The Effects of Season, Habitat, Hydroperiod and Water Chemistry on the Distribution of Turlough Aquatic Invertebrate Communities

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Declaration

I declare that this thesis is entirely my own work, except where otherwise stated, and that it has not previously been submitted to this or any other university. I give my permission to the library to lend or copy this thesis on request.

Gwendolin Porst

Summary

The aim of this study was to investigate the effects of season, habitat, hydroperiod and water chemistry on the distribution of turlough aquatic invertebrate communities. Twenty-two turloughs, selected as representative of geographical distribution and hydrological conditions were included in the study. A comparative study of eight turloughs representing a nutrient gradient determined macroinvertebrate community distinctiveness in a stratified sampling design and related assemblage structures to environmental variables. Assessment of macroinvertebrate temporal and spatial variation was the objective of separate studies conducted in a subset of four turloughs, varying in hydrological and nutrient regimes. The influence of disturbance and habitat characteristics on macroinvertebrate community dynamics was tested. Across twenty-two turloughs macroinvertebrate and cladoceran zooplankton communities were analysed and their relation to varying trophic, hydrological and morphological regimes identified.

For a comparative study of macroinvertebrates eight turloughs were selected to represent a gradient of total phosphorus (TP) concentrations. To allow comparability of turlough macroinvertebrate communities, samples were collected from one habitat type (submerged grassland) in April 2007 using a simple box sampler. Five replicates were collected in every turlough by rapidly lowering the box to the substratum and removing trapped organisms with a net. Community analysis identified highly distinct macroinvertebrate assemblages, indicating that a single or pooled sample can provide a reliable description of turlough macroinvertebrate communities. Hydroperiod influenced mean taxon richness and abundance of macroinvertebrates but no correlation was found between nutrient status and either mean taxon richness or abundance.

In order to study temporal dynamics of macroinvertebrates in turloughs, littoral faunal samples were collected over a one to two year period in four turloughs with differing hydrological and nutrient regimes. Sampling was carried out using a standardised sampling approach. Five replicate samples were collected every month using a box sampler from the dominant turlough habitat, submerged grassland. Macroinvertebrate biodiversity and community structure varied monthly and interannually. A two-phased hydrocycle was identified with permanent residents dominating during the start of the hydrocycle, with an increase of ephemeral taxa over time. Disturbance, as demonstrated by short hydroperiod and high areal reduction rate had an important effect on macroinvertebrate community structure in turloughs, with high disturbance generally supporting lower faunal diversity. Influence of disturbance generally decreased over time leading to a stabilization of macroinvertebrate communities.

For the study of spatial variation of macroinvertebrates in turloughs two habitats were sampled in two turloughs during sampling season 2006/2007 using a box sampler and five replicates were collected in each habitat. Within-habitat variability was assessed by collecting five replicate macroinvertebrate samples from four different submerged grassland habitat sites in four turloughs in sampling season 2007/2008 using the box sampler. While habitat specific preferences were found for some taxa of conservation concern variability of macroinvertebrates within turloughs was nevertheless identified to be smaller than among turloughs. Macroinvertebrate samples collected in any location of the dominant turlough habitat (submerged grassland) were identified as reliable indicators of ecological change of turloughs.

A comparative study of macroinvertebrates and cladoceran zooplankton communities was conducted across twenty-two turloughs, representing a wide hydromorphological and geographical range. Macroinvertebrate samples were collected in November 2006 and April 2007 using a stratified sampling approach. All available habitats in a turlough were sampled proportional to their availability using sweeps with a standard FBA pond net. Three minute sampling time was subdivided proportionally to each habitat's availability. Cladoceran zooplankton and separate chydorid samples were collected from twenty turloughs in April 2007 by horizontal hauls with a zooplankton net from the shore and a perspex tube, respectively. Varying associations of macroinvertebrate as well as zooplankton communities to environmental variables season, TP concentrations, number of habitats sampled and hydroperiod of turloughs were detected. Some macroinvertebrate orders and zooplankton species showed significant relationships with chemical descriptors of nutrient enrichment.

Turlough macroinvertebrate communities are highly distinct and conducive to time and cost-effective monitoring. Collection of a single submerged grassland sample reduces inherent 'noise' and is suited for the detection of pressure gradients. The number of habitats sampled should, however, depend on the objective of the sampling. Sampling for more holistic purposes should be carried out using a multi-habitat sampling approach to obtain a more comprehensive survey of turlough biodiversity. Season had an important influence on macroinvertebrate community structures. Turlough sampling regimes need a flexible approach with timing and frequency of sampling depending on sampling protocol objectives and should be geared towards the start of the flooding season and variable hydrocycles. Turloughs are inherently variable systems which might negate the development of simple type-specific reference conditions as required for lakes under the WFD.

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1 Introduction

1.1 General Research Aims

The overall aim of this study was to investigate the effects of season, habitat, hydroperiod and water chemistry on the distribution of turlough aquatic invertebrate communities. This included comparative studies of the macroinvertebrate and cladoceran zooplankton communities across twenty-two turloughs, representing a wide hydromorphological and geographical range. It was investigated how differences in hydrological, geomorphological and trophic regimes would affect turlough invertebrate biodiversity and community structure. Macroinvertebrate communities of eight turloughs selected to represent a gradient of total phosphorus were studied using a stratified sampling approach and their relation to environmental variables was investigated. Separate studies examined the spatial and temporal variability of macroinvertebrate communities in a subset of turloughs with varying hydrological and nutrient regimes, testing the influence of different disturbance regimes and habitat characteristics on community dynamics.

This project was part of the broader Turlough Conservation Project 'Assessing the Conservation Status of Turloughs' (Turlough Conservation Project: http://www.tcd.ie/Botany/turlough_conservation/). This multidisciplinary project included four PhD projects and two Post-doctoral subprojects, focussing on a range of interconnected aspects of the turlough habitat: Hydrology, algae and hydrochemistry, vegetation, soils, aquatic invertebrate communities, and catchment-scale and within-site management.

1.2 Thesis Outline

This thesis comprises seven chapters, starting with a general introduction and a methods section, followed by four data chapters and concludes with a general discussion and final conclusions. The introduction presents a summary of background information on turloughs, relevant legislation and aquatic invertebrates. The turlough site selection procedure and a summary of general methods used in the subsequent data chapters are outlined in Chapter two. A comparative study of eight turloughs determines the distinctiveness of macroinvertebrate communities and investigates their relationship to selected environmental variables in Chapter three.

This is followed by a more detailed study on the temporal patterns of macroinvertebrate communities in turloughs investigating the importance of disturbance on successional processes of macroinvertebrates. Chapter five explores the among- and within-habitat variability of littoral macroinvertebrate communities and tests the usefulness of a single grassland habitat sample collected in any location of a turlough for monitoring purposes. Chapter six assesses macroinvertebrate and cladoceran zooplankton community structures across a range of turloughs and investigates the effect of differing hydrological, morphological and trophic regimens on the faunal communities. The final chapter discusses the overall findings of the research and draws conclusions for monitoring and conservation of turloughs and their invertebrate communities.

1.3 Turloughs

Temporary wetlands are common throughout the world (Studinski and Grubbs, 2007; Williams, 2006). However, some temporary wetland types such as turloughs (temporary filling carboniferous limestone ponds or lakes) are restricted geographically owing to climate and geology (Reynolds *et al.*, 2004). Turloughs are most abundant and found in their greatest variety throughout the Western third of Ireland, a region characterized by frequent rainfall and karstified carboniferous limestone (Sheehy Skeffington *et al.*, 2006). Particularly the karstic limestone regions of south County Galway, north County Clare, County Mayo, including the Burren region, and County Roscommon where thin or no glacial drift cover is found, harbour a large number of turloughs (Ní-Bhriain *et al.*, 2003; Ní-Bhriain *et al.*, 2002; Reynolds, 1982; Sheehy Skeffington *et al.*, 2006). More isolated turloughs occur in Counties Cork, Donegal, Fermanagh, Kilkenny, Leitrim, Limerick, Longford, Monaghan, Sligo, Tipperary and Westmeath (Goodwillie, 2003; Reynolds, 1982, 1996; Sheehy Skeffington *et al.*, 2006). Turlough-like water bodies have also been described in Wales at Pant-y-llyn (Blackstock *et al.*, 1993), in Catalonia (Boix *et al.*, 2001), in Slovenia and eastern Canada (Coté *et al.*, 1990), although these differ from turloughs in terms of seasonality, hydrology, size or geomorphology (Coxon, 1986).

Carboniferous limestone differs from many other rock types owing to its solubility by rainwater. It can hold large volumes of water hidden in cracks and cavities or

leading them underground through channels either to a spring or into the sea (Goodwillie and Reynolds, 2003). In most rock types, groundwater flows very slowly (from just a few centimetres to a few meters per day), but in karstified limestone the flow rate can be, in some cases, up to 100 metres per hour or more (Coxon and Drew, 1986; Drew, 1990). When the underground water, which is carrying dissolved limestone as calcium bicarbonate comes in contact with air, CO_2 is released, leading to the deposition of marl or calcite in the basin (Goodwillie *et al.*, 2003). As a result turloughs typically have high alkalinities and high pH (Goodwillie, 2003).

Turloughs are not true lakes, even though they support an aquatic fauna, as they reveal a variety of wet grassland and fen type vegetation when drying up in summer (Sheehy Skeffington *et al.*, 2006). They usually fill and empty through underground passages and estavelles (sinkholes that also act as a spring) with some turloughs obtaining their major water input from inflowing streams or rivers (Coxon, 1986; Goodwillie, 1992; Goodwillie *et al.*, 2003). Although not strictly seasonal, turloughs generally flood in response to variations in the local water table in autumn and empty in spring (Figure 1.1) (Ní-Bhriain *et al.*, 2003). However, water levels may also rise sporadically during periods of high rainfall, reflecting local weather conditions (Reynolds *et al.*, 1998; Visser *et al.*, 2006). Owing to differences in size, depth and karstic bedrock, speed at which turloughs fill and empty can vary enormously, as does the modality of increase and decrease in water levels during the flooded period. Coxon (1986) derived associations with both duration and depth of inundation and soil composition. She associated turloughs containing sand/silt and silt/clay mixtures with short flooding durations. Turloughs with peat and marl were shown to be associated with longer duration of flooding. Silt/clay or peat type turloughs tend to be shallow (<1 m or 1-2 m), while marl can be found in slightly deeper turloughs (2-3 m), sometimes acting as a barrier against drainage, which may cause some water to be retained (Goodwillie *et al.*, 2003). Turloughs are generally dry and used as pastures in summer (Reynolds, 1982), yet, some basins may contain still or flowing waters throughout the year (Goodwillie *et al.*, 2003). Owing to their temporary nature, Reynolds (1996) described turloughs as ‘ecotones’, zones of transition between aquatic and terrestrial systems.

Turloughs are variable in size, extending from a few hundred square metres to several square kilometres (Coxon, 1987b). To date over 300 active turloughs have been documented and the size of about 100 is known (Sheehy Skeffington *et al.*, 2006) most of which are smaller than 10 ha. The distribution and extent of turloughs are remnants of a vast complex of turloughs and other wetlands that have been drained during successive waves of state- and EU-funded arterial drainage works mainly to increase agricultural land (Visser *et al.*, 2007). Following drainage schemes from the 19th century to the present, only one turlough larger than 200 ha remains (Rahasane in Co. Galway; approximately 260 ha). In a study on 90 turloughs over 10 ha in size Coxon (1986, 1987a) identified one third as irreversibly damaged by drainage. The land in which turloughs are located is often owned as 'commonage' by numerous landowners and frequently used as pastures for cattle, sheep and even horses or domestic geese (Sheehy Skeffington *et al.*, 2006). The intensification of grazing practices and the introduction of agriculture of greater intensity also cause a major threat to the turlough environment, by potentially increasing nutrient inputs (manure or fertilizer) to the system (Goodwillie, 2001; Ní-Bhriain *et al.*, 2003; Ní-Bhriain *et al.*, 2002).

Figure 1.1: Garryland turlough July 2006 (top) and November 2006 (bottom). The arrow indicates the same tree in both pictures.

1.4 Legislation affecting Turloughs

Turloughs are classified as priority habitats under the European Habitats Directive (92/43/EEC) (EEC, 1992) and many are candidate Special Areas of Conservation (cSACs). A priority habitat is classified as a natural habitat that is in danger of disappearing. The purpose of the directive is to 'maintain or restore at a favourable conservation status, natural habitats and species of wild fauna and flora of Community interest' by designation of Special Areas of Conservation (SACs). To allow this, relevant landowners have been issued with a list of 'notifiable actions', which restricts certain activities to be carried out within the 'buffer area', comprising 50 m from the level of high water of a turlough, without prior ministerial consent. There are seventeen main 'notifiable actions' for turloughs, ten of which are related to agriculture such as grazing above a 'sustainable level' (according to definition in farm plans) or fertilizer application of any type within the buffer zone (Goodwillie, 2001; Ní-Bhriain *et al.*, 2003). In Ireland, owners of land formally designated as SACs are bound to manage these areas according to management plans drawn up by the Irish National Parks and Wildlife Services or alternatively adopt a Rural Environmental Protection Scheme (REPS) plan (Ní-Bhriain *et al.*, 2003). Under Article 17 Member States are required to report on the implementation of the Habitats Directive including conservation status, at time intervals of six years.

Currently, in the Republic of Ireland, seventy-one turloughs are included in forty-three candidate SACs, of which eight are identified as Special Protection Areas (SPA) under the Birds Directive (EEC, 1979) and one is a Nature Reserve (Sheehy Skeffington *et al.*, 2006; Working Group on Groundwater, 2004). Additional turloughs are likely to be designated as Natural Heritage Areas under the Wildlife (Amendment) Act, 2000.

