would have succeeded in breaking down the stratification. Findings more comparable to those from Moor House were reported by Condie and Webster (2002) from Rushy Billabong in south-eastern Australia, where vertical temperature gradient of up to 10 °C developed in the top 1 m during the day, followed by a complete mixing of the water column between midnight and 06:00. A study based in the Netherlands which measured temperature profiles in a very small, experimental pool (diameter 1.10 m, depth 0.25 m) reported diurnal surface (2 cm) fluctuations of ~ 10 ° C which dropped to ~6 °C at 20 cm (Jacobs et al., 2008). The pool studied by Jacobs et al. (2008) is the most similar in dimensions (although even shallower) to the Moor House pool and displayed similar fluctuations at 20 cm (MHM01 fluctuated by 5.5° C at 20 cm on 1st June). However, as the sides of pool in Jacobs et al. (2008) were constructed from 3 mm PVC which severely restricted heat loss, this somewhat confounds direct comparison with MHM01 in which heat would have transferred to the surrounding peat.

The results from my study indicate that the severity of the diurnal stratification cycle was linked to surface area, evidenced by the largest pool at Forsinard displaying markedly less thermal stratification than the pools at Moor House or Abisko. This was to be expected as reduced water volume will result in greater diurnal temperature fluctuation with increased temperature maxima (Macan, 1974). Also, the increased fetch over a larger expanse of water will provide more opportunity for turbulent mixing by wind, which reduces stratification (MacIntyre and Melack, 2010). However, the smaller pool at Forsinard (FORS02 – surface area 32 m^2) displayed a maximum temperature gradient (between 10 and 50 cm) of 4.6 °C, whereas that in ABSK02 (surface area 31 m^2) was much larger at 10.3 °C. This was because, although both pools had similar surface (10 cm) temperature ranges (FORS02 ranged from 12.0 to 22.2 °C, and ABSK02 from 13.5 to 21.7 °C) the temperatures at 50 cm depth behaved very differently. In FORS02 the temperature at 50 cm depth ranged from 12.0 to 18.6 °C whereas in ABSK02 it was much more stable, ranging from 11.2 to 11.6 °C. The lower water strata in ABSK02 also appeared to be permanently separate from the layers above, whereas the water strata in FORS02 mixed completely during the night. This apparently more permanent stratification in ABSK02 could be explained by the higher levels of DOC recorded there, as studies have shown that turbid or opaque ponds, and those with high densities of phytoplankton, are more prone to stratification due to the reduced light attenuation as more solar radiation is trapped by particles in the surface layers (Mazumder and Taylor, 1994, Hansson, 1992, Snucins and John, 2000). ABSK02 also had 100% vegetation cover (90% *Sphagnum*, 10% *Eriophorum*), whereas FORS02 was mainly open-water, so this may also have acted as a buffer to prevent radiation from reaching the pool bottom and thus maintaining the stratification.

6.4.2 DO profiles

This study was originally conceived in response to the evening DO 'spikes' found regularly in the Moor House pools (see Chapter 5). Other studies have also reported after-dark rises in levels of DO and attributed them to DO rich pockets of water moving past the sensor, either vertically or horizontally (Gelda and Effler, 2002, Hanson et al., 2008). In chapter five, the DO spikes at Moor House had been recorded at a pool depth of 20 cm. In the current study, it became clear that the DO spikes originated in the surface waters (10 cm depth) and were then replicated down through the water column as the temperatures cooled and water merged with the strata below.

The DO spikes at lower depths clearly aligned with the point at which the temperatures (and presumably water) mixed with the layer above. However, the cause of the initial spike at 10 cm depth is less clear. As DO concentrations further down the water column were lower than at the surface, the extra influx of oxygen must have come either from above (i.e. from the atmosphere) or a horizontal movement of oxygen-rich water from the littoral zone. In larger ponds and lakes there is evidence for the latter, as the littoral area has been shown to be more metabolically active and may be the source of oxygenated pockets of water moving by advection to the pelagic zone (Lauster et al., 2006). However, the Moor House pools are so small that this theory seems unlikely; there is little demarcation between the pelagic and littoral zones. This leaves the atmospheric diffusion theory, which also feels counter-intuitive as atmospheric diffusion is generally a gradual process and seems an unlikely candidate to explain such sudden spikes. For example, in MHM01 on 31st May, the DO spike at 10 cm depth occurred between 20:45 and 21:00 when DO concentrations rose from 7.36 to 9.51 mg L^{-1}, which corresponded to an increase in O_2 % saturation from 73% to 94% (U.S.G.S., 2014). The rate of cooling in the pool had been speeding up: between 17:45 and by 20:15 (2.5 hrs) the temperature at 10 cm depth had reduced by 1.2 °C, from 16.1 to 14.9 °C. Then, between 20:15 and 21:15 (1 hr) it further reduced by 1.1 °C from 14.9 to 13.8 °C. Thus, the speed of diffusion of atmospheric O_2 was increasing, but there is nothing obvious to account for such a sudden, sharp rise. The spike was not caused by an increase in aeration as the prevailing average wind speed between 20:45 and 21:00 actually reduced slightly, from 1.5 to 1.1 m s^{-1}. So, this issue still needs further clarification. Future studies could consider placing probes horizontally across the water column as well as vertically down, to pick up any patterns of DO movement across the pool surface, potentially from patches of littoral *Sphagnum* which have been photosynthesising during the day. On the evening of 30th May, when the pools had thermally stratified during the day, there was no vertical pattern of DO spikes, with the single spike occurring at 20 cm when the temperatures at this depth mixed with those at 10 cm. The lack of DO spikes at 10, 30 or 40 cm depths may have been related to the substantial mixing event overnight on the 29th / 30th May when DO levels at 50 cm depth had risen sharply with the breakdown of thermal stratification, and perhaps suggests that the DO stratification/turnover cycle does not resume immediately after a large mixing event.

DO patterns in FORS01 and FORS02 were very different to those recorded at Moor House. Concentrations of DO in the natural Forsinard pools were consistently high and virtually unchanging. This corresponded well to the general lack of / reduced thermal stratification seen in the natural pools at Forsinard, indicating that DO was not restricted by thermal boundaries in the water column. The only exception to this generally smooth DO pattern was the sudden, unexplained drop in DO levels in FORS02 at around 08:50 on 27th June, 2014. In contrast to the natural pools at Forsinard, the two drain-blocked pools (FORS03 and FORS04) showed marked variation in levels of DO. Probably due to their small size, the drain blocked pools at Forsinard behaved more like the Moor House pools. However, the DO spike seen at 10 cm depth in FORS04 on the evening of 25th June, 2015, when concentrations jumped from 6.38 to 10.04 mg L^{-1} in the space of 15 minutes, did not correspond to an unusually fast rate of cooling at the same depth (10 cm). In the hour leading up to the spike, the surface temperatures that evening had cooled from 13.8 to 13.2 °C, a drop of only 0.6 °C compared to the 1.1 °C seen over the same time period in MHM01 on 31st May prior to the spike.