The Water Framework Directive (2000/60/EC) (WFD) was established in response to increasing anthropogenic pressures on aquatic systems in the European Union (EC, 2000). It establishes a comprehensive basis for the management of water resources in Europe and rationalises and updates several pre-existing Directives in the area of water policy. The WFD encompasses all inland flowing and standing surface waters, transitional waters, coastal waters and groundwaters and stipulates the need for an integrated strategy to protect and manage river basins, thus including

turloughs within an appropriate 'river basin district' (EC, 2000). For the purpose of the WFD, turloughs are classified as Groundwater Dependent Terrestrial Ecosystems (GWDTE) as their aquatic phase is not permanent. They represent an extreme case of this category as they are connected directly to the groundwater table (Kilroy *et al.*, 2005; Working Group on Groundwater, 2004). The Directive requires the establishment of a typology for all surface water bodies ('ecotypes') and the definition of respective reference conditions, but the requirements for GWDTE are presently unclear. The WFD demands that European member states achieve at least 'good ecological status' for all European water bodies through 'programmes of measures' by 2015 and has initiated changes of water quality concepts and assessment (Solimini *et al.*, 2006). Annex five of the directive explicitly requires that biological variables are considered as indicators of water quality, thus, including the 'composition and abundance of benthic invertebrate fauna' for all surface water systems. In order to obtain 'good ecological status' under the WFD, turloughs must meet their Habitats Directive objective of 'favourable conservation status' where it is dependent on their water needs.

1.5 Littoral Benthic Macroinvertebrates

The littoral zone of freshwater systems is the part of the benthos and its overlying water which falls between the shore and the deepest point at which sufficient light for photosynthesis for plants or algae can penetrate, representing the extent of the euphotic zone (Moss, 1998; Wetzel, 2001). The littoral zone can play an important part in the energy budget of lentic ecosystems and whole-lake functioning (Blumenshine *et al.*, 1997; Vadeboncoeur *et al.*, 2002). In shallow lakes, which include most turloughs, the littoral zone can be extensive, increasing its influence on within-lake processes compared with deeper, stratified lakes. It generally supports diverse biotic communities owing to *inter alia* high habitat heterogeneity, good light, food and oxygen conditions (Brodersen *et al.*, 1998).

Littoral benthic macroinvertebrates inhabit the bottom substrates of littoral freshwater habitats for at least part of their lifecycles (Rosenberg and Resh, 1993a). They range in size from only a few millimetres to several centimetres, but are generally visible by the naked eye. Macroinvertebrates are commonly defined as the part of the faunal community which can be retained by mesh sizes of ≥200-500 μm,

comprising a variety of taxa, including insects, annelids, molluscs, flatworms and crustaceans. They play an essential role in key ecological processes in the littoral zone by forming an important link between primary producers, detrital deposits and higher trophic levels in aquatic food webs (Stoffels *et al.*, 2005; Vadeboncoeur *et al.*, 2002; Blumenshine *et al.*, 1997). Macroinvertebrates can occupy a variety of substrates ranging from fine to coarse sediments, submerged and emergent vegetation, debris, filamentous algae to various other natural or artificial habitats (Rosenberg and Resh, 1993b). Not only habitat is important for distribution patterns of macroinvertebrates (Hinden *et al.*, 2005; Stoffels *et al.*, 2005; Tolonen *et al.*, 2001; White and Irvine, 2003). Habitat stability and macroinvertebrate adaptations to droughts, floods or other disturbances have been described to fundamentally influence macroinvertebrate community structures of temporary freshwater habitats (Collinson *et al.*, 1995; Schneider and Frost, 1996; Wiggins, 1980; Williams, 2006). Proximity of habitats for oviposition (Brooks and Lewington, 1997), nutrient trophic state (Brauns *et al.*, 2007; Brodersen *et al.*, 1998; Rader and Richardson, 1994) and seasonal variation in life-cycles, macroinvertebrate succession and seasonal influx of aerial colonizers (Boix *et al.*, 2004; Brooks, 2000; Cayrou and Céréghino, 2005; Jocqué *et al.*, 2007) among other variables also contribute significantly to ecological processes and dynamics in macroinvertebrate communities.

Benthic macroinvertebrates are most frequently recommended as monitoring tools for the assessment of water quality in rivers (Hellawell, 1986). Although chemical and physical measurements are also used to define the ecological status of surface waters, these variables only reflect conditions encountered at time of sampling (Resh *et al.*, 1996). In contrast, biotic elements such as littoral macroinvertebrates represent past and present conditions of water and ecological quality. Their sedentary nature, rather long life histories, diversity, sensitivity to changes in their environment and ubiquitous distribution allows for efficient spatial analysis of pollutants or other anthropogenic influences and disturbance effects (Abel, 1996; Rosenberg *et al.*, 1993a). The occurrence of relatively large numbers of invertebrate species offers a wide spectrum of response to different kind of stress (Hellawell, 1986). While responses of macroinvertebrates to various stressors including nutrient pressures have been studied in less complex habitats of the lake profundal (Brodersen and Lindegaard, 1999; Langdon *et al.*, 2006), research on littoral

macroinvertebrate communities experienced increased research in lakes only in recent years (e.g Brauns *et al.*, 2007; Pinel-Alloul *et al.*, 1996; Tolonen *et al.*, 2001). However, studies on the dynamics and ecology of littoral macroinvertebrates in turloughs are comparatively scarce.

The European Water Framework Directive (WFD) requires assessment of ecological quality of all standing waters (including turloughs), and specifically the inclusion of biotic elements, such as macroinvertebrates, in the assessment and monitoring of lake/turlough ecological status. This, however, requires the prior knowledge of basic community dynamics and ecology, including temporal and spatial variability of macroinvertebrates and response of communities and taxonomic structures to single or multiple stressors.

1.6 Cladoceran Zooplankton

The term 'zooplankton' usually refers to small animals that inhabit the open-water. However, the cladoceran zooplankton also includes the group of Chydoridae (Anomopoda), which are primarily littoral dwellers. Zooplankton are common inhabitants of shallow lakes and ponds. They act as primary consumers of phytoplankton and serve as food source for invertebrate and vertebrate predators, thus representing an important part of lentic freshwater food webs (Irvine *et al.*, 2001a; Mckee *et al.*, 2002). Most cladoceran zooplankton possess a carapace covering the body and include herbivorous types such as *Daphnia* or *Bosmina* and carnivores such as *Polyphemus*, preying on small zooplankton. Grazing by zooplankton can regulate phytoplankton growth (Sterner, 1989) and might stabilize plant communities by improving light conditions through the removal of periphyton (Mckee *et al.*, 2002). The majority of the Chydoridae are detritus feeders and associations with distinct habitats have been found (de Eyto *et al.*, 2003).

Changes in water quality can have an effect on zooplankton communities, either through direct physiological or indirectly through food web processes. Nutrient enrichment, which is one of the major threats to ecological quality of freshwater systems in Ireland, affects zooplankton mainly through greater primary productivity and, thus, enhanced secondary production. Eutrophication and associated high concentrations of filamentous phytoplankton can, furthermore, cause a shift from

large-bodied to smaller bodied species of zooplankton (Moss *et al.*, 1991). Certain chydorid taxa and assemblages have been described as useful indicators of ecological quality of lakes, including turloughs (Duigan and Kovach, 1991; de Eyto *et al.*, 2002; de Eyto *et al.*, 2003; Duigan and Kovach, 1994). Furthermore, chydorid taxon richness has a potential for the assessment of water quality (Irvine *et al.*, 2001a). Increased nutrient input to lakes may result in higher chydorid species diversity through greater nutrient availability. This, however, may result in a subsequent decrease of diversity with increasing eutrophication associated with a switch from plant to phytoplankton dominated habitats, and thus a change in habitat and food availability (de Eyto and Irvine, 2001). This may lead to monospecific chydorid communities of species which can cope with both littoral as well as pelagic food sources (Duigan and Murray, 1987a).

With the aim to fulfil the requirement of the EC Habitats Directive and the WFD of achieving 'favourable conservation status' and 'good ecological status', respectively, understanding the ecology and relation of different biotic groups to multiple stress factors is indispensable. While zooplankton are not referred to in the WFD, their identified response to different stressors in lentic freshwater environments suggests them as useful surrogates for determining ecological change of turloughs.

2 Site Selection and Methodology

2.1 Turlough Selection

In Ireland, turloughs occur most frequently in areas where the extensive carboniferous limestone has only thin or no deposits of glacial till (Coxon, 1987b). Highest densities of turloughs can be found in Counties Clare, Galway, Mayo and Roscommon. Over 300 active turloughs are known and combined hydrological and ecological information, of varying forms and standards, is available for approximately 60 of them (Coxon, 1986; Goodwillie, 1992; Southern Water Global, 1998; Tynan *et al.*, 2005). Twenty-two turloughs were selected for study on the basis of existing hydrological data founded on the hypothesis by Mitsch and Gosselink (2000) that hydrology is the key determinant for the establishment and maintenance of wetland processes. The site selection process was driven by the Project Management and Steering Committee of the broader project 'Assessing the Conservation Status of Turloughs' (Turlough Conservation Project: http://www.tcd.ie/Botany/turlough_conservation/). The twenty-two turloughs were selected in order to represent the hydromorphological and geographical range of turloughs in Ireland (Table 2.1 & Figure 2.1).

Selection of turloughs was based, as far as respective information was available, on the Karstic Flow System hypothesis which suggests that turloughs associated with specific types of karstic flow system (e.g. shallow epikarst, conduit) are associated with specific ecological conditions (Drew, 1990; Southern Water Global, 1998; Tynan *et al.*, 2005). The concept of turlough hydrology is currently subject to change. Where a preliminary classification of karstic flow system was unavailable, selection was based on surrogate hydrological data from Coxon (1986) and other data sources given in Table 2.1. The criteria included information on the mosses *Cinclidotus fontinaloides* and *Fontinalis antipyretica* as a surrogate for duration of flooding of turloughs and on height of *C. fontinaloides* as a measure of depth of flooding of turloughs. Information on groundwater tracing data, deposits and swallow holes was considered as secondary data in the selection process. Access to turloughs was clarified with landowners prior to the start of the project and the finalisation of the site selection. With the exception of Brierfield, Carrowreagh and

Rathnalluleagh, all selected turloughs are designated as candidate Special Areas of Conservation (cSAC) under the EC Habitats Directive (92/43/EEC) (EEC, 1992).

Table 2.1: List of twenty-two turloughs studied, their ID, location, reference to source of hydrological information used for selection and information of karstic flow system.

Turlough	***ID***	***County***	***Hydrological Data Source***	***Postulated Karstic Flow System***
Ardkill	1	Mayo	Coxon (1986), Drew (pers. comm.)	N/A
Ballindereen	2	Galway	Coxon (1986)	N/A
Blackrock	3	Galway	Tynan *et al.* (2005)	Conduit
Brierfield	4	Roscommon	Coxon (1986), Drew (pers. comm.)	N/A
Caherglassaun	5	Galway	Tynan *et al.* (2005)	Conduit
Caranavoodaun	6	Galway	Southern Water Global (1998), Tynan *et al.* (2005)	Shallow epikarst
Carrowreagh	7	Roscommon	Coxon (1986), Drew (pers. comm.)	N/A
Coolcam	8	Galway/ Roscommon	Coxon (1986), Drew (pers. comm.)	N/A
Croaghill	9	Galway	Coxon (1986), David Drew (pers. comm.)	N/A
Garryland	10	Galway	Southern Water Global (1998)	Conduit
Kilglassan	11	Mayo	Coxon (1986), Drew (pers. comm.)	N/A
Knockaunroe	12	Clare	Drew (1990)	Shallow epikarst
Lisduff	13	Roscommon	Coxon (1986), David Drew (pers. comm.)	N/A
Lough Aleenaun	14	Clare	Southern Water Global (1998), Drew (pers. comm.)	Shallow epikarst
Lough Coy	15	Galway	Southern Water Global (1998), Tynan *et al.* (2005)	Conduit
Lough Gealain	16	Clare	Drew (pers. comm.)	Shallow epikarst
Rathnalulleagh	17	Roscommon	Coxon (1986), Drew (pers. comm.)	N/A
Roo West	18	Galway/Clare	Tynan *et al.* (2005)	Shallow epikarst
Skealoghan	19	Mayo	Coxon (1986), Drew (pers. comm.), Moran (2000)	N/A
Termon	20	Galway/Clare	Southern Water Global (1998)	Shallow epikarst
Tullynafrankagh	21	Galway	Southern Water Global (1998), Tynan *et al.* (2005)	Shallow epikarst
Turloughmore	22	Clare	Coxon (1986)	N/A

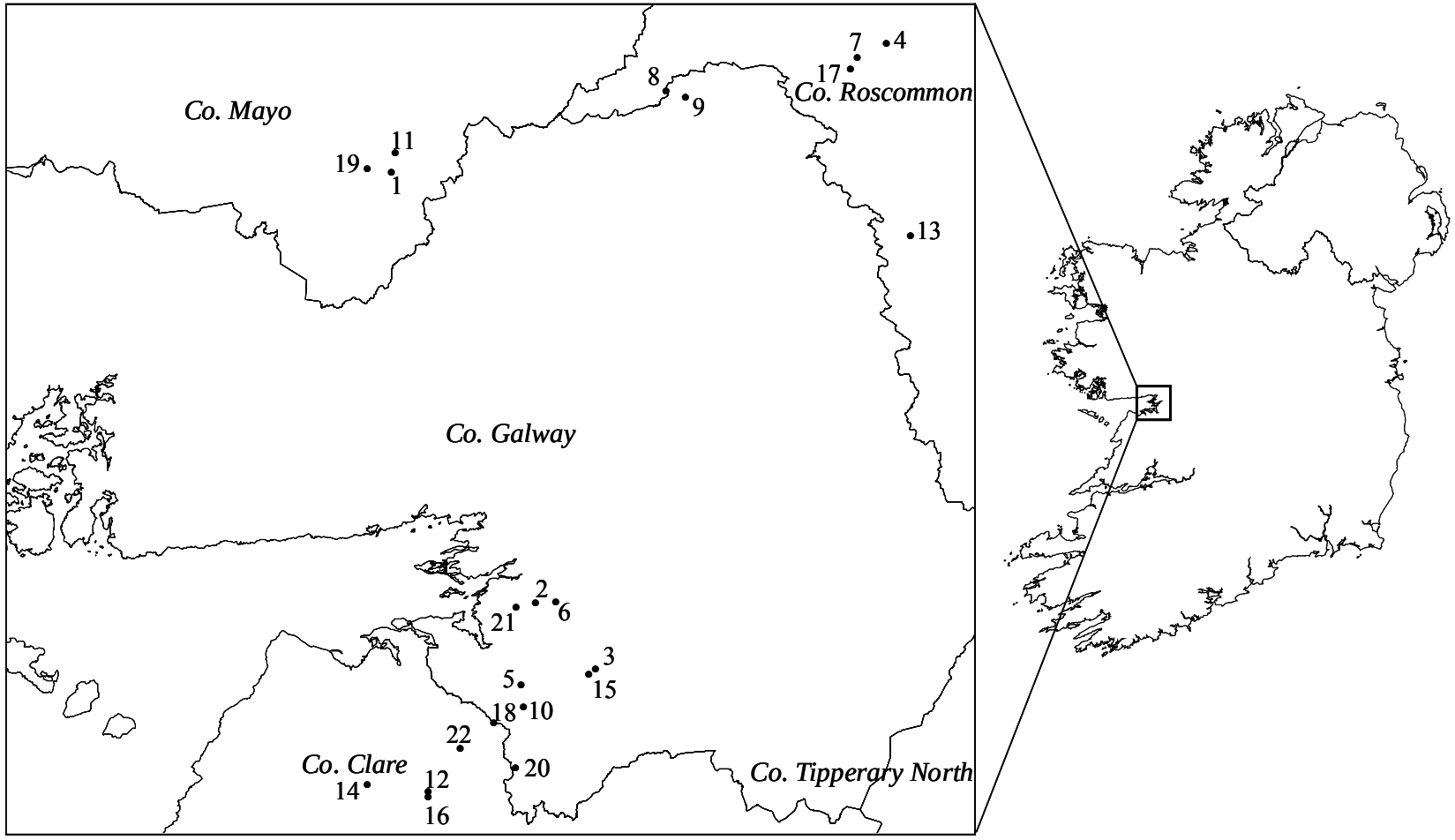


Figure 2.1: Map of Ireland showing the location of twenty-two turloughs selected for study (numbers refer to turlough IDs as indicated in Table 2.1).