In the Abisko pools, concentrations of DO at 50 cm depth were consistently low (just above 0 mg L^{-1}) throughout the sampling period in all three pools. This could be accounted for by weak night-time mixing which failed to reach down to the bottom sediments, so that temperatures at 10 and 30 cm depth became aligned (and water presumably mixed) but those at 50 cm depth remained cooler. Therefore, the DO consumed by bacterial processing at the pool bottom was not being replenished from above, leading to a permanent state of anoxia. However, in ABSK02, levels of DO at 30 cm depth were also almost constantly just above 0 mg L^{-1}, despite the temperatures at 10 and 30 cm depth aligning overnight, and this remains unexplained. It is possible that the influx of DO provided by the breakdown of thermal stratification was used up almost instantly by the microbes at 30 cm depth, but as this did not happen in any of the other pools it seems unlikely.

Another notable aspect of the DO patterns at Abisko was the appearance of more 'standard' diel curves at 10 cm depth, most notably in ABSK01. These did not appear in any of the other pools sampled as part of this study (the apparent curve in FORS03 on 25th June actually started at 18:45, so was not mirroring PAR levels for the day). The most likely driver of the curves would be higher rates of photosynthesis driven by an increased number of autotrophic organisms. However, it is interesting that, out of the three Abisko pools, the one with by far the highest vegetation cover (ABSK02) arguably showed the least defined PAR curves, suggesting that phytoplankton, as opposed to moss or macrophyte cover, is more important in driving photosynthesis in these pools. One variable not measured in this thesis, which could have been informative, was Chlorophyll *a*, as a proxy for phytoplankton biomass (Staehr et al., 2010a) and it is recommended that future studies looking at the metabolism of peatland pools measure Chlorophyll *a*.

6.4.3 Metabolism estimates

The results from this study found that placing a DO probe at different depths could result in different metabolism estimates. Generally, the vertical placement of the DO probes was less important on colder days, when stratification was minimised or absent, and also in larger pools. For example, the two natural pools at Forsinard (FORS01 and FORS02) exhibited so little stratification that the metabolism estimates were very similar at all depths. NEP values in FORS01 and FORS02 changed from positive to negative depending on probe depth, but these pools were far less metabolically active than either the Moor House or Abisko pools so the NEP values, in effect, varied very little. For example, in FORS01 (2014) they ranged between -1.08 (40 cm depth) to 0.83 g (10 cm depth) O_2 m^{-3} d^{-1}, whereas NEP in MHM01, although always negative, varied more, i.e. on 1st June NEP ranged from -5.66 (10 cm depth) to -15.63 g O_2 m^{-3} d^{-1} (40 cm depth).

Other metabolism studies have reported that DO patterns vary with depth in shallow waterbodies. For example Kersting (1983) reported bimodal diel DO curves at the bottom (50 cm depth) of a polder ditch in Holland but a unimodal curve at the top (10 cm depth) which the author attributed to diurnal thermal stratification. In the polder ditch the water stratified during the day with a temperature gradient of up to 3.6 °C in the top 30 cm. The bottom bimodal curves were caused by (1) an initial burst and decline of photosynthesis and (2) a breakdown of thermal stratification later in the afternoon when the more oxygenated surface waters mixed with the lower layers. The lack of bimodal, or indeed of any real DO curves found in the lower strata of the pools I studied is probably due to the high levels of light attenuation (and therefore low rates of photosynthesis) at depth in the coloured, dystrophic waters, as well as a lack of night-time mixing. Indeed, one very clear conclusion from my study is that the DO probes should not be placed towards the bottom of pools, when attempting to measure R and GPP, due to the almost constant state of anoxia often found there; the diel DO change technique by definition requires a detectable diel oxygen signal. Instead, the probes need to be placed at a depth where they can detect changes in oxygen caused by both biological (e.g. photosynthesis) and physical (e.g. atmospheric diffusion) processes. It seems clear from the results of this study that probes should be placed in the top 10-20 cm of the water column, where solar radiation is available to drive photosynthesis and oxygen supplies can be replenished from the air. In the Abisko pools the probes were clearly best placed at 10 cm depth where the standard diel DO curves occurred. Although no probes were deployed at 20 cm depth in the Abisko pools, it is possible that similar curves may have been found at that depth as well, although they had mainly diminished by 30 cm depth. In the Moor House pools, probes placed at 10 cm depth tended to produce positive GPP figures whereas those at 20 cm depth were more likely to be negative. This can in part be explained by the probable increase in rates of photosynthesis at 10 cm depth due to the higher incident UV radiation. However, it is also the case that the sharp DO spike often found at Moor House occurred earlier at 10 cm depth (e.g. usually within daylight hours) so is incorporated into the NEP_{hr} during the day figures, when concentrations of DO are expected to be increasing anyway.

Modifying the calculation of metabolism by using a fluid Z_{mix} value compared to a fixed Z_{mix} value was shown to alter metabolism estimates on days when thermal stratification was more severe. In such cases, both the increase in R and the decrease in GPP could be attributed to the calculations, rather than to any underlying physical processes. This is because both R and GPP are extrapolated out from NEP_{hr} values, which in turn are calculated using:

$$\Delta DO_{hr} - (F/Z_{mix})$$

where ΔDO_{hr} is the rate of change in DO levels over the last time step (one hour) and F is atmospheric O_2 exchange (see Chapter 5 for more details). As the Z_{mix} value becomes shallower, the corresponding NEP_{hr} value decreases. When the number of daylight hours exceed dark hours, these decreases have a larger impact on the average NEP_{hr} during the day than the average NEP_{hr} at night, simply because there are more values from which an average is taken. This is important because R is based purely on the NEP_{hr} night values, whereas GPP incorporates both NEP_{hr} at night and during daylight. So, whilst R is impacted by the change in Z_{mix}, GPP is impacted more.