2.2 Methodology

2.2.1 Water Chemistry Sampling and Analysis

On every sampling occasion water was sampled using a weighted 5 litre plastic bottle which was attached to a rope and thrown out from the turlough shore. Water samples were analysed for alkalinity, chlorophyll *a*, colour, conductivity, dissolved oxygen, molybdate reactive phosphorus (MRP), pH, silicate, temperature, total nitrogen (TN), total phosphorus (TP), turbidity, the anions chlorine, sulphate, nitrate and the cations calcium, magnesium, potassium and sodium following standard methods in cooperation with a separate PhD study (Helder Pereira) on algae and hydrochemistry of turloughs.

Temperature and dissolved oxygen concentrations were assessed directly in the field using a thermometer and a WTW Oxi 330i water proof dissolved oxygen meter with a CellOx 325 probe. Temperature and dissolved oxygen were not assessed during the second year field season in 2007/2008. Depending on turlough water sample turbidity, 0.3-1.0 L of each sample was immediately filtered in the field station through Whatman® GF/C filter papers using a vacuum filtration system. Each filter paper was stored in a polypropylene centrifuge tube containing 10 ml of methanol and kept in the fridge. The filtrate was kept for subsequent analysis. Back in the laboratory samples were analysed for chlorophyll *a* following methods by the Standing Committee of Analysts (1983). Samples were heated in a water bath at ~ 65-70 ºC until the methanol was boiling and left boiling for 10 second to extract further pigment from the filter papers. After cooling the filter papers were removed and samples centrifuged (8 minutes at 3500 rpm). Chlorophyll *a* contents were assessed by measuring absorbance against a methanol blank at both 665 nm (the chlorophyll *a* peak) and 750 nm (turbidity correction) using a Shimadzu® UV-1700 UV-Visible spectrophotometer.

Turbidity of turlough waters was assessed using a HACH® turbidity meter 2100P on triplicate unfiltered samples. True colour was quantified with a HACH® DR2000 direct reading spectrophotometer by measuring triplicate filtered turlough samples. Silicate concentrations were measured using previously filtered turlough water samples following methods by Grasshoff *et al.* (1999). After preparing a range of

standards (0, 0.5, 1 and 2 mg L^{-1} Si), duplicate water samples and standards were mixed with 0.2 ml of acid molybdate reagent to form silicomolybdic acid (yellow colour) followed by 0.2 ml of oxalic acid reagent and 0.1 ml of ascorbic acid after 10-20 minutes to produce an intensely coloured blue complex. Silicate concentrations were measured after 30-60 minutes at 810 nm on a Shimadzu® UV-1700 UV-Visible spectrophotometer.

Turlough water was analysed for pH by inserting a pH-electrode into 50 ml of unfiltered turlough sample. The pH-electrode and pH-meter were calibrated prior to analysis using Reagon buffer of pH 4 and 7 following recommendations by Davison (1990). pH was read once the reading had stabilised. Alkalinity of turlough waters was measured on 50 ml of turlough sample following methods by Clesceri *et al.* (1998) for high alkalinity lakes. A Metrohm 715 Dosimat automatic dispenser was used to titrate 0.01 M H_2SO_4 into the sample until the pH endpoint 4.5 was reached. Titration was finished within 2 minutes using a magnetic stirrer throughout to ensure that gentle mixing occurred. The millilitres of titrant used were recorded and subsequently multiplied by 20 to obtain turlough alkalinity (mg L^{-1} Ca CO_3). Conductivity of turlough water was measured on approximately 100 ml of sample in a glass beaker using a WTW multimetre Cond 197i; Probe: TetraCon® 325WTW and reported as μsiemens cm^{-1}.

Total phosphorus concentrations were measured using triplicate unfiltered turlough water samples and PO_4-P standards according to the methods by Eisenreich *et al.* (1975). This method is based on the oxidisation of organic matter in samples by acid persulphate (potassium peroxide sulphate $K_2S_2O_8$) digestion at 120ºC converting organically bound phosphorus to phosphate which can be subsequently measured using colorimetry. A volume of 25 ml of each sample and standard was pipetted into an autoclaveable glass bottle and 5 ml digestion reagent added. Bottles were loosely covered with caps and samples autoclaved at 15 psi for 30 minutes. After letting them cool down to room temperature, samples were mixed with 5 ml mixed reagent (containing H_2SO_4, antimony stock, molybdate stock and ascorbic acid). Sample absorbance was measured after colour development on a Shimadzu® UV-1700 UV-Visible spectrophotometer at 882 nm. Molybdate reactive phosphorus (MRP) was measured on filtered turlough samples, immediately on return to a field station,

based on the reaction of phosphate ions (PO_4) with sodium molybdate and antimony potassium tartrate after Murphy and Riley (1962). The resulting compound is reduced to 'molybdenum blue' by ascorbic acid which can be determined spectrophotometrically. 5 ml of each filtered sample were mixed with 1 ml of mixed reagent (containing H_2SO_4, antimony stock, molybdate stock and ascorbic acid) and colour let develop for at least 15 minutes. Concentrations in turlough samples and 2 standards were read at 882nm.

Concentrations of total nitrogen in turlough water samples were determined in triplicate according to Grasshoff *et al.* (1999). This method is based on alkaline persulphate digestion at 120 ºC converting organically bound nitrogen and ammonia to nitrate. Triplicate 50 ml samples and nitrate standards were filled into polypropylene bottles and 5 ml of oxidising reagent added. Samples were autoclaved at 15 psi for 30 minutes and cooled down over night. Nitrate concentrations were measured using a continuous flow auto-analyser (AutoAnalyzer 3, Bran and Luebbe® AACE 5.40).

Nitrate, chloride and sulphate were analysed on turlough water filtrate in duplicate by self regenerated electrolytically suppressed ion chromatography (Dionex-ICS-1500 Ion-chromatographer System; Dionex AS40 automated sampler) (Clesceri *et al.*, 1998). Reading of concentrations of respective anions followed calibration using five standards and calibration was tested using a quality control solution after every ten samples. Calcium, magnesium, potassium and sodium concentrations were measured on filtered turlough samples by flame atomic absorption (Perkin Elmer 3100 Spectrometer) and inductively coupled plasma atomic emission spectroscopy (ICPAES). Samples were mixed with lanthanum chloride to a concentration of 0.4% and 0.1% CsCl contained in a 1% HNO_3 matrix for the different methods, respectively. Duplicate samples were read after calibration with four standards per cation using the flame atomic absorption method, and calibration was checked after every ten samples using one standard and if necessary a reslope factor. For ICPAES turlough samples were read after calibration with five standards and calibration tested after every ten samples using a quality control solution.

For quality control (QC), samples of known concentration were run along with turlough water samples for analysis of total and molybdate reactive phosphorus (TP

and MRP), total nitrogen (TN), silicate, anions and cations. QC solutions were prepared from different stock reagents to those used for preparing concentration standards. For total and molybdate reactive phosphorus analysis, the QC concentration used was 25 μg L^{-1} TP and MRP, while for nitrogen analysis the QC concentration was 2.1 mg L^{-1} NO_3-N. Concentrations of QCs for the anion analysis were 10 mg L^{-1} chloride and sulphate, respectively, and 1 mg L^{-1} NO_3-N. QC concentrations for cations were 2.5 mg L^{-1} calcium, 0.25 mg L^{-1}magnesium, 1 mg L^{-1} potassium and 0.5 mg L^{-1} sodium. The concentration of the silicate QC was 1 mg L^{-1}. For further quality assurance certified lake water (Ontario-99, lot 406) was run together with samples for analysis of anions and cations. Only the key water chemistry variables TP, TN, Chl *a*, turbidity and conductivity were considered relevant for analysis in subsequent data chapters.

2.2.2 Invertebrate Sampling and Identification

Field sampling of turloughs for this study was carried out during two successive flooding seasons (2006/2007 and 2007/2008). Macroinvertebrates were collected from the littoral zone of turloughs following different sampling approaches as outlined in each of the following data chapters. The comparability of different methods was assessed by means of hierarchical cluster analysis. Clustering of turloughs sampled in April 2007 using the two different sampling strategies (multi-habitat sweep net and single-habitat box sampling) resulted in a similar grouping of turloughs, demonstrating reliable comparability of methods (Figure 3.4 & Figure 6.2b).

Macroinvertebrates were identified using the keys by Ashe *et al.* (1998), Brooks and Lewington (1997), Edington and Hildrew (1995), Elliott and Mann (1979), Elliot *et al.* (1988), Fitter and Manuel (1986), Friday (1988), Gledhill *et al.* (1993), Holland (1972), Hynes (1977), Macan (1977), Miller (1996), Nilsson (1997), Reynoldson and Young (2000), Richoux (1982), Savage (1989), Savage (1999) and Wallace *et al.* (2003). Macroinvertebrates were identified to the lowest taxonomic level, generally species. However, Diptera and Trichoptera pupae, Hydrachnidia, Ostracoda and Oligochaeta were identified to order and all Diptera and Collembola to family level only. Random samples were identified by an independent individual to ensure quality assurance of identification. Identifications of rare species were

verified by established experts. Cladoceran zooplankton and separate chydorid samples were collected from twenty turloughs in April 2007 using methodologies described in Chapter 6 and identified using keys by Scourfield and Harding (1966) and Amoros (1984). Quality of identification was assured by cross-identification of random samples by established experts.

2.2.3 Hydrological Parameters

Detailed hydrological data was assessed through a separate PhD study (Owen Naughton) on hydrology of turloughs that provided estimates for hydrological metrics such as 'hydroperiod' and 'areal reduction rate'. Estimates of hydroperiod were based on detailed water level records and defined as the time each turlough was inundated during one year. A turlough was defined as 'dry' when the diver, which was placed at the lowest point in each turlough, clearly identified a dry spell (no water) or when only a minimal amount of water e.g. little puddle or water in swallow hole was remaining. Multimodal flooding events were factored in the calculations to give a total number of days of inundation.

Areal reduction rate was calculated for a subset of turloughs with the purpose to provide a metric for the speed at which water levels change in each turlough. It was calculated as the average rate of decrease in planar flooded area between the time of maximum and minimum areal inundation. The maximum areal inundation was defined as the maximum stage and volume of each turlough, whereas the minimum areal inundation coincided with the drying of the turlough, or, if a permanent water body was present throughout the year, the surface area of the permanent water body was used (dA/dT m^2/Day where dA= -maximum areal inundation and dT=time between maximum areal inundation and emptying of turlough/non permanent water body).

3 Distinctiveness of Macroinvertebrate Communities in Turloughs (Temporary Ponds) and their Response to Environmental Variables[1]

3.1 Abstract

1. Turloughs are a prime example of a water body type that interfaces with both the European Habitats Directive (92/43/EEC) and Water Framework Directive (2000/60/EC) (WFD), highlighting the need for an integrated strategy to protect and manage surface waters and groundwaters. To date, research on turloughs, including their invertebrate communities is limited.

2. Eight turloughs were sampled for their macroinvertebrate communities and water chemistry in April 2007. Faunal samples were collected by means of a simple box sampler.

3. Replicate samples within each turlough clustered together, indicating that a single sample can provide a meaningful description of the turlough invertebrate community. Variation of invertebrate communities within turloughs was nested among turloughs.

4. Hydroperiod influenced mean abundance and taxon richness of macroinvertebrates, but no correlation was found between nutrient status and either mean abundance or taxon richness.

5. Turloughs are priority habitats under the EU Habitats Directive, requiring maintenance of 'favourable conservation status', which needs to be assessed through monitoring and effected through appropriate management plans. While the distinctiveness of macroinvertebrate communities across turloughs is conducive to simple and cost-effective monitoring, this also challenges the applicability of the concept of type-specific communities across these highly dynamic ecosystems.

[1] Porst G, Irvine K. 2009. Distinctiveness of macroinvertebrate communities in turloughs (temporary ponds) and their response to environmental variables. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**: 456-465.

3.2 Introduction

Turloughs are periodically flooded karst wetland ecosystems. They are common in the western third of Ireland, where the dominant bedrock is carboniferous limestone, with or without shallow deposits of glacial till (Coxon, 1987b). Turloughs support both aquatic fauna during the flooding period, typically over the winter, and wet grasslands and fen type vegetation over the summer (Sheehy Skeffington *et al.*, 2006). They usually flood with rising water tables through springs and fissures in the limestone in autumn and empty, often through the same fissures or 'swallow holes', in spring (Ní-Bhriain *et al.*, 2003). Filling and emptying can vary enormously among turloughs and water levels may rise sporadically during periods of high rainfall (Reynolds *et al.*, 1998; Visser *et al.*, 2006). In summer turloughs are generally dry and used as pastures (Reynolds, 1982), although some may contain still or flowing waters throughout the year (Goodwillie and Reynolds, 2003).

Turloughs are classified as priority habitats under the European Habitats Directive (92/43/EEC) (EEC, 1992). Article 2 of the EU Directive requires Member states to ensure maintenance of biodiversity through the conservation of natural habitats and of wild fauna and flora. Under the Water Framework Directive (WFD) (EC, 2000) turloughs are classified as groundwater dependent terrestrial ecosystems (GWDTE). The WFD has stimulated increased research on littoral invertebrates in lakes (García-Criado *et al.*, 2005; Moss *et al.*, 2003; Sondergaard *et al.*, 2005; Tolonen *et al.*, 2001; White and Irvine, 2003) but work on the invertebrate fauna of Irish wetlands, including turloughs remains very limited (Reynolds, 2000; Reynolds *et al.*, 1998). While hydrographic studies exist for relatively large temporary water bodies in some areas (counties Clare and Galway) (Coxon, 1987a), and Goodwillie (1992) mapped vegetation for over 80 turloughs, most data on aquatic turlough invertebrate communities are not recent (Lansbury, 1965; Reynolds, 1982, 1985a, b; Reynolds, 1997), focuses on single taxon groups (Donaldson *et al.*, 1979; Duigan and Kovach, 1991; Grainger, 1991) and does not consider conservation issues *per se*. Studies encompassing the macroinvertebrate community as a whole have not been conducted to date.

Coxon (1986) considered that approximately one third of all turloughs over 10 hectares were damaged irreversibly by drainage. Nutrient enrichment, together with changes in stocking densities, is a current major threat to turloughs (Ní-Bhriain *et al.*, 2003; Ní-Bhriain *et al.*, 2002; Sheehy Skeffington *et al.*, 2006) that can alter biotic communities, including macroinvertebrates (Working Group on Groundwater, 2004). In addition, temporary waters are important for the survival of rare and restricted species (Collinson *et al.*, 1995), and regional biodiversity (Oertli *et al.*, 2005; Williams, 1997). Maintaining ecological integrity is required by both the Habitats and Water Framework Directive. The macroinvertebrates provide an essential component for the assessment of conservation status of turloughs, and the understanding of biotic response to changing catchment pressures and hydrological regimes (Reynolds, 1996; Sheehy Skeffington *et al.*, 2006).

The aim of the work reported here was to compare macroinvertebrate community structures in eight turloughs, selected along a nutrient gradient of total phosphorus, and identify their conservation value for rare and restricted species, and their response to a range of environmental variables.

3.3 Methods

3.3.1 Site Selection

Eight turloughs were selected to represent a gradient of total phosphorus (TP) concentrations (Table 3.1 & Figure 3.1). Phosphorus concentrations of twenty-two turloughs were determined prior to the selection of sites. Except Brierfield, all the sites are designated as candidate Special Areas of Conservation (cSAC) under the Habitats Directive.

Table 3.1: Summary of turloughs, their location and concentrations of key water chemistry variables and hydroperiod.

Turlough	*County*	*Irish National Grid*	*TP* [1] *(µg L^{-1})*	*Turbidity (NTU)*	*Chl a* [1] *(µg L^{-1})*	*TN* [1] *(mg L^{-1})*	*Conductivity* [1] *(µS cm^{-1})*	*Hydroperiod* [2] *(days)*
Ballindereen	Galway	M3852016100	5	1.41	1.54	0.579	405	239
Brierfield	Roscommon	M8160076560	15	2.2	1.06	0.425	393	331
Caherglassaun	Galway	M4155006340	38	4.53	13.52	0.936	388	365
Caranavoodaun	Galway	M4545015450	11	4.05	1.31	0.750	461	228
Kilglassan	Mayo	M2786064550	18	3.25	1.95	0.221	357	365
Lisduff	Roscommon	M8425055500	8	1.96	0.78	1.218	393	256
Roo West	Galway	M3863002210	8	1.57	1.27	0.370	307	231
Termon	Galway	R4092097350	11	1.69	4.35	0.347	418	365

[1] Data provided by Helder Pereira
[2] Data provided by Owen Naughton

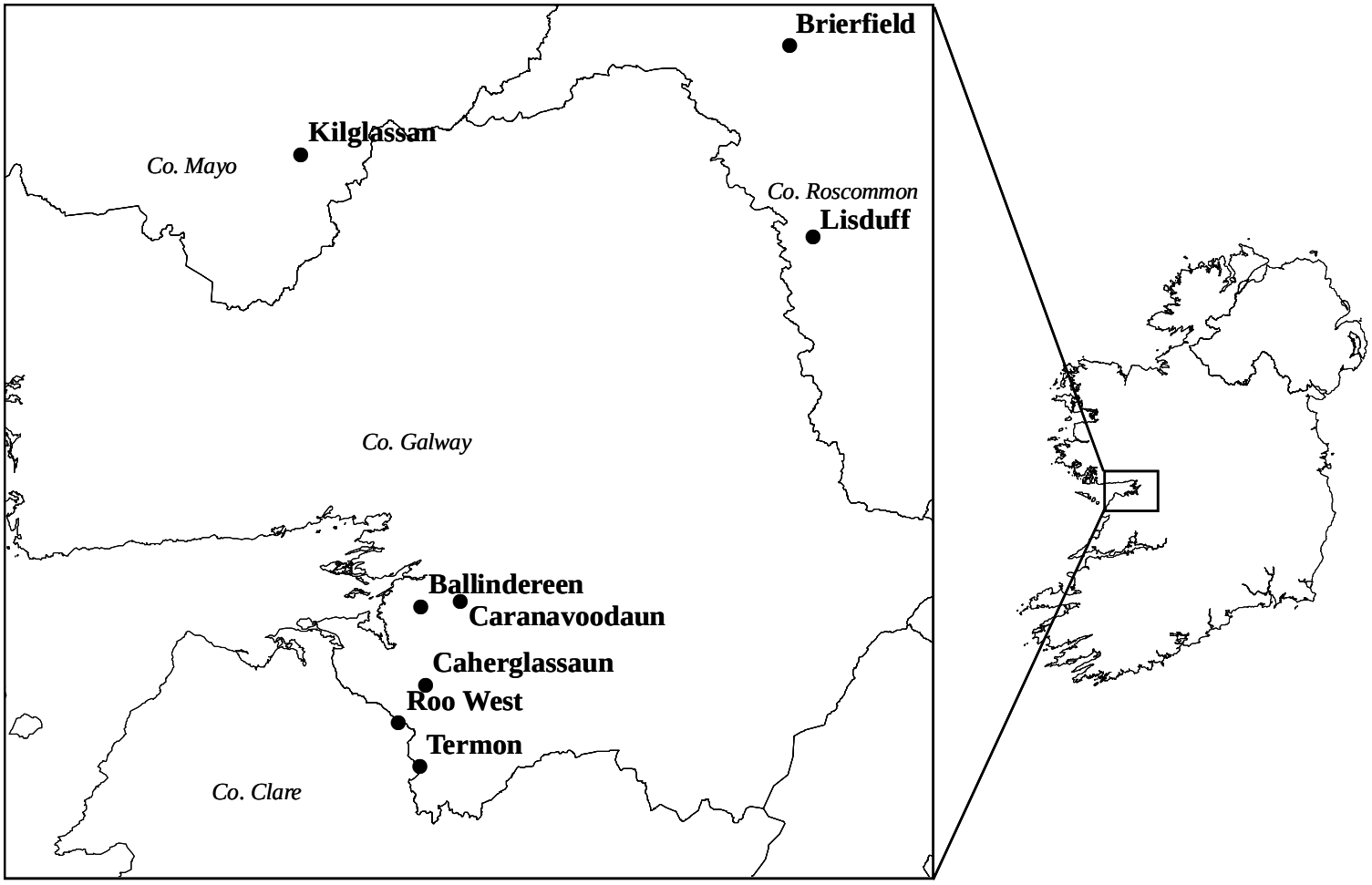


Figure 3.1: Map of the sampling region showing the eight turloughs studied.

3.3.2 Macroinvertebrate Sampling

Turloughs were sampled in April 2007 with a simple box sampler (50 cm long x 40 cm wide x 50.5 cm high), created by cutting out the bottom of a sturdy plastic storage box, modified after O'Connor *et al.* (2004). Turlough littoral zones can comprise different habitat types varying from grassland, limestone pavement, and stone walls to thick stands of sedges or reeds. To allow comparability of littoral macroinvertebrate communities among turloughs, one habitat type (submerged grassland) was selected, which occurred extensively in all of the eight turloughs. Five replicate samples were collected from each turlough by rapidly lowering the box on to the substratum. Organisms trapped within the box where then removed with a small net with a mesh size of 1mm, sieved, washed into collection bottles and preserved in 90% industrial methylated spirits (IMS) for later sorting and identification. In the laboratory macroinvertebrates were identified under a dissecting stereomicroscope to the lowest taxonomic level possible (typically species). Identifications of rare species were verified by established experts.

3.3.3 Water Chemistry Sampling

At every turlough a water sample was collected using a weighted 5 L plastic bottle attached to a rope, and thrown out from the shore. Water samples were analysed for turbidity (HACH Portable Turbidity Meter 2100P), conductivity (WTW multimetre Cond 197i; Probe: TetraCon® 325), chlorophyll *a* (Standing Committee of Analysts, 1983; SHIMADZU UV-VIS Spectrophotometer UV-1700), total nitrogen (TN) (Grasshoff *et al.*, 1999; Bran+Luebbe AutoAnalyzer 3) and total phosphorus (TP) (Eisenreich *et al.*, 1975; SHIMADZU UV-VIS Spectrophotometer UV-1700).

3.3.4 Statistical Analysis

To test for differences among turloughs a one-way analysis of variance (ANOVA) was performed on total abundance and taxon richness of samples. The relationship between nutrient status and invertebrate communities was assessed using Pearson product-moment correlation (comparing, respectively, mean abundance and log-transformed mean taxon richness, with log-transformed TP and TN concentrations) and Spearman rank-order correlation to compare, respectively, mean abundance and

log-transformed mean taxon richness with turbidity, chlorophyll *a*, conductivity and hydroperiod. Hydroperiod was estimated as the period of time each turlough was inundated during the sampling period. Data normality was verified using the Shapiro Wilk test and homogeneity of variance checked with the Leven's test before choosing parametric or nonparametric statistical analysis.

Cluster Analysis and Multi-Dimensional Scaling (MDS) ordination on log(x+1) transformed total abundance macroinvertebrate data assessed similarity of samples. Cluster Analysis and MDS are based on a Bray-Curtis similarity matrix, with clusters formed using the average group linkage method. The similarity profile (SIMPROF) permutation test, which tests for statistically robust clusters, not defined *a priori* into groups (Clarke and Gorley, 2006), was incorporated into the Cluster Analysis. Contributions of individual species to sample similarities or differences to the grouping of clusters or MDS plots was done using the similarity percentages routine SIMPER (PRIMER® 6). This method decomposes Bray-Curtis similarities among all pairs of samples, within *a priori* defined groups, into percentage contributions from each species to the respective similarities (Clarke and Warwick, 2001).

3.4 Results

3.4.1 Abundance and Taxon Richness

Taxon richness and abundance of invertebrates were significantly different among turloughs (one-way ANOVA: $F_{7,39}$=5.515 and $F_{7,39}$=9.84, respectively; P<0.001 in both cases). Pair wise comparisons between turloughs using the least significant differences (LSD) test for post hoc testing identified differences between samples in 19 (abundance) and 9 (taxon richness) of the possible 28 comparisons (P<0.05 in both cases). Mean sample abundances varied considerably among turloughs (Figure 3.2), with highest numbers in Termon (146.6±18.6 95% *c.I.*; n=5), the most permanent of the eight turloughs investigated and lowest in Caranavoodaun (56±13.9 95% *c.I.*; n=5). Highest mean taxon richness (Figure 3.3) occurred in Kilglassan (18.4±2.6 95% *c.I.*; n=5) and lowest in Ballindereen (10.8±1.6 95% *c.I.*; n=5) and Caranavoodaun (10.8±3.6 95% *c.I.*; n=5). Average taxon richness in all eight turloughs was 14, with a range from 7 to 21 species. A significant positive correlation was found between mean abundance and log-transformed mean taxon richness (R=0.71; P<0.05). No significant correlations were found between either mean abundance or log-transformed mean taxon richness and log_TP, log_TN, turbidity, chlorophyll *a* and conductivity, respectively. Hydroperiod correlated positively with mean abundance and mean taxon richness (R=0.88; P<0.01 and R=0.74; P<0.05, respectively).

Macroinvertebrate community structure varied among turloughs (Table 3.2, 3.3). For example, Lisduff was dominated by Coleoptera, Isopoda and Oligochaeta, while Caherglassaun had high abundances of Diptera and Gastropoda. Highest mean numbers of Coleoptera were found in Kilglassan, highest proportions of Isopoda were found in Lisduff and very high abundances of Diptera were found in Brierfield, Caherglassaun and Termon. High numbers of Odonata (both *Lestes* sp. and *Sympetrum sanguineum*) were found only in Caranavoodaun. Six rare/restricted species of conservation concern were found in five of the eight turloughs studied (Table 3.2).