6.4.4 Other biogeochemical implications

Diurnal thermal stratification has consequences for biogeochemical processes other than levels of DO and pool metabolism. For example, a study by Watras et al. (2015) analysed the dynamics of chromophoric dissolved organic matter (CDOM) fluorescence (used as a proxy for levels of DOM / DOC) in the oxic and anoxic strata of Crystal Bog and Trout Bog lakes in Wisconsin (USA) (both listed in Table 5.6), and identified two distinct diel cycles. In the oxygenated epilimnion, CDOM fluorescence decreased during the day and increased at night, whereas in the anoxic hypolimnion it was relatively stable at night before gradually increasing during the day to a midday maximum. The authors tentatively linked the oscillations to a rapid biological turnover of a small, labile fraction of DOM, theorised to exist among the larger pool of much more recalcitrant DOM usually associated with bog lakes (Wetzel, 2001). Furthermore, the existence of a diel CDOM fluorescence cycle which mirrored the diel solar cycle but at depths beyond the reach of UV light suggested the existence of vertical interactions, e.g. the diel vertical migration (DVM) of zooplankton or the settlement of zooplankton fecal pellets. The implications for DOC sampling are that samples taken from the upper layer of a stratified pool may not reflect DOC concentrations in the pool as a whole. Furthermore, as levels of UV in the surface waters of a stratified pool are high, this will lead to increased photo-mineralisation of DOC into DIC and UV-induced transformations of DOM into lower molecular weight organic carbon substrates which are easier for microbes to consume (Sulzberger and Durisch-Kaiser, 2009, Watras et al., 2015). This photodegradation effect may also be enhanced by the acidity of the pools, as Anesio and Granéli (2004) demonstrated that low pH lakes, especially humic lakes, experienced higher rates of photochemical mineralisation than lakes with ambient pH. Therefore, the heating of a shallow surface layer in peatland pools may initially increase carbon losses to the atmosphere, although the depleted DOC loads would not be replenished from below until the waters destratified.

Stratification controls the movement of CH_4 throughout the water column as CH_4, produced by methanogenesis in the bottom sediments cannot diffuse up through thermal boundaries into the surface waters. This is especially relevant to peatland pools which are considered to be hotspots for methane release (Baird et al., 2009, Holden et al., in press). For example, Ford et al. (2002) studied the effects of water-column stability on methane and oxygen dynamics in a shallow floodplain lake in south-eastern Australia, and reported that diurnal thermal stratification in summer led to oxygen maxima in the surface waters whilst restricting CH_4 to the lower strata. Overnight cooling and mixing then removed the thermal boundary, resulting in the more even distribution of both gases throughout the water column. As a result, summer CH_4 concentrations in the surface waters varied by an 18-fold range during the course of a diel cycle, compared to a 2-fold range in autumn when stratification was absent (Ford et al., 2002). This has implications for measurements of CH_4 across the air-water interface, for example using floating chambers, as the rate of diffusion cannot be assumed to be constant. For example, daytime measurements taken when most of the CH_4 is trapped at the bottom of the pool and extrapolated out across 24 hours may underestimate the diffusive component of CH_4 emissions.

Another consequence of the separation of DO and CH_4 into the upper and lower strata of a waterbody is the potential to modify rates of planktonic methanotrophy (the oxidation of CH_4, resulting in CO_2 and H_2O) which requires the presence of both oxygen and methane. Methanotrophy is a vital biogeochemical process in peatlands as it helps to prevent sediment-derived CH_4 (which is a more potent greenhouse gas than CO_2) from reaching the atmosphere, and CO_2 derived from methane-oxidising bacteria has also been shown to partially sustain autotrophic communities in bogs pools in raised bog pools in Estonia (van Duinen et al., 2013). In the study by Ford et al. (2002), nocturnal mixing led to relatively uniform oxygen and methane distribution throughout the water column in the early morning (albeit at low oxygen concentrations), resulting in an increased area over which methanotrophy could theoretically take place. With the onset of stratification, however, DO / CH_4 interaction, and thus methanotrophy, would be restricted and centre on the boundary of the epilimnion and hypolimnion (i.e. the point at which the product of the concentrations of methane and oxygen is at a maximum). Furthermore, the nightly influx of dissolved oxygen down into the pool bed where anoxic sediments are often found should act to inhibit microbial methanogenesis (the production of methane). The extent to which any of these processes would impact on methanotrophic capacity is unclear but merits further investigation due to the potential importance for carbon cycling in peatland pools.

6.4.5 Conclusions

This study indicates that care should be taken when using the diel DO change technique to estimate metabolism in peatland pools, as the diurnal thermal stratification regimes vary both within and between sites. It is recommended that depth profiles for both DO and temperature should be obtained prior to probe deployment for R and GPP calculations in order to establish the optimum vertical positioning of the probes. The findings above suggest that this will usually be within the top 10 to 20 cm of the pool water column. If possible, during the sampling period, a string of thermistors should be deployed (starting at 0 cm depth and progressing in suitable increments to the pool bottom) to allow for detection of thermal stratification and the incorporation of fluid Z_{mix} values into the metabolism calculations. The diel DO change technique is perhaps more valid when used in pools which show a distinct DO diel curve, as in the Abisko pools. However, even in pools with less obvious diel signals, the technique will provide a good indication of NEP as long as anomalies resulting from physical processes such as evening DO spikes are identified and accounted for. The technique can also provide further benefits when deployed alongside water and gas samples for carbon cycle related research, so that processes influencing fluxes and concentrations of dissolved matter and gases can be better understood.

Chapter 7: An integrated assessment of physicochemical dynamics, biodiversity and ecosystem functioning in peatland pools

7.1 Introduction

The previous chapters of this thesis have provided valuable new insights into the ecology and physicochemistry of peatland pools, which has wider relevance for understanding ecosystems in many different types of small or shallow waterbodies around the globe. This chapter will summarise the research findings and present an updated version of the conceptual schematic included in Chapter 2. It will then highlight key findings and discuss their implications for both peatland restoration schemes and the management of other small or shallow water bodies, before concluding with the main contributions that the work has made to the field of peatland restoration research.

7.2 Research synthesis

Chapter 2 presented a literature-based conceptual schematic (Figure 2.3) which outlined a theorised evolution of drain-blocked pools over time with regards to both biotic and abiotic processes. The schematic presented several possible research questions and highlighted the ones to be answered by this thesis. Figure 7.1 now advances this schematic based on the results of my research; Figure 7.1 (a) shows the original schematic with red text indicating the selected research questions and 7.2 (b) provides answers to the questions, with red text indicating evidence-based findings.

Chapter 3 answered the first research question (do macroinvertebrate communities in drain-blocked pools resemble those of natural pools?) in the

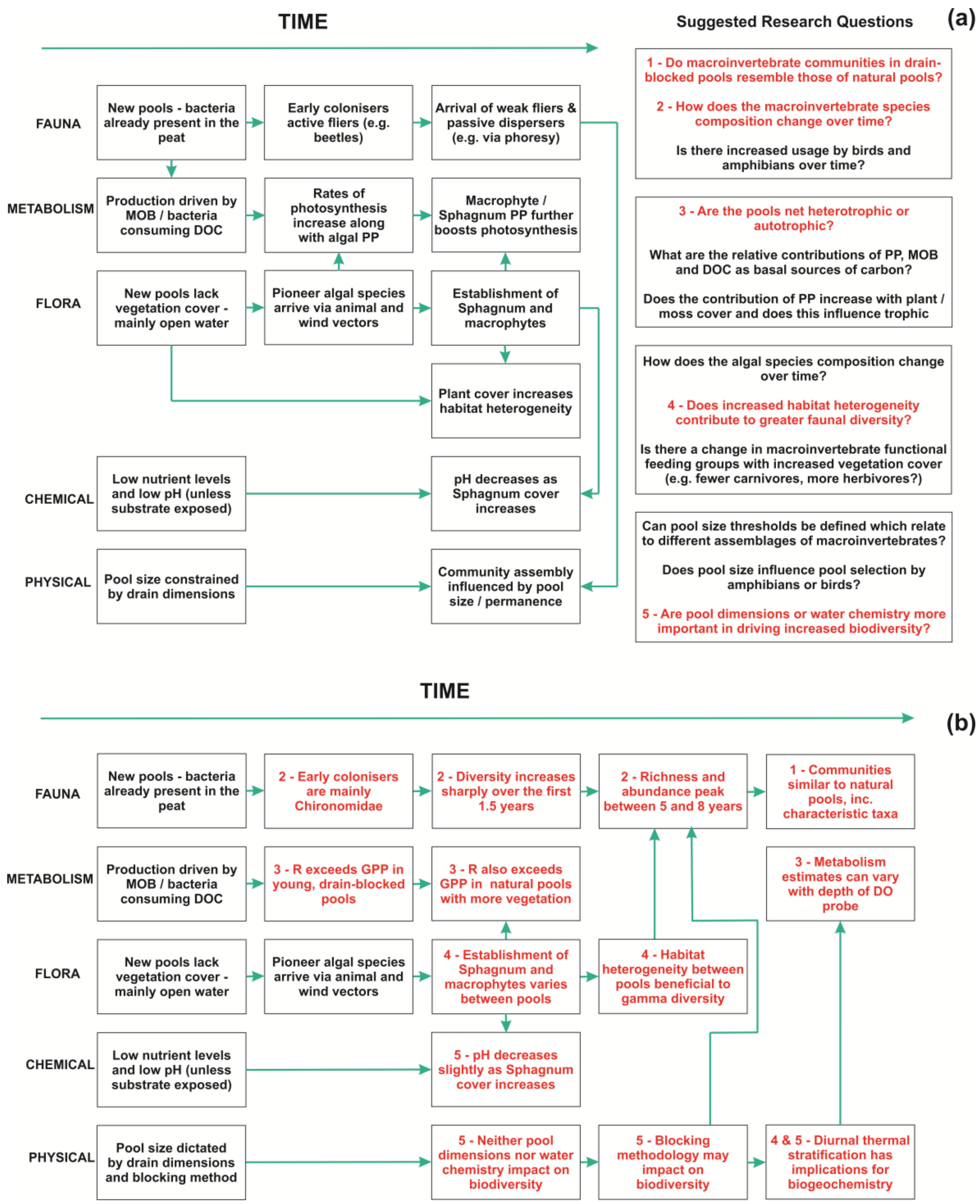

Figure 7.1. Updated conceptual schematic (a) The original conceptual schematic from Chapter 2, and (b) an updated schematic based on thesis finding. Answers to the research questions highlighted in red in panel (a), are highlighted in red in panel (b), along with corresponding research question numbers.

affirmative. Both blocked and natural pools were dominated by Chironomidae, with a good representation of Coleoptera and a mix of other typical bog pool taxa (e.g. Hemiptera, other Diptera, Trichoptera and Odonata). Although the ANOSIM tests in

Chapter 3 reported a significant difference between blocked and natural pool communities, the global R statistic was low (0.319) and the differences appeared to be driven mainly by one natural site (Butterburn Flow) which showed distinct clustering on the nMDS ordination. However, this difference between Butterburn Flow, which was the only truly natural peat pool complex I was able to locate in the Pennines, and the other natural pools in the study, which were more isolated features in otherwise intact peatlands, is interesting in itself. The Butterburn Flow pools were far less diverse as measured by the biodiversity metrics, but were home to the only two ‘notable’ species found; *Enochrus affinis* and *Enochrus ochropterus*. Also, although no rare or endangered taxa were identified, several taxa classified as acid-mire obligates, specialists or preferentials were identified. The distribution of the acid mire taxa between the natural and blocked pools was very similar, although *E. affinis* was found only in the natural pools and the odonate *Aeshna juncea* only in the L-shaped pools. Furthermore, there were tentative suggestions that the blocking methodology of reprofiling may benefit biodiversity more than creating L-shaped pools, as evidenced by the significantly higher taxon richness in the reprofiled pools and the significantly lower 1-Simpsons and higher Berger-Parker scores in the L-shaped pools. However, Chapter 3 did not find any evidence that gradients in either pool dimensions or water chemistry drove macroinvertebrate biodiversity (research question 5) (Figure 7.1a). Only two significant relationships between the biodiversity metrics and the environmental variables were found; negative relationships between abundance and (i) vegetation cover and (ii) Cl, the former of which may have been at least partially due to the sampling technique used and the latter of which was considered to be a statistical outlier. It may well be that the dimensions and water chemistry of these pools are so restricted in range that there is little scope for a noticeable impact on biota, suggesting a stochastic rather than deterministic community assembly process. This chapter builds on previous work comparing macroinvertebrate communities in natural and artificial peatland pools (van Duinen et al., 2003, Mazerolle et al., 2006, Hannigan et al., 2011, Brown et al., submitted) and is the first study to look at how blocking methodologies might impact on aquatic biodiversity.

Chapter 4 set out to provide answers to the second research question; how does the macroinvertebrate species composition change over time? The original schematic had predicted that active fliers would be the first to arrive, followed by passively dispersed taxa. My findings contradicted this by showing that the bulk of early colonisers were chironomids (weak fliers mainly dispersed by the wind during swarming events), with beetles slower to arrive. However, pools in newly-blocked drains were generally colonised quickly, and both taxon richness and abundance continued to rise sharply until 1.5 years, with a continued although more sedate rise resulting in peak richness and abundance in pools aged 5 to 8 years. The 5 to 8 years pools also housed the largest number of acid mire taxa, although the total abundance of acid mire individuals was greatest in the 10+ years pools. The increased diversity in the 5 to 8 year old pools was most likely explained by the larger inter-pool variation in vegetation cover compared to pools in the other age classes. The disparity in % vegetation cover provided some evidence that increased habitat heterogeneity between pools contributed to greater overall faunal diversity, thus addressing the fourth research question on Figure 7.1 (a). Chapter 4 constitutes the first study to be undertaken anywhere in the world to analyse how communities initially assemble and change over time in artificial peatland pools.