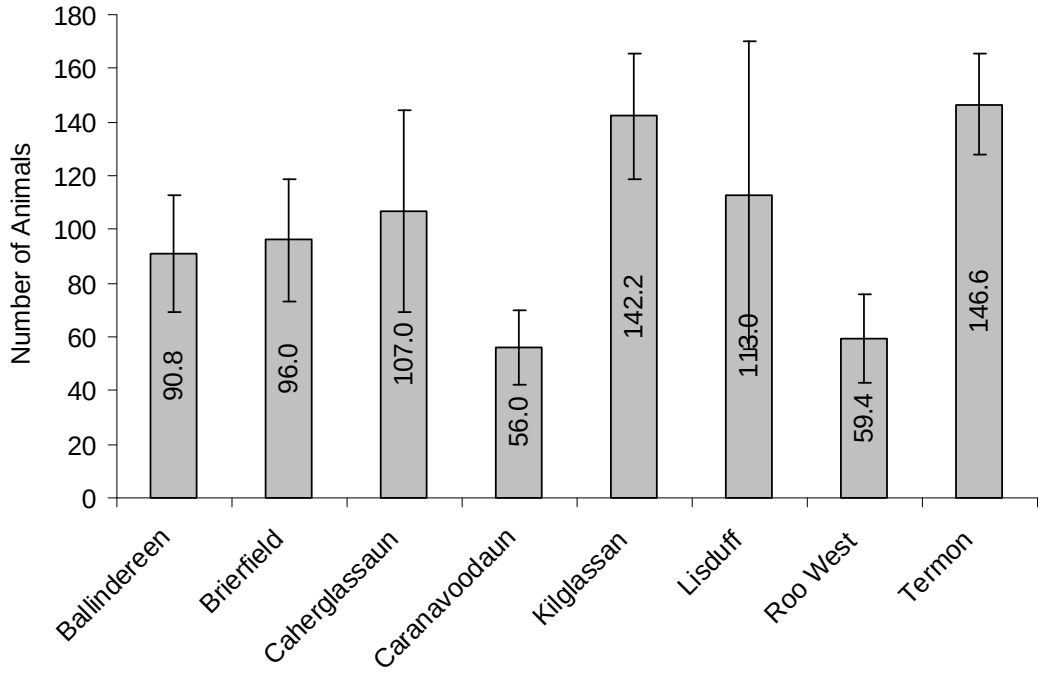


Figure 3.2: Mean abundance of macroinvertebrates recorded per turlough. Error bars are 95% *c.I.* (n=5).

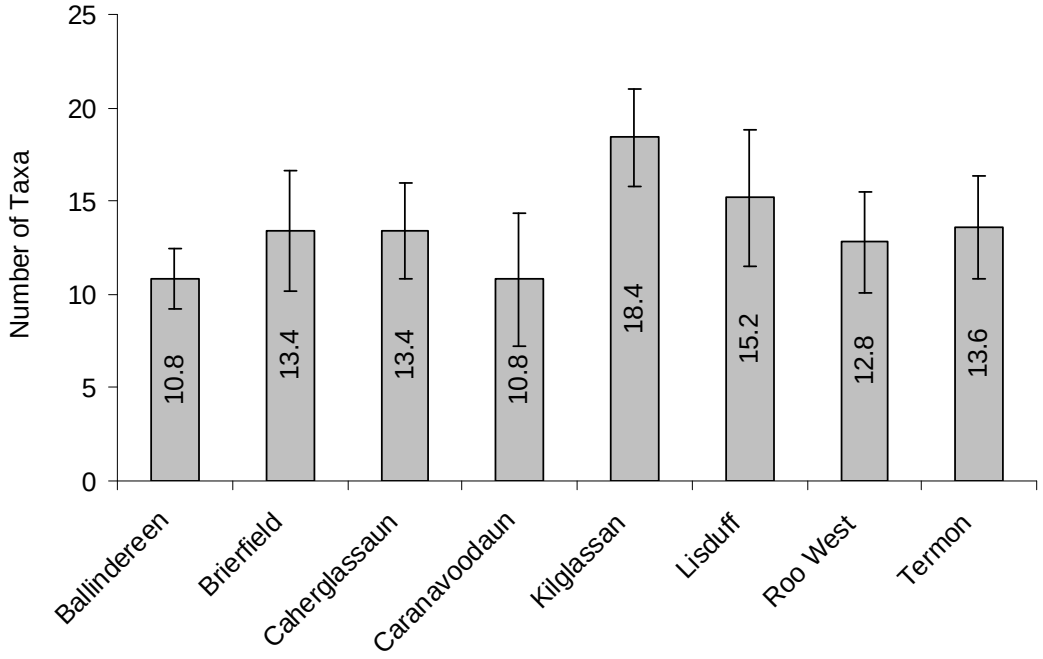


Figure 3.3: Mean number of macroinvertebrate taxa recorded per turlough. Error bars are 95% *c.I.* (n=5).

3.4.2 Cluster Analysis

Hierarchical cluster analysis grouped all replicate samples within turloughs together (Figure 3.4). The similarity profile test (SIMPROF) indicated no significant differences among replicate samples per turlough. The six turloughs Ballindereen, Brierfield, Kilglassan, Lisduff, Roo West and Termon clustered at about 43%. This group was only being joined by Caherglassaun turlough at about 34% and finally by Caranavoodaun at about 28 % similarity.

The average similarity of replicate samples of the six turloughs Ballindereen, Brierfield, Lisduff, Roo West and Termon was identified as 48% by the SIMPER routine. *Chironomidae* sp., *Oligochaeta* sp. and *Agabus* sp. *larvae* contributed 24%, 23.4% and 22.4%, respectively, to average similarity of this group. The high presence of *Planorbis conturtus* and *Asellus meridianus* and the absence of *Agabus* sp. *larvae* in Caherglassaun samples accounted for, respectively, 10.5%, 5.9% and 9.4% of the average dissimilarity (66.3%) of this turlough compared with the other six. Caranavoodaun differed from the group of six turloughs by 70.6%. The dissimilarity was mainly caused by the high occurrence of *Sympetrum sanguineum*, *Anisoptera* sp. *larvae* and *Culicidae* sp. (respectively, 9.7%, 7.3% and 6.4% of dissimilarity).

3.4.3 Non-Metric Multidimensional Scaling (MDS)

The non-metric multidimensional (MDS) scaling plot concurred with results from the Cluster Analysis and the SIMPER routine. The six turloughs Termon, Brierfield, Roo West, Kilglassan, Ballindereen and Lisduff showed higher similarities to each other compared with Caranavoodaun and Caherglassaun. Replicate samples clustered together, with almost no overlap with other turloughs (Figure 3.5).

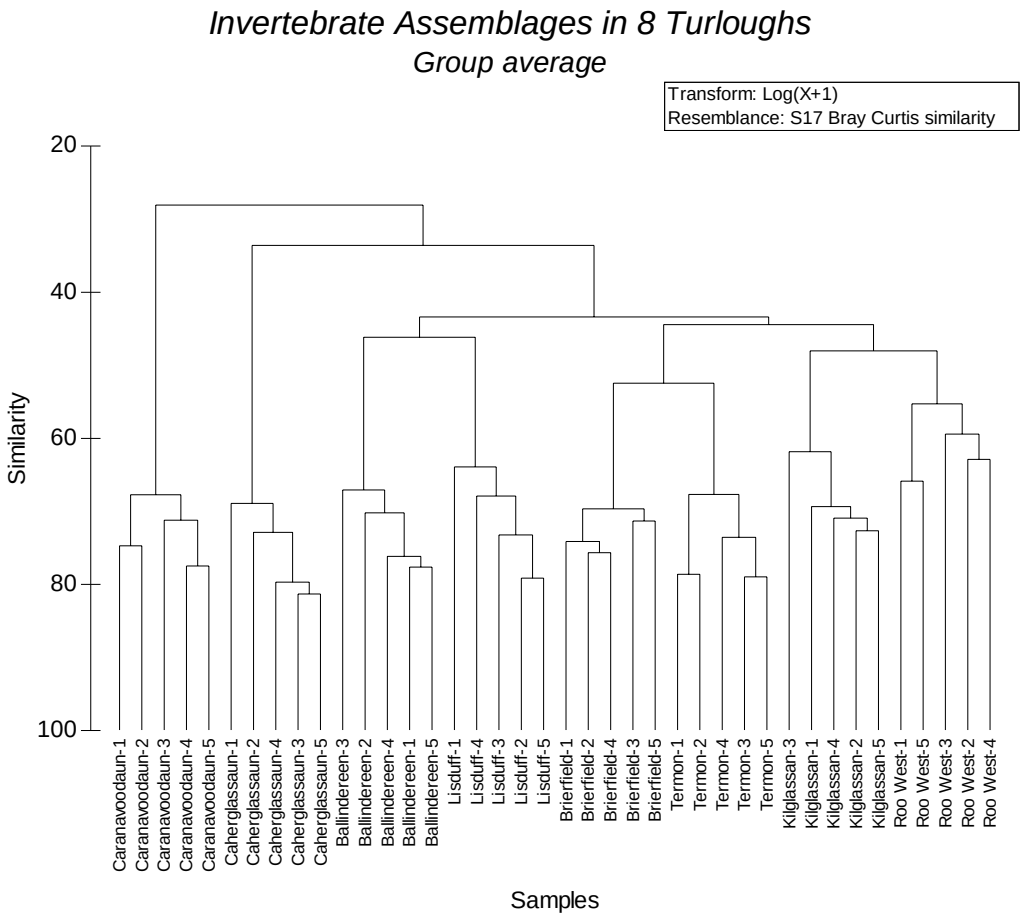


Figure 3.4: Hierarchical cluster analysis dendogram of macroinvertebrate species log(x+1) transformed total abundance data of eight turloughs (n=5 per turlough).

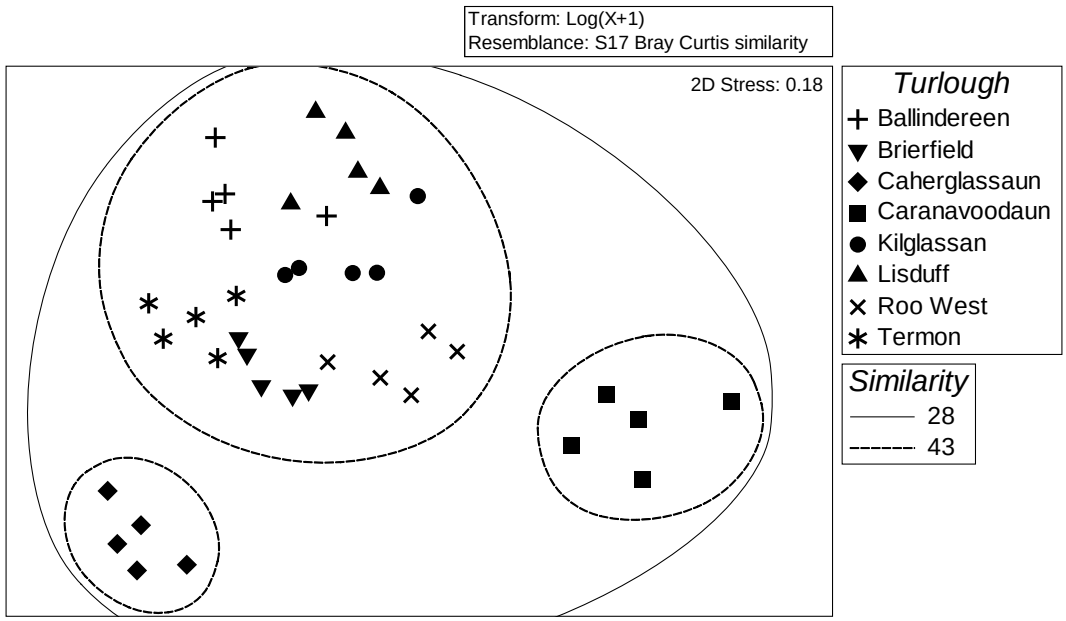


Figure 3.5: MDS plot of macroinvertebrate species log(x+1) transformed total abundance data of eight turloughs (n=5 per turlough), overlaid with similarity levels from Cluster Analysis.

Table 3.2: Pooled species abundances of macroinvertebrates found in eight turloughs. BN=Ballindereen; BF=Brierfield; CN=Caherglassaun; CV=Caranavoodaun; KN=Kilglassan; LF=Lisduff; RO=Roo West; TN=Termon (n=5 per turlough). Species marked with ***** are considered rare/restricted species, e.g. their occurrence can be restricted to the turlough environment and is considered to be of high conservation value.

Class/Order	*Family*	*Species*	*BN*	*BF*	*CN*	*CV*	*KN*	*LF*	*RO*	*TN*
Acari	Hydrachnidia	*Hydrachnidia* sp.	4				2	14		2
Amphipoda	Gammaridae	*Gammarus lacustris*	1						11	
		Gammarus sp. *juveniles*							1	2
Araneae	Argyronetidae	*Agyroneta aquatica*						1		
Coleoptera	Chrysomelidae	*Halticinae* sp.	7	8						1
		Donacia sp (larvae)						2		
	Curculionidae	*Curculionidae* sp.	2				2			
	Dryopidae	*Dryops* sp.					1			
		Dryops sp. *(larvae)*		1	2		3	3	2	1
	Dysticidae	*Dytiscus* sp. *(larvae)*								1
		Ilybius sp. *(larvae)*	2	1			2		1	8
		Rhantus sp. *(larvae)*	1	4			14	5	2	6
		Agabus bipustulatus	3							
		Agabus labiatus *****						1	1	
		Agabus nebulosus	2		1		1			
		Agabus sp. *(larvae)*	116	63		20	181	49	65	31
		Hydaticus sp. *(larvae)*				1				2
		Graptodytes bilineatus *****		14				102	2	
		Hydroporus erythrocephalus						5		1
		Hydroporus palustris		4	4				2	
		Hydroporus pubescens	3							
		Hygrotus inaequalis	2	1		2	2	1		
		Hygrotus impressopunctatus						1	2	
		Hygrotus quinquelineatus *****			5	1			2	
		Hygrotus sp. *(larvae)*	2			2	11		8	
		Laccophilus minutus			1				1	
		Laccophilus sp. *(larvae)*			1		10			4
		Rhantus exsoletus				1				1
	Haliplidae	*Haliplus fulvus*						1	1	
		Haliplus sp. *(larvae)*			1				1	1
	Hydraenidae	*Ochthebius minimus*	3				2			
	Hydrophilidae	*Berosus signaticollis* *****				7		7	2	
		Cercyon tristis					1			
		Helophorus brevipalpis	7	1		1	7	5	2	
		Hydrobius fuscipes					1			
Diptera	Ceratopogonidae	*Ceratopogonidae* sp.								4
	Chironomidae	*Chironomidae* sp.	56	214	209	13	96	31	79	216
	Culicidae	*Culicidae* sp.		13		33		4		
	Psychodidae	*Psychodidae* sp.			1					1
	Stratiomyidae	*Stratiomyidae* sp.		1						
	Tabanidae	*Tabanidae* sp.								5
	Tipulidae	*Tipulidae* sp.		3					1	11
		Diptera pupae	4	4	25	1	1	1	2	2

Table 3.2 (Contd.): Pooled species abundances of macroinvertebrates found in eight turloughs. BN=Ballindereen; BF=Brierfield; CN=Caherglassaun; CV=Caranavoodaun; KN=Kilglassan; LF=Lisduff; RO=Roo West; TN=Termon (n=5 per turlough). Species marked with ***** are considered rare/restricted species, e.g. their occurrence can be restricted to the turlough environment and is considered to be of high conservation value.