Chapter 5 emphatically answered the fourth research question; are the pools net heterotrophic or autotrophic? The Moor House pools were found to be strongly heterotrophic, with rates of R exceeding those of GPP on all sampling occasions. The high rates of R appeared to be driven by high concentrations of DOC and the relatively large sediment-water interface found in the small pools. Furthermore, comparisons with other standing freshwater-body studies showed that the Moor House pools regularly returned lower (i.e. more negative) NEP values, meaning that they acted as a stronger carbon source to the atmosphere. Chapter 6 also contributed evidence to this question by showing that natural pools at Abisko, including one with 100% vegetation cover, also returned negative NEP values, although sampling here was only for three pools over two days. However, the two natural pools at Forsinard both returned positive NEP values at a probe depth of 10 cm, indicating that some peatland pools may be autotrophic, at least in summer. Although other authors have used the diel DO change method to estimate the metabolism of larger dystrophic waterbodies (Hanson et al., 2003, Lauster et al., 2006, Staehr et al., 2010b), Chapter 5 is the first study to apply the method to small, peatland pools, and provides empirically-derived recommendations to improve future metabolism investigations of very small or shallow lentic systems.

The discovery of regular evening spikes in DO concentrations in the Moor House pools led to further investigation, outlined in Chapter 6, resulting in some important findings regarding temporary (usually diurnal) thermal stratification in the pools. On warmer days, the Moor House pools experienced quite severe diurnal thermal stratification, which lessened or disappeared at night as the surface waters cooled. Extreme diurnal stratification was also seen in the larger, natural Abisko pools and in small, drain-blocked pools at Forsinard. In contrast, thermal stratification in the larger, natural pools at Forsinard was much less evident or even non-existent. This stratification was shown to impact on metabolism estimates depending on the depth of the DO probe and also has wider implications for peatland pool biogeochemistry, including greenhouse gas fluxes. Thus, future studies could address research questions concerning the relationship between temporary stratification and both the biogeochemistry (e.g. gas fluxes and carbon cycling) and also the biota (e.g. possible diurnal vertical migrations related to temperature differentials) of pools. Other studies have reported diurnal thermal stratification in shallow waterbodies (Ganf, 1974, Ford et al., 2002, McEnroe et al., 2013) but Chapter 6 is the first to investigate the temperature and DO profiles in artificial peatland pools.

7.3 Key findings and wider implications

This study has greatly increased our knowledge of the ecology and functioning of natural peatland pools and artificial peatland pools created by damming drainage ditches. The findings, particularly those related to pool thermal stratification and metabolism, are relevant to many other shallow lentic systems such as Australian billabongs (Bunn and Boon, 1993, Ford et al., 2002), everglades (Hagerthey et al., 2010), urban and stormwater ponds (McEnroe et al., 2013, Hassall, 2014), estuaries (Caffrey, 2004, Cornell and Klarer, 2008), temporary forested ponds (Holgerson, 2015), abandoned quarries (Christensen et al., 2013), aquaculture ponds (Losordo and Piedrahita, 1991) and rice paddy fields (Saito et al., 2005). For example, low concentrations of DO at the bottom of commercial aquaculture systems can cause stock mortality (Losordo and Piedrahita, 1991). However, the results also pose a question of priorities for land managers involved in future drain-blocking schemes; rewetting measures which involve the creation of pools on areas on blanket bog are undoubtedly good for aquatic biodiversity but could increase carbon emissions per unit area of peatland.

7.3.1 Macroinvertebrate biodiversity

The overarching finding from Chapters 3 and 4 is that the creation of drain-blocked pools on areas of blanket bog benefits aquatic biodiversity by creating suitable living space for aquatic taxa, some of which are characteristic of acid-mire pool habitats (Boyce, 2004). This is a key finding given the importance of the British Isles as a host of globally-scarce blanket bog habitat (Lindsay, 2010). There was evidence that the reprofiling methodology led to increased macroinvertebrate diversity within the pools when compared to the creation of L-shaped pools. This was true for all taxa combined, as well as for the chironomid and beetle datasets. Indeed, reprofiled pools appeared to be as biodiverse as natural pools with regards to beetle communities. The reasons for increased biodiversity in reprofiled pools are unclear, but it may be that, as the method involves redistributing existing vegetation onto the reprofiled drain edges, a more complex submerged vegetation structure exists within the pool, thus increasing habitat heterogeneity. However, although the L-shaped pools were less diverse overall, they were found to be important habitats for Odonata, which, in Chapter 3, were found almost exclusively at one site with L-shaped pools (Yad Moss).Although there was no significant relationship between pool dimensions and biodiversity, the research indicated some potential benefits to be gained by creating larger pools. Firstly, larger, deeper pools are more likely to persist (i.e. it would take longer for them to in-fill) allowing time for the more characteristic bog pool communities to assemble, which ties in with the findings from the chronosequence study reported in Chapter 4. Furthermore, Odonata, which are among the most charismatic taxa found in peatland pools, and may reasonably be considered as a flagship taxon by which to measure the success of restoration programs, displayed higher abundance in the largest pools (Chapter 3) and also the oldest pools (Chapter 4). Finally, the reprofiled pools, which were on average more diverse than either the other two pool types, were also among the deepest, despite the general aim of method being to create a shallower drain profile. This is most likely because reprofiling is often carried out in areas with larger drains, partly to facilitate the escape of any wildlife or livestock from the ditches (Armstrong et al., 2009). However, it is likely that some conservation bodies presently create shallow pools deliberately, with a view to them infilling and revegetating, as the regeneration of peat-forming vegetation typically associated with bog landscapes is often a rationale underpinning restoration schemes (Armstrong et al., 2009). The benefits to terrestrial plant diversity afforded by this approach would negate the some of the benefits to aquatic diversity (and the associated benefits to moorland birds which feed on the aquatic taxa) identified by this study, so there is a need to communicate this information to conservation agencies.

The results from this thesis also suggest that creation of uniformly deep pools in every blocking scheme will not provide the optimum conditions for gamma diversity. This was evidenced firstly by the fact that the most taxonomically rich site in Chapter 3 was Harwood Fell, where the two natural pools had a mean depth of only 11 cm. Secondly, the benefit of maintaining some shallow pools was suggested by the exclusive presence of the two ‘notable’ beetle species; *E. affinis* and *E*. *ochropterus*, along with by far the largest population of the acid-more specialist beetle; *H. obscurus,* at Butterburn Flow. This site had relatively low taxonomic richness and abundance, with very shallow pools full of mainly decaying *Sphagnum*, so the presence of the aforementioned beetles there illustrates that even sites which may superficially appear to be ecologically poor can be vital in supporting biodiversity at a landscape level (Williams et al., 2003, Biggs et al., 2005). It is also worth noting that Butterburn Flow was the most northerly site, nearest to the border with Scotland, which suggests a geographical bias with regards to the presence of rare and endangered bog pool taxa. Indeed, the only IUCN Red Data Book taxon identified on mainland Britain as part of the literature review in Chapter 2, the caddisfly species *Nemotaulius punctatolineatus*, was found in the Flow Country in Scotland (Towers, 2004). This may be because some peat landscapes in Scotland host far more natural pool complexes than do those in England, so it may simply be a matter of time before the rare taxa which have established there can effectively disperse to the new habitat further south. Thus, continued and broader-scale monitoring of pools created by ditch blocking is recommended to identify colonisation by any rare or endangered taxa.

The importance of between-pool heterogeneity was also highlighted in Chapter 4, wherein I found that pools in the 5-8 years age class had the highest levels of taxonomic richness and abundance. Whilst this could have been due to their comparatively larger size, it could also have been explained by the greater variation in inter-pool vegetation cover compared to the younger pools (mainly open water) and older pools (nearly all 100% cover). This tentative finding is worth further research and could extend blocking recommendations to include, not just initial blocking methodology, but also management of the vegetation cover in the years following blocking. Overall, it is recommended that drain-blocking programs wishing to maximise benefits for aquatic taxa aim to create a range of pools of different sizes to enhance gamma diversity. A more tentative recommendation to increase gamma diversity involves maintaining vegetation cover at different levels in different pools.

The results of my study generally agree with others undertaken across the northern hemisphere, which show that pools created by peatland rewetting measures are beneficial to peatland aquatic biodiversity (Table 7.1). In the UK this expansion of aquatic habitat on areas of blanket bog is undoubtedly beneficial to peatland aquatic biodiversity. However, in areas where there is a wider range of existing aquatic habitat, such as on heterogeneous raised bog in the Netherlands, the homogenising effect of rewetting measures has been shown to be detrimental, by destroying niche habitats inhabited by rare and endangered taxa (Verberk et al., 2010a).

Table 7.1. A comparison of the key findings and conclusions with other studies looking at the ecology of lentic habitat on restored peatlands across Europe and North America. Abbreviations: A = Artificially-created pool; N = naturally-formed pool; P = plants; Am = amphibians, B = birds. Elo et al. (2015) focused only on Odonata. Adapted from Brown et al. (submitted)

	UK		Netherlands			Canada	Ireland	Finland
Key findings/conclusions	**This thesis**	**(Brown et al., submitted)**	**(van Duinen et al., 2003)**	**(Verberk et al., 2006b)**	**(Verberk et al., 2010a)**	**(Mazerolle et al., 2006)**	**(Hannigan et al., 2011)**	**(Elo et al., 2015)**
Physicochemistry similar across pool types	x	✓			✓	pH: A>N	✓	
Invertebrate taxonomic richness higher in artificially-created pools	✓	✓	A ~ N			A < N	A ~ N	
Similar invertebrate community structure in artificial and natural peat pools	✓	✓		✓	✓		✓	
Important habitats for diverse assemblages of Chironomidae	✓	✓	✓	✓	✓		✓	
Coleoptera colonised artificially-created pools readily	✓	✓	✓	✓	✓	✓	✓	
Odonate populations establish in artificially-created pools	✓	✓	✓	✓	✓	✓	✓	✓
Potential benefits for organisms other than invertebrates	✓Am, B	✓Am, B	✓P			✓P, Am		

Overall, though, it is probable that the benefits to UK aquatic taxa evidenced by my research will also be felt in other countries where significant new expanses of water have been created by peatland rewetting measures, e.g. in Canada (Mazerolle et al., 2006, Waddington and Day, 2007), Ireland (Hannigan et al., 2011, Wilson et al., 2013) and countries in Northern Europe such as Estonia, Sweden and Finland (Tuittila et al., 2000, Vasander et al., 2003, Elo et al., 2015). Although my research concentrated on macroinvertebrates, other benefits to biodiversity are apparent. For example, the blocked pools at Moor House provided the first ever UK specimens of the green alga *Saturnella saturnus* (Beadle et al., 2014), whilst other studies have recorded benefits for amphibians and aquatic plants (Table 7.1). During the course of my fieldwork, I also encountered adult and juvenile amphibians at several sites, and the potential benefits of pool creation to moorland bird populations, in the form of additional food and water resources, are large. Furthermore, the creation of new freshwater habitat may provide future refuge for aquatic taxa forced to migrate upwards / polewards in the face of climate change (Walther et al., 2002, Rosset and Oertli, 2011). These ideas require further study to be substantiated, but its seems highly likely that there are combined ecological benefits to be afforded by peatland pool creation, which should provide management agencies with further justification to continue with future peatland restoration that includes new waterbody creation.

7.3.2 Pool metabolism and biogeochemistry

The main finding from Chapter 5, that newly drain-blocked pools are strongly heterotrophic, and that they tend to emit more carbon per unit area than other types of lentic waters and also than surrounding terrestrial peat, is obviously one that needs to be taken into consideration when planning future drain-blocking schemes. The best mitigation measure to prevent net CO_2 release would be to infill drains completely or use reprofiling alongside damming to create shallow pools which will infill more quickly than those which are simply dammed. This would, however, negate most of the benefits to biodiversity, outlined in section 7.3.1, that larger-scale pool creation would afford. Also, the negative impact of drain-blocking on aquatic carbon emissions needs to be viewed in the light of its potential to reduce terrestrial carbon emissions. Increasingly, the role of drain-blocking in restoring peatland C-sink function has been cited as a benefit (Green et al., 2014). This is because peatland restoration (if successful) raises the water table (brings it closer to the surface), thus reducing the thickness of the aerobic layer which, in turn, should reduce overall rates of aerobic peat decomposition and consequently CO_2 losses to the atmosphere (Green et al., 2014). So, although small, drain-blocked pools in the UK number in the hundreds of thousands (a conservative estimate), their cumulative surface area is tiny in comparison to the overall surface area of blanket bog in the UK, meaning that blocking could still return peatlands that are net C sources into sinks. However, to quantify this broad theory, more data on the comparative size of aquatic and terrestrial surface areas and the corresponding CO_2 fluxes from each are required. Furthermore, the presence of pools might make the terrestrial peatland more resilient to drought events with regards to carbon loss and peat decay.