Class/Order	*Family*	*Species*	*BN*	*BF*	*CN*	*CV*	*KN*	*LF*	*RO*	*TN*
Ephemeroptera	Baetidae	*Cloeon dipterum*			23	11	19	1	12	4
	Baetidae	*Cloeon simile*			1			4	1	2
	Caenidae	*Caenis horaria*			14					
	Leptophlebiidae	*Leptophlebia vespertina*		4			5			
Gastropoda	Gastrodontidae	*Zonitoides* sp.		1				1		
	Lymnaeidae	*Galba truncatula*				1	3	1		
		Lymnaea fusca	93							
		Lymnaea stagnalis					1			
		*Omphiscola glabra**		20						
		Radix balthica	1		1	1	1	2	4	
		Succinea putris					21	3		
	Physidae	*Physa fontinalis*			1					
	Planorbidae	*Planorbis contortus*			133					
		Planorbis crista		2			4	1		
		Planorbis planorbis							7	
	Valvatidae	*Valvata cristata*		2						
Heteroptera	Corixidae	*Corixa punctata/iberica*		1						
		Sigara falleni			2					
	Corixinae	*Corixinae Instar I & II*	1				18			2
	Notonectidae	*Notonecta glauca*							1	1
	Velidae	*Microvelia reticulata*								1
Hirudinea	Glossiphonidae	*Glossiphonia complanata*					1	1	1	
	Gnathobdellae	*Haemopis sanguisuga*				1		1		
Isopoda	Asellidae	*Asellus aquaticus*	92	2	22		29	155		27
		Asellus meridianus			28					
Odonata	Lestidae	*Lestes* sp.				7				
		Lestes dryas *				11				
	Libellulidae	*Sympetrum sanguineum*	1			113	20	5	22	
		Anisoptera sp. *(larvae)*				33			2	
		Zygoptera sp. *(larvae)*		1			5			
Oligochaeta		*Oligochaeta* sp.	46	58	22	16	225	109	40	312
Ostracoda		*Ostracoda* sp.	3	53	11	1	5		8	84
Plecoptera	Nemouridae	*Nemoura cinerea*	1			1				
Trichoptera	Limnephilidae	*Limnephilus auricula*				1	2			
		Limnephilus centralis					7	24	3	
		Limnephilus lunatus		2						
		Limnephilus marmoratus					1	3		
		Anabolia brevipennis			3	1				
		Trichoptera sp. *pupae*	1							
Turbellaria	Turbellaria	*Polycelis nigra/tenuis*		2	24		7	21	8	

Table 3.3: Mean abundance of macroinvertebrate orders (± s.e.) found in samples of eight turloughs (n=5).

	Ballindereen	***Brierfield***	***Caherglassaun***	***Caranavoodaun***	***Kilglassan***	***Lisduff***	***Roo West***	***Termon***
Acari	0.8 ± 0.4				0.4 ± 0.2	2.8 ± 0.4		0.4 ± 0.4
Amphipoda							2.4 ± 1.2	0.4 ± 0.2
Araneae						0.2 ± 0.2		
Coleoptera	30 ± 7.7	19.4 ± 3.6	3 ± 2.1	7 ± 3.4	47.6 ± 8	36.4 ± 9.3	18.8 ± 5.9	11.4 ± 4.2
Diptera	12 ± 2.2	47 ± 8.3	47 ± 4.4	9.4 ± 1.9	19.4 ± 2.9	7.2 ± 1.8	16.4 ± 2.8	47.8 ± 9.9
Ephemeroptera		0.8 ± 0.6	7.6 ± 2.4	2.2 ± 0.6	4.8 ± 2.3	1 ± 0.8	2.6 ± 1.2	1.2 ± 0.8
Gastropoda	18.8 ± 4.6	5 ± 2.0	27 ± 11.6	0.4 ± 0.4	6 ± 2.4	1.6 ± 1.4	2.2 ± 0.8	
Heteroptera	0.2 ± 0.2	0.2 ± 0.2	0.4 ± 0.2		3.6 ± 1.4		0.2 ± 0.2	0.8 ± 0.6
Hirudinea				0.2 ± 0.2	0.2 ± 0.2	0.4 ± 0.4	0.2 ± 0.2	
Isopoda	18.4 ± 2.3	0.4 ± 0.2	10 ± 3.1		5.8 ± 2.2	31 ± 10.5		5.4 ± 1
Odonata	0.2 ± 0.2	0.2 ± 0.2		32.8 ± 4.8	5 ± 1.6	1 ± 0.5	4.8 ± 2.7	
Oligochaeta	9.2 ± 2.3	11.6 ± 1.7	4.4 ± 1.4	3.2 ± 0.8	45 ± 3.7	21.8 ± 5.2	8 ± 1.1	62.4 ± 4.2
Ostracoda	0.6 ± 0.4	10.6 ± 2.3	2.2 ± 0.8	0.2 ± 0.2	1 ± 0.3		1.6 ± 0.7	16.8 ± 4.4
Plecoptera	0.2 ± 0.2			0.2 ± 0.2				
Trichoptera	0.2 ± 0.2	0.4 ± 0.2	0.6 ± 0.4	0.4 ± 0.4	2 ± 1.1	5.4 ± 3.1	0.6 ± 0.7	
Turbelaria		0.4 ± 0.2	4.8 ± 1.2		1.4 ± 0.6	4.2 ± 1.2	1.6 ± 1.2	
Total	90.6	96	107	56	142.2	113	59.4	146.6

3.5 Discussion

3.5.1 Comparison of Macroinvertebrates among Turloughs

Hierarchical Cluster Analysis, MDS and the SIMPER routine identified a strong individual character of turloughs with macroinvertebrate community compositions varying markedly among the eight turloughs studied. Caranavoodaun and Caherglassaun separated clearly from the remaining six turloughs in all methods, suggesting discrete turlough invertebrate communities. Caherglassaun, which had highest turbidity (4.53 NTU), total phosphorus (38 µg L^{-1}) and chlorophyll *a* concentrations (13.5 µg L^{-1}), and reported high cattle stocking densities (Ní-Bhriain *et al.*, 2003) had abundant Diptera (mainly *Chironomidae* sp.) and Gastropoda (mainly *Planorbis contortus*). This concurs with a tolerance to nutrient enrichment by Gastropoda and Diptera suggested by Hellawell (1986) and Rosenberg and Resh (1993a). Water level in Caherglassaun had dropped dramatically in April 2007 and water at sampling locations was extremely turbid owing to a great amount of soft, muddy sediment. The high occurrence of *Sympetrum sanguineum* observed in Caranavoodaun reflects its preference for shallow well-vegetated ponds, situated in woodland. Its adults typically perch in bankside trees while feeding (Brooks and Lewington, 1997). *S. sanguineum* as well as the scarce emerald damselfly *Lestes dryas* complete their live cycle within one year, allowing them to breed in seasonal pools with thick vegetation such as Caranavoodaun (Brooks *et al.*, 1997). *L. dryas* is considered the rarest Irish damselfly and is especially threatened by intensive grazing, which removes shelter for adult damselflies and reduces suitable areas for reproduction (Nelson and Thompson, 2004). Thus, the comparably low grazing pressure (Ní-Bhriain *et al.*, 2002) and relatively low nutrient status (TP=11 µg L^{-1}; Chl *a*=1.31 µg L^{-1}), together with its surrounding hazel woodland and well vegetated littoral/shore zone make Caranavoodaun an ideal habitat for both Odonata species. Their mutual occurrence furthermore agrees with findings by Moore (1980), who reported *S. sanguineum* in two out of four *L. dryas* freshwater sites in Ireland. The seasonality of turloughs and hence the absence of larger predatory invertebrates and fish in many sites seems also crucial for the survival of *L. dryas* (Nelson and Thompson, 2004). The occupation of mainly aerial colonizers in Caranavoodaun

furthermore represents an adaptation of aquatic invertebrates to turloughs, which also include resistance to desiccation and resting stages (Reynolds, 2003).

The mayfly *Cloeon simile* Eaton, which occurred in four of the eight turloughs studied, has been reported to produce only one generation per year in two upland turloughs, whereas normally it has a bivoltine lifestyle (Byrne, 1981). Other typical aquatic macroinvertebrates of turloughs comprise *inter alia Cloeon dipterum*, the molluscs *Radix balthica* and *Galba truncatula*, the flatworm *Polycelis nigra/tenuis*, *Ostracoda* sp., caddis-fly species of the family Limnephilidae, the amphipods *Gammarus* sp. and *Asellus* sp. and various beetle species including *Hydroporus palustris* and *Hygrotus impressopunctatus* (Reynolds, 1982, 1985b, 1996; Reynolds, 1997; Reynolds, 2003). This fauna typically inhabits small ponds (Reynolds, 2000) and were all found in the surveyed turloughs.

Small fish were discovered in Termon, which has a permanent water body all year round, and Kilglassan, which also holds a considerable area of puddles and drainage ditches supporting fauna with life-spans exceeding one year. The smooth newt *Triturus vulgaris* was detected in Brierfield, a turlough which usually holds some water even during summer when newt tadpoles metamorphose. *T. vulgaris* is probably the top-predator in this turlough during spring, but large beetle larvae such as *Rhantus* sp. can also prey on amphibians in turloughs (Sheehy Skeffington *et al.*, 2006). Temporal and spatial habitat complexity was suggested by Reynolds (2000) to allow for the coexistence of predators with characteristic turlough invertebrates.

The distinctiveness of turlough macroinvertebrate assemblages was demonstrated by the clear clustering of replicate samples. Temporal and spatial sampling of three of the studied turloughs (Caranavoodaun, Roo West and Termon) and one additional one confirmed these results (see Chapter 4 & 5). This also suggests that single or pooled invertebrate samples are sufficient to describe the aquatic macroinvertebrate communities of turloughs, at least from individual habitat types. White and Irvine (2003) found variation of littoral macroinvertebrates within lakes nested among lakes across a range of lake types. This suggests that standing waters in general have distinct invertebrate communities. Turloughs, with their ephemeral character, may provide extreme examples of community response to local regional variations that favour distinctive, well adapted macroinvertebrate assemblages (Reynolds, 2003).

Furthermore, like other temporary waters (Collinson *et al.*, 1995; Williams, 1996; Williams *et al.*, 2003), turloughs tend to have highly individual physico-chemical features and hydrological regimes, plus small catchment areas that provide relative isolation from other water bodies (Sheehy Skeffington and Gormally, 2007). These facets, and the evidence from the sampling programme, emphasize both the importance of turloughs as important conservation sites, but also the likely distinctiveness of the habitats.

3.5.2 Macroinvertebrate Response to Environmental Variables

While hydrogeomorphological characteristics and land use practices of turlough basins would be expected to influence their ecology strongly (Sheehy Skeffington *et al.*, 2006), our study did not find any evidence for the influence of water chemistry on mean abundance or taxon richness. This is in agreement with Reynolds (2000), who found nutrient concentrations to be unimportant in determining faunal community diversity in turloughs. Yet, further research is needed to investigate the relationship between water chemistry variables and macroinvertebrate community composition in turloughs. The data confirmed, however, the influence of duration of flooding on mean macroinvertebrate abundance and taxon richness in the eight turloughs studied. The most permanent turlough, Termon, had highest numbers of macroinvertebrates and relatively high mean taxon richness. Caranavoodaun, a turlough which usually dries out completely during the summer months, had the lowest mean abundance and mean taxon richness. Correlation of permanence of temporary ponds with invertebrate taxon richness and abundance has also been found in several studies of ponds (Collinson *et al.*, 1995; Duigan, 1988; Eitam *et al.*, 2004; Spencer *et al.*, 1999; Tavernini *et al.*, 2005). The exclusion of riparian species such as rove beetles (Staphylinidae), ground beetles (Carabidae) or shore bugs (Saldidae), which might be a significant component of the faunal community of turloughs during the dry phase (Williams, 1997), may contribute, however, to an underestimation of taxon richness associated with temporary ponds (Collinson *et al.*, 1995; Della Bella *et al.*, 2005).

The question of taxonomic resolution is controversial (Bailey *et al.*, 2001). While some benthologists argue that the lowest resolution gives the best information on variability in aquatic macroinvertebrate communities (Resh and Unzicker, 1975),

others have found that the lower taxonomic resolution has little effect on multivariate statistics (Hewlett, 2000; Marshall *et al.*, 2006). In this study most of the specimens could be identified to species (Table 3.2). However, Diptera and Trichoptera pupae, oligochaetes and ostracods were identified to order and all the dipterans to family level only. The statistical analysis of the macroinvertebrate data was nevertheless based on the displayed species list, which included different taxonomic levels. Similar results were, however, obtained when the data was transposed to order and family levels, demonstrating the validity of the reported results at a mixed but lower taxonomic resolution.