Drain-blocking may increase terrestrial CH_4 fluxes because, as the aerobic layer decreases, the anaerobic layer increases, potentially leading to increased rates of methanogenesis (CH_4 production) and also reducing the area over which methanotrophy (methane consumption) can occur (Baird et al., 2009). As CH_4 is a more potent greenhouse gas than carbon dioxide, this may negate the decrease in terrestrial CO_2 emissions brought about by drain-blocking. Estimates of aquatic CH_4 fluxes of were not obtained by my study, as one of the recognised drawbacks of the diel DO change technique is that it does not account for anaerobic respiration (i.e. CH_4 losses). However, the DO profiles obtained in Chapter 6 allow me to infer that CH_4 may build up at the anoxic pool bottoms, when pools are stratified due to the overlying thermal boundary, and that this will eventually result in increased fluxes to the atmosphere. Such fluxes may not be immediate, as the gas cannot diffuse easily through thermally stratified boundaries, but these boundaries will break down at some point (typically diurnally), enabling the methane to reach the surface waters where it can diffuse out into the air. Results from an experimental study based at the Migneint, North Wales, suggested that CO_2 and CH_4 fluxes were not significantly different between blocked and open ditches, including both pool and terrestrial habitat comparisons (Green et al., Unpublished). However, these results came with the caveat that the effect of drain-blocking on the water table level at the site was minimal.

Based on my findings, the impact of temporary thermal stratification on the biogeochemistry, not just of peatland pools but in all types of shallow lentic habitats, warrants further research. As well as potentially influencing gas fluxes, carbon cycling and the movement of aquatic biota, diurnal stratification has important consequences for basic sampling methodologies (e.g. metabolism estimates and measurements of DOC) which may provide invalid results if stratification is not accounted for. The extent of shallow aquatic habitat, globally, is potentially huge. Scheffer (1998) asserts that in some countries, such as the Netherlands and Denmark, almost all the lakes are shallow, and studies of shallow lakes have been conducted in the UK (James et al., 2003) China (Xing et al., 2005), Africa (Ganf, 1974), Brazil (Jeppesen et al., 2007) and Japan (Takamura et al., 2003). Shallow stormwater ponds have been created extensively across North America, due to the assumption that small depths means ponds are well mixed both horizontally and vertically (Persson, 2000). My research provides strong evidence that this assumption might be erroneous, and gives extra impetus to authors who are now questioning the validity of this assumption and studying the possible consequences of temporary stratification in stormwater ponds (McEnroe et al., 2013).

7.3.3 An holistic overview

This thesis has generally dealt with the biodiversity, metabolism and stratification of peatland pools as separate entities when, obviously, all three are closely entwined. For example, without pool biota there would be no metabolism, and the balance of autotrophic to heterotrophic organisms together with prevailing environmental conditions combine to determine the balance of oxygen to carbon dioxide. Similarly, the severe diurnal thermal stratification experienced by many peatland pools will impact strongly not only on the gas cycling regimes, as gases are unable to diffuse through the thermal boundaries, but also on the biological communities. Stratified pools display extreme variation in temperature throughout the water column, which changes rapidly in the course of 24 hours. This temperature gradient is associated with a corresponding depletion or accumulation of gases at different depths (e.g. oxygen depletion and methane build-up at the pool bottom). Thus the biota which inhabit the pools need either to be able to migrate vertically to find optimum conditions (i.e. strong swimmers like dytiscid beetles) or be able to tolerate extreme conditions (i.e. like chironomids in the pools sediments). Diurnal stratification may therefore act as a long-term stressor, and may help to explain both the community assembly and generally low biodiversity in small, peatland pools as much as aspects like low nutrient levels and acidic conditions.

7.3.4 Key contributions of the thesis to knowledge of artificial peatland pool ecosystems

This thesis set out to increase our understanding of the environmental characteristics, macroinvertebrate communities and metabolism of drain-blocked pools located on blanket bog in the UK, and to compare them to naturally-occurring pools. This has been achieved by:

1. Increasing our current understanding of the environmental characteristics and macroinvertebrate communities of both natural and drain-blocked pools, as well as analysing the potential impacts on biodiversity of two different and widely-used blocking methods.
2. Demonstrating how the macroinvertebrate communities of drain-blocked pools change over time, and identifying the main potential drivers behind such changes.
3. Advancing our knowledge of the role that newly-blocked pools play in the peatland carbon cycle and identifying the potential impacts that temporary thermal stratification may have on their biogeochemical processes.

This study has significantly improved our understanding of the spatial and temporal distribution of macroinvertebrate communities in peatland pools and their response to drain-blocking. It has also demonstrated the importance of incorporating carbon fluxes from drain-blocked pools into peatland carbon budgets, whilst refining the methods for doing so, particularly to account for inconstant gas fluxes caused by temporary stratification events. Previous research analysing the effects of drain-blocking has concentrated almost exclusively on hydrological aspects such as loads of DOC and discoloration in upland streams (Wallage et al., 2006, Armstrong et al., 2010).

However, my research has provided a step-change in the evidence base on peatland aquatic biodiversity and ecosystem functioning, by undertaking the most comprehensive study of UK artificial peatland pool ecosystems to date. Stakeholders including upland management organisations, conservation groups, regulators and policy makers now need to incorporate this detailed new evidence into their future peatland restoration policy making process, to ensure that peatland restoration and management decisions are made with due regard to the whole range of system properties (e.g. biodiversity, water quality, hydrology, C sequestration).

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Appendices

Appendix A List of taxa

A list of all taxa identified by chapter, along with acid mire designation, where applicable, based on Boyce (2004). For the purposes of statistical analysis, taxonomic adjustment was applied by combining the following taxa: (i) *Limnephilus* spp and *Limnephilus coenosus*, (ii) *Plectrocnemia* spp and *Plectrocnemia conspersa*, (iii) *Nemoura spp* and *Nemoura cambrica*, (iv) Gerridae nymphs and *Gerris costae*, (v) Corixidae nymphs and *Callicorixa wollastoni* (vi) Anisoptera nymphs and *Aeshna juncea*, (vii) Zygoptera nymphs and *Pyrrhosoma nymphula* and (viii) Tanypod spp and *Macropelopia*.

Order	**Taxon**	**Chapter 3**			**Chapter 4 Moor House**	**Chapter 4 Chronosequence**			**Acid Mire Status**
		Natural	**Reprofiled**	**L-shaped**	**4 - 18 months**	**<3 years**	**5-8 years**	**10+ years**	
Coleoptera (adults)	*Agabus bipustulatus*	✓	✓	✓	✓	✓	✓	✓	
	Agabus congener						✓		B
	Agabus guttatus		✓						
	Anacaena globulus	✓	✓	✓		✓	✓	✓	
	Enochrus affinis	✓							A
	Enochrus ochropterus	✓							
	Gyrinus Substratiatus				✓		✓		
	Helophorus aequalis					✓	✓		
	Helophorus flavipes	✓		✓	✓	✓	✓	✓	C
	Hydrobius fuscipes	✓	✓			✓	✓		
	Hydroporus discretus	✓	✓	✓	✓				

	Hydroporus gyllenhalii	✓	✓	✓		✓	✓	✓	B
	Hydroporus incognitus	✓	✓				✓		
	Hydroporus melanarius		✓			✓		✓	C
	Hydroporus memnonius		✓				✓		
	Hydroporus morio Aube	✓	✓		✓	✓	✓	✓	B
	Hydroporus nigrita		✓	✓	✓	✓	✓	✓	
	Hydroporus obscurus	✓	✓	✓			✓		B
	Hydroporus palustris	✓							
	Hydroporus pubescens	✓	✓	✓	✓	✓	✓	✓	
	Hydroporus tristis	✓	✓	✓	✓	✓	✓	✓	C
Coleoptera (larvae)	Chrysomelidae larvae	✓							
	Dytiscidae larvae	✓	✓	✓	✓	✓	✓	✓	
	Hydrophilidae larvae	✓							
	Scirtidae larvae	✓	✓	✓					
Collembola	Collembola spp	✓	✓	✓	✓		✓	✓	
Diptera (chironomidae)	*Ablabesmyia*				✓				
	Acamptocladius reissi						✓	✓	
	Acricotopus lucens							✓	
	Chaetocladius dentiforceps					✓		✓	
	Chironomus anthracinus	✓	✓	✓	✓	✓	✓		
	Chironomus plumosus	✓	✓	✓	✓	✓	✓		
	Chironomini spp		✓		✓	✓	✓		
	Corynoneura arctica	✓		✓	✓	✓	✓	✓	
	Corynoneura scutellata				✓		✓		
	Corynoneura type A		✓		✓		✓	✓	
	Corynoneura spp.	✓	✓	✓	✓	✓	✓	✓	
	Glyptotendipes barbipes	✓	✓	✓	✓	✓	✓	✓	

	Limnophyes		✓		✓		✓	✓	
	Macropelopia	✓	✓	✓	✓	✓	✓	✓	
	Metriocnemus eurynotus					✓		✓	
	Metriocnemus terrester						✓		
	Microspectra contracta		✓						
	Microspectra junci			✓	✓			✓	
	Microspectra spp					✓			
	Orthoclad sp	✓	✓		✓	✓			
	Parametriocnemus				✓	✓			
	Polypedilum nubeculosum	✓	✓	✓		✓	✓		
	Procladius				✓				
	Psectrocladius obvius	✓	✓	✓	✓	✓	✓	✓	
	Pseudorthocladius				✓	✓			
	Stempellinella/Zavrelia	✓							
	Tanypodinae spp	✓	✓	✓		✓		✓	
	Tanytarsus mendax	✓	✓	✓	✓	✓			
	Tanytarsus pallidicornis	✓	✓	✓	✓	✓	✓		
	Tanytasini sp	✓	✓	✓	✓	✓	✓	✓	
	Zalutscia mucrontata	✓	✓	✓	✓	✓	✓	✓	
Diptera (other)	*Ceratopogininae*	✓						✓	
	Chaoborus spp.			✓			✓		
	Eutonia spp.	✓			✓	✓	✓	✓	
	Pedicia spp.			✓				✓	
	Phalacrocera replicata					✓	✓		
	Pilaria spp.	✓	✓						
	Tabanidae							✓	
	Tipula spp.	✓			✓	✓			

Hemiptera	*Callicorixa wollastoni*	✓	✓	✓	✓	✓	✓		C
	Corixidae nymphs	✓	✓	✓	✓	✓	✓	✓	
	Gerris costae	✓	✓	✓	✓	✓	✓		B
	Gerridae nymphs	✓	✓	✓	✓	✓	✓		
	Sigara nigrolineata				✓				
	Immature velia		✓				✓	✓	
Megalopetra	*Sialis lutaria*	✓	✓	✓					
Odonata	*Aeshna juncea*			✓			✓	✓	C
	Anisoptera nymph						✓	✓	
	Pyrrhosoma nymphula			✓			✓	✓	
	Zygoptera nymph						✓		
Oligochaeta	*Enchytraidae* spp				✓	✓		✓	
	Lumbriculidae spp							✓	
	Tubificidae spp					✓			
Plecoptera	*Nemoura cambrica*		✓	✓	✓	✓	✓	✓	
	Nemoura spp		✓		✓		✓	✓	
Trichoptera	*Limnephilus coenosus*	✓	✓	✓	✓	✓	✓	✓	A
	Limnephilus centralis							✓	
	Limnephilus spp						✓	✓	
	Plectrocnemia conspersa		✓	✓	✓	✓	✓	✓	
	Plectrocnemia spp				✓		✓		
Trombidiformes	Hydracarina	✓		✓			✓	✓	

Appendix B List of sampling dates for Chapter 5

		May-13	Jun-13	Jul-13	Aug-13	Sep-13	Oct-13	Nov-13	Dec-13	Jan-14	Feb-14	Mar-14	Apr-14	May-14
Core Pools	**MHM01**	14-May	^		20-Aug	10-Sep	10-Oct		04-Dec			11-Mar	09-Apr	28-May
	MHM02	14-May	11-Jun		20-Aug	10-Sep	10-Oct		04-Dec			11-Mar	09-Apr	28-May
	MHM03	14-May	11-Jun		20-Aug	10-Sep	10-Oct		04-Dec			11-Mar	09-Apr	28-May
	MHM04	14-May	11-Jun		20-Aug*	10-Sep	10-Oct		04-Dec			11-Mar	09-Apr	28-May
	MHM05	14-May	11-Jun		20-Aug	10-Sep	10-Oct		04-Dec			11-Mar	09-Apr	28-May
Summer Pools	**MHM06**			13-Jul										
	MHM07			13-Jul										
	MHM08			24-Jul										
	MHM09			24-Jul										
	MHM10				14-Aug									
	MHM11				14-Aug									
	MHM12				18-Aug									
	MHM13				20-Aug									
	MHM14				22-Aug									
	MHM15				22-Aug									

^ No data obtained for this pool on this date due to equipment failure

* No water chemistry data available for this sample due to spoilt water sample