3.5.3 Temporal Effects

This study emphasizes the importance of drying out of ponds for the occurrence of rare and restricted species. Up to four rare/restricted taxa of the six uncommon species discovered during this study were found in five of the studied turloughs. This finding also highlights the contribution of turloughs to regional biodiversity and their high conservation value. Similar importance of temporary pond conditions was found in studies comparing the conservation value of temporary and permanent ponds (Collinson *et al.*, 1995; Della Bella *et al.*, 2005). The coleopterans recorded also comprise species of a characteristic 'edge-moss-dwelling' turlough community, identified by Bilton (1988), which is considered of high conservation value and unknown from Great Britain (Foster *et al.*, 1992). This assemblage, which is reported to be very susceptible to disturbance by anthropogenic sources such as heavy grazing and nutrient enrichment, includes the 'nationally notable B species' (Great Britain) *Hygrotus quinquelineatus*, *Agabus labiatus* and *Berosus signaticollis*. They are frequently accompanied by other typical turlough beetles including *Agabus nebulosus* (Foster), *Hygrotus impressopunctatus* (Schaller) and *Helophorus* sp. (Bilton, 1988), which were also documented in this study. The Red Data Book category three species (rare and threatened) *Graptodytes bilineatus* (Shirt, 1987), together with *Agabus labiatus* and *Dryops similaris* (not recorded in this study) were, furthermore, described as most sensitive to disturbances (Bilton, 1988). The mutual occurrence of *G. bilineatus* and *A. labiatus* in the nutrient poor turloughs Lisduff and Roo West suggests relatively low disturbance of these sites. The mud snail *Omphiscola glabra* (UK RDB category one – vulnerable) is known as a temporary pond specialist and typically found on its own or accompanied only by

very few molluscs species (Bratton, 1991). In this survey it was only recorded from Brierfield, a turlough which usually dries out for a considerable amount of time during the year, together with just one other, not truly aquatic snail species (*Zonitoides* sp.). However, the fully aquatic species such as snails and the crustaceans *Gammarus* and *Asellus* (also reported in this study) are known to adapt to the changing turlough environment by reproducing quickly after onset of flooding. Moreover, they can survive dry periods in refugia such as swallow holes or little puddles (Sheehy Skeffington *et al.*, 2006).

3.6 Conclusions

In order to comply with the requirements of the WFD and the EC Habitats Directive of achieving and maintaining good ecological status and favourable conservation status, respectively, adequate monitoring and management plans have to be developed for turloughs in the near future. If littoral macroinvertebrates are to be used to assess the ecological status of Irish turloughs, our findings are important for the design of monitoring, suggesting assessment of the macroinvertebrates can be carried out in a cost and time effective way. Owing to the strong individuality of turlough macroinvertebrate communities, a single box sample taken from the most dominant turlough habitat, submerged grassland, appears sufficient to provide comparison of the macroinvertebrate community among turloughs. However, for the assessment of maximum species diversity of single turloughs we recommend a more intensive sampling approach, including all available habitats in each turlough in agreement with Della Bella *et al.* (2005). Yet, the understanding of the relative effect of hydrology and nutrient status requires further work. Turloughs are of high conservation importance, supporting invertebrate species and assemblages of restricted distribution and high conservation value, and are susceptible to inputs from both surface land use, and alterations to groundwater regimes (Drew and Coxon, 1988; Sheehy Skeffington *et al.*, 2006). Assessment of conservation value of turloughs should not discriminate against low diversity sites, as this is the natural character of these ecosystems. A net of turlough SAC sites should reflect the biodiversity gradation from low to high. However, the highly dynamic nature of turlough hydrology may negate simple classification or even development of a typology (Visser *et al.*, 2006). This conclusion contrasts strongly with the current

vogue (under the WFD) to classify water bodies within types and estimating type-specific reference communities. As sites that fall outside the normal classification and monitoring paradigm of the WFD, turloughs may not be subject to some of the naïve ecological assumptions that underpin the implementation of the WFD (Hatton-Ellis, 2008; Moss, 2008). A major challenge for turlough monitoring and management is how to provide general guidance useful for sites that have extremely variable and often unpredictable hydrology, and hence disturbance, within and among years.

4 The Importance of Disturbance for Seasonal and Inter-annual Succession of Macroinvertebrates in Turloughs

4.1 Introduction

Turloughs are ephemeral, usually grass floored, karst wetlands restricted to limestone regions in the West of Ireland (Coxon, 1987b; Reynolds, 1982). They are recognised as habitats of national and international conservation importance (Sheehy Skeffington *et al.*, 2006), listed as priority habitats under the European Habitats Directive (92/43/EEC) (EEC, 1992). Several are designated as candidate Special Areas of Conservation (cSAC). Under the EC Water Framework Directive (2000/60/EC) (EC, 2000), turloughs are designated as groundwater dependent terrestrial ecosystems (GWDTE). Ephemeral standing waters are at risk worldwide (Oertli *et al.*, 2005). Contemporary threats to turloughs are diverse and include agricultural intensification (Nicolet *et al.*, 2004), drainage (Coxon, 1986) and climate change (Jeffries, 2005; Sweeney *et al.*, 2003).

Turloughs and other ephemeral waters support a largely specialised fauna (Reynolds, 1982; Reynolds, 2003) of which aquatic invertebrates comprise an important part (Lahr *et al.*, 1999; Waterkeyn *et al.*, 2008; Williams, 1987). The dominant taxa are usually microcrustaceans, mites, and three insect groups: true bugs, beetles and midges (Williams, 1987). Duration of flooding, probably the most influential variable affecting aquatic invertebrate communities in ephemeral waters (Jocqué *et al.*, 2007; Williams, 2006), can vary enormously among turloughs (Sheehy Skeffington *et al.*, 2006). Structuring processes and dynamics in communities are generally closely related to frequency, scale and regularity of disturbances (White and Pickett, 1985), often exercising a dominant factor for community composition in wetlands (Schneider and Frost, 1996; Wiggins, 1980). The dry phase of an ephemeral wetland can be defined as an ecological disturbance for its aquatic fauna and flora and a wetlands disturbance regime can be characterised by hydroperiod or habitat duration (Schneider, 1999), with reduction of biotic interactions among species in highly disturbed waters (Schneider, 1999; Wilbur, 1987). Temporary waters with a long inundation cycle, providing a comparatively low disturbance frequency are, thus, expected to offer a more stable

habitat and facilitate continued colonization of invertebrates (Holland and Jenkins, 1998; Williams, 1997). This consequently favours higher species diversity in lakes with increased habitat persistence compared with waters with a shorter and more variable inundation period (Duigan, 1988; Jocqué *et al.*, 2007; Spencer *et al.*, 1999).

Temporary wetland invertebrates have to mature, reproduce or disperse before the end of the wet cycle and their life histories need to be responsive to effects and duration of disturbance (Williams, 2006). Survival strategies include the production of resting eggs (crustaceans), the migration of adults to permanent waters (hemipterans, coleopterans), and the survival as terrestrial adults when only the larval stages are aquatic (mayflies, damselflies, dragonflies) (Lahr, 1997; Lahr *et al.*, 1999; Williams, 1987). Temporary wetland invertebrates can, furthermore, be categorised broadly into passive and active dispersers. Passive dispersers, such as snails or crustaceans, typically recolonize the temporary habitat shortly after reflooding through the hatching of resting stages or recolonization from refugia (e.g. sinkholes or puddles) (Jocqué *et al.*, 2007; Reynolds, 1982, 1996). Active dispersers, characterised by rapid larval development and excellent colonization abilities (Wiggins, 1980), comprise most insects, typically colonizing the habitat later in the season (Jocqué *et al.*, 2007).

While macroinvertebrate succession has, for example, been studied in temporary rock pools of eastern Botswana (Jocqué *et al.*, 2007), in Sahelian and Mediterranean temporary ponds (Boix *et al.*, 2000; Lahr *et al.*, 1999) and in seasonal forest ponds in central Massachusetts (Brooks, 2000), research on temporal variability in turlough aquatic invertebrate communities has been limited (Reynolds, 1996). Owing to the rather irregular nature of the turlough environment, invertebrate species occurrence and diversity is postulated to depend on the variable availability of colonizers at times of flooding (Reynolds, 1996; Reynolds *et al.*, 2004). Despite the importance of turloughs as hot spots for biodiversity (Biggs *et al.*, 2005; Scheffer *et al.*, 2006; Williams *et al.*, 2003), there is an absence of studies on colonization and ecological succession (Reynolds *et al.*, 2004). Knowledge of successional patterns of aquatic invertebrates of temporary wetlands establishes a reference point for judging whether or not a site is subject to subsequent degradation (Linke *et al.*, 1999; Trigal *et al.*, 2006).

The aim of this study was to assess seasonal and inter-annual variation in macroinvertebrate community structures, and community response to disturbance in four turloughs differing in hydrological and nutrient regimes.

4.2 Methods

4.2.1 Study Sites

From a data set of twenty-two turloughs, located in counties Clare, Galway, Mayo and Roscommon, which represents the morphological and geographical range of turloughs in Ireland (see section 2.1 in Chapter 2 for details), four turloughs were selected for study of macroinvertebrate succession. Turloughs were chosen to represent different recurrent nutrient and hydrological regimes (Table 4.1, Figure 4.1). Blackrock is an example of a turlough with a hydrological regime that responds rapidly to local rainfall and weather conditions, characterised by a relatively short hydroperiod and a high areal reduction rate (dA/dT (m^2/Day) = average rate of change of area between the time of maximum areal inundation and the emptying of a turlough). A high areal reduction rate implies rapid changes in water levels and, thus, disturbance in the littoral zone. This turlough has, furthermore, comparatively high nutrient concentrations. Caranavoodaun represents a turlough with a low nutrient status and a comparatively low areal reduction rate. Roo West's areal reduction rate is slightly faster, while possessing a similar hydroperiod and nutrient concentrations to Caranavoodaun. Termon has the lowest areal reduction rate and contains a permanent water body throughout the year, with nutrient concentrations a little higher than those of Caranavoodaun and Roo West (Table 4.1). All four turloughs are designated as cSACs under the EC Habitats Directive (EEC, 1992).

Table 4.1: Sampling sites, their nutrient status, areal reduction rates and hydroperiod of two sampling seasons 2006/07 and 2007/08 of the four turloughs studied.

Turlough	*Mean TP ± s.e. (ug/L)**	*Areal reduction rate dA/dT (m^2/Day)[1]*	*Hydroperiod (weeks) 2006/07 & 2007/08*
Blackrock	52±7.2	-10875	28 – 19
Caranavoodaun	11±1.4	-3479	32.6 – 26
Roo West	10±1.4	-3734	33 – 26
Termon	15±2.7	-1042	52 – 52

[1] calculated as the average rate of change of area between the time of maximum areal inundation and the emptying of turlough (dA= - maximum areal inundation; dT=time between max areal inundation and emptying of turlough). Data provided by Owen Naughton.
* mean of collected monthly TP concentrations during sampling season October 2006 – June 2007. Data provided by Helder Pereira.

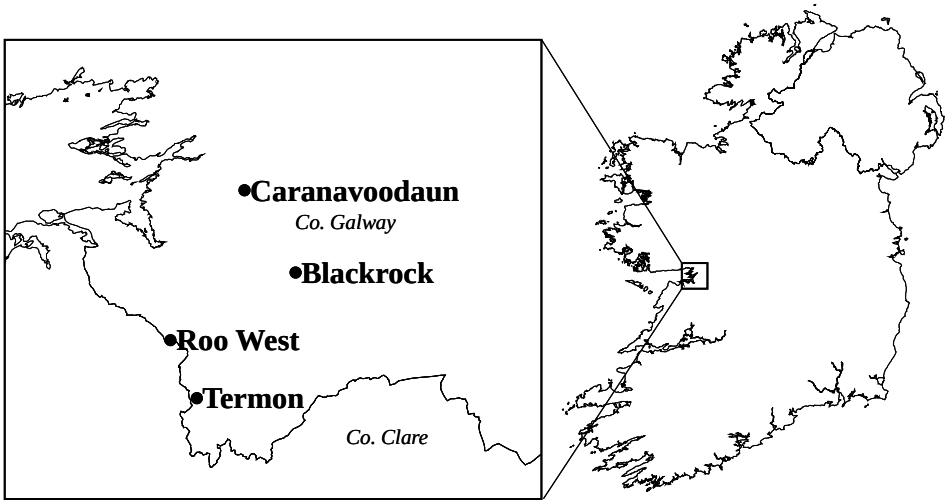


Figure 4.1: Map of Ireland showing the location of the four turloughs studied.

4.2.2 Macroinvertebrate Sampling

The four turloughs were sampled monthly for their macroinvertebrate communities from December 2007 to April 2008 (seasonal data set) using a box sampler (50 cm long x 40 cm wide x 50.5 cm high), modified after O'Connor *et al*. (2004). Caranavoodaun was sampled additionally in May 2008 and Termon in June 2008. In order to investigate the stability of turlough invertebrate communities and diversity among years, samples collected in the proceeding sampling season 2006/07 using the same sampling methodology were incorporated into the analysis (interannual data set). At each sampling occasion (Table 4.2), five replicate samples were

collected in each turlough from submerged grassland habitat (the dominant habitat of turloughs studied). Samples were collected in the accessible, wadable littoral zone, moving with the turlough shore line along a transect with increasing or decreasing water level. Macroinvertebrates caught within the box were removed with a small 1 mm mesh size net, sieved through a 500 µm sieve and preserved in 90% industrial methylated spirits (IMS). In the laboratory macroinvertebrates were identified to the lowest taxonomic level possible (typically species).

Table 4.2: Sampling dates of turloughs studied over 2 years.

Sampling date	*Sampling season*	*Blackrock*	*Caranavoodaun*	*Roo West*	*Termon*
November-06	1	x			x
January-07	1	x			x
April-07	1		x	x	x
June-07	1				x
December-07	2	x	x	x	x
January-08	2	x	x	x	x
February-08	2	x	x	x	x
March-08	2	x	x	x	x
April-08	2	x	x	x	x
May-08	2		x		
June-08	2				x

4.2.3 Statistical Analysis

4.2.3.1 Temporal Variation in Invertebrate Taxon Richness

The effect of time on macroinvertebrate species richness of the four turloughs was investigated using repeated measures ANOVA in SPSS 15 (SPSS-Inc., 2006) on synchronized, consecutive sampling data (December 2007 - April 2008/seasonal data set). For this analysis recorded taxa were divided into permanent and ephemeral residents after Williams (1987) and Lahr (1997). Permanent residents comprised mainly crustaceans (amphipoda and isopoda), bivalves, gastropods, flatworms, leeches, ostracods, oligochaetes and collembolans. Ephemeral residents encompassed primarily coleopterans, trichopterans, dipterans, hemipterans, ephemeropterans and Odonata species. Repeated measures ANOVA was carried out on the whole community and permanent and ephemeral residents separately, including all replicate samples. Least significant difference (LSD) and Bonferroni

procedure were used for post hoc testing. Variability of taxon richness within replicate samples was estimated by the coefficient of variation (C.V.):

$$CV = s.d. / \overline{x} * 100$$

4.2.3.2 Temporal Variation in Invertebrate Community Composition and Co-occurrence of Taxa

The effect of time on invertebrate community composition was investigated using PERMANOVA (Anderson *et al.*, 2008) with 9999 permutations on invertebrate community compositions over consecutive sampling data (December 2007 - April 2008/seasonal data set). Analysis was carried out on the whole invertebrate community data as well as for the separate life-cycle groups (permanent and ephemeral residents) using a two-way crossed design (factors time and turlough), including all replicates. Data were log(x+1) transformed and analysis was carried out on a Bray-Curtis dissimilarity matrix. Pair-wise comparisons among all pairs of levels of the factor time were carried out in a separate run of the PERMANOVA routine.

Patterns of co-occurrence of taxa over time in the seasonal data set were tested with ECOSIM (Gotelli and Entsminger, 2006), using C-score settings, which measures the average number of 'checkerboard units' between all possible pairs of species (Stone and Roberts, 1990) and default settings (fixed sum) for both row and column constraints. ECOSIM tests for non-random patterns of co-occurrence using a presence/absence matrix. P-values indicate probability of observed index value to be greater than or equal to the expected index values based on Monte Carlo permutations (5000 randomizations). Average values of replicate samples per month were included in the calculations.

Seasonal and interannual differences in community structures in each turlough were analyzed using the similarity percentages routine SIMPER (PRIMER® 6). By decomposing Bray-Curtis similarities among all pairs of samples, within *a priori* defined groups, SIMPER computes the percentage contributions of individual species to respective sample differences (Clarke and Warwick, 2001). Similarity of samples was moreover assessed using log(x+1) transformed total abundance macroinvertebrate data for Multi-Dimensional Scaling (MDS) ordination.

4.3 Results

4.3.1 Temporal Variation in Invertebrate Taxon Richness

Average monthly taxon richness (n=5 per turlough) during sampling season 2007/2008 varied from 2.6±0.6 s.e. (January 07) to 8.6±1 s.e. (Dec 07) in Blackrock, 6.6±0.5 s.e. (February 08) to 18.4±1.5 s.e. (May 08) in Caranavoodaun, 4.8±0.4 s.e. (December 07) to 12.2±0.7 s.e. (March 08) in Roo West and 3.8±0.8 s.e. (January 07) to 23.6±0.7 s.e. (June 08) in Termon (Figure 4.2a). Highest seasonal average taxon richness (n=5x5=25 in Blackrock and Roo West and n=5x6=30 in Caranavoodaun and Termon) during sampling season 2007/2008 was detected in Termon (13.4±2.3 s.e.) and lowest in Blackrock (7.2±0.8 s.e.), which concurs with respective hydroperiods. Comparatively low average seasonal taxon richness in Blackrock suggests a negative effect of high areal reduction rates on taxon richness (Figure 4.2 b).

Repeated measures ANOVA revealed a significant influence of time (month of sampling) on the taxon richness of the whole invertebrate community, as well as permanent and ephemeral residents' taxon richness (Table 4.3). Taxon richness in sampling periods December 07-February 08 (1-3) and March-April 08 (4-5) differed significantly from each other, suggesting two successional phases in the macroinvertebrate community (Table 4.3).

The ratio of permanent/ephemeral residents changed over time towards higher abundances of ephemeral taxa later in the season in Caranavoodaun, Roo West and Termon (Figure 4.3). This trend was also seen in Blackrock during the first year's sampling season and the start of year two, but changed from February 2008 towards an increase in permanent residents in March and April 2008. Variation in taxon richness generally decreased until February/March 2008, with an increase from March/April as the turloughs started to drain, and displayed a negative trend with turlough hydroperiod (Figure 4.4 a & b).

Table 4.3: Results of repeated measures ANOVA testing for effects of time on taxon richness for the whole community and different life-cycle groups in turloughs for consecutive sampling months December 07 – April 08 (seasonal data set) (n=5 per turlough in each month; d.f., degrees of freedom; MS, mean sum of squares; *Significant (P<0.05) Bonferroni and LSD pair-wise tests).

Groups	*d.f.*	*MS*	*F-value*	*P-value*	*Post hoc*
Whole community	4,99	53.62	19.88	<0.001	1-3*4-5
Permanent residents	4,99	10.94	7.84	<0.001	2*5, 3*4-5
Ephemeral residents	4,99	25.53	13.67	<0.001	1*4-5, 2*3-5

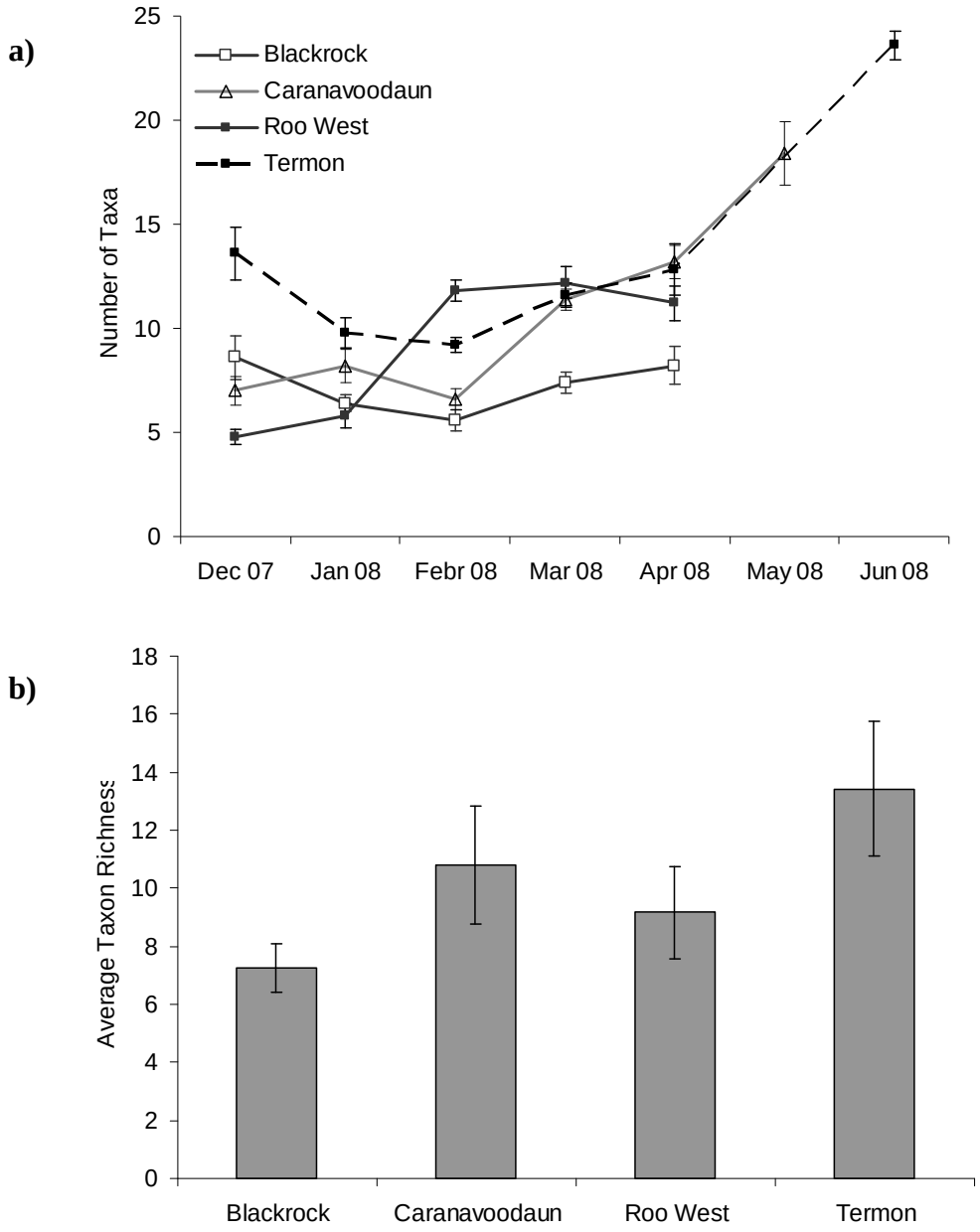


Figure 4.2: a) Seasonal variation of average number of macroinvertebrate taxa recorded per turlough (n=5). **b)** Seasonal average taxon richness during sampling season 2007/2008 per turlough (n=25 in Blackrock and Roo West; n=30 in Caranavoodaun and Termon). Error bars indicate standard error.

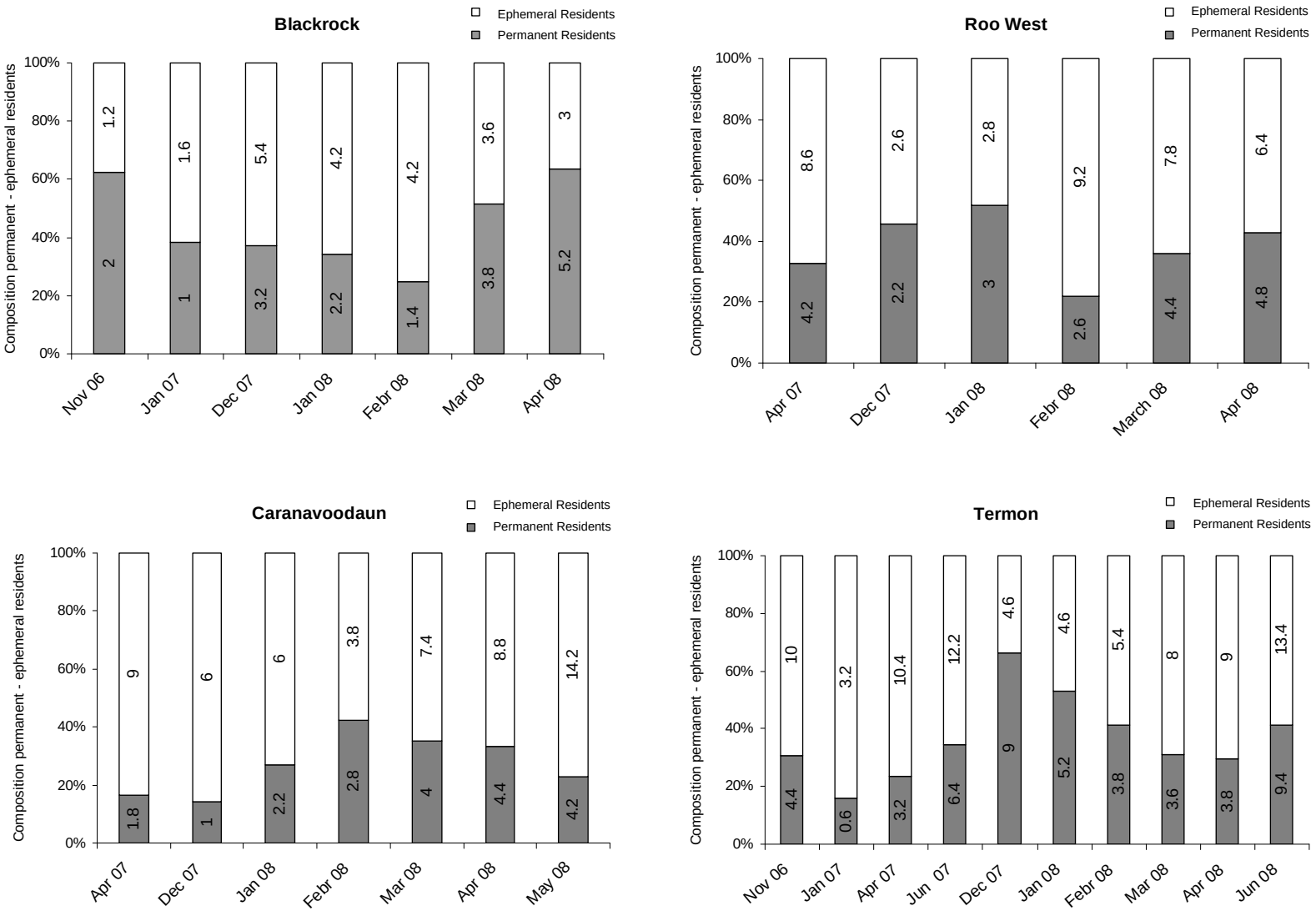
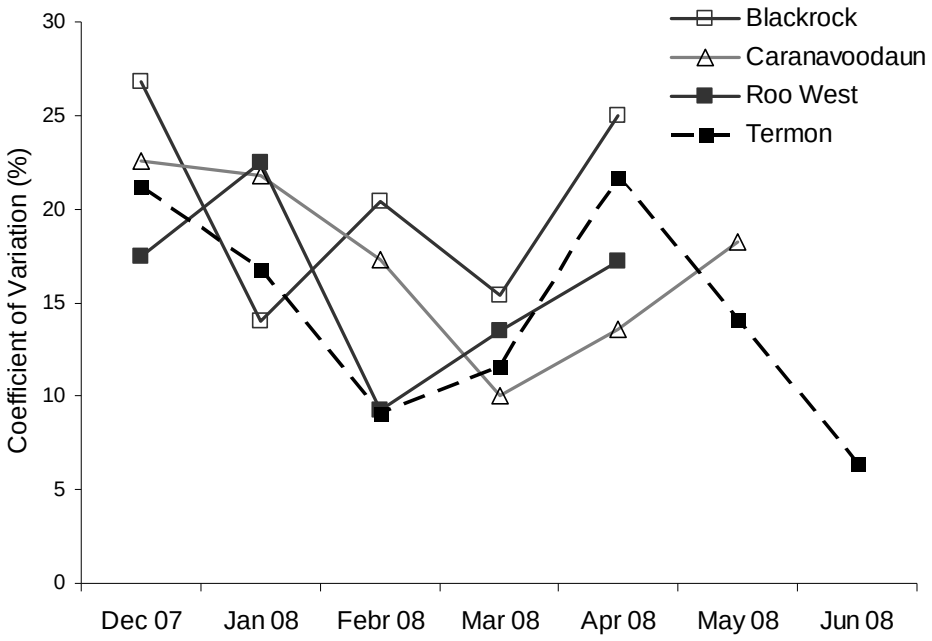


Figure 4.3: Temporal changes in the taxon richness of permanent and ephemeral residents in four turloughs. Numbers in stag columns represent the average taxon richness of respective resident groups (n=5 per turlough in each month).

a)



b)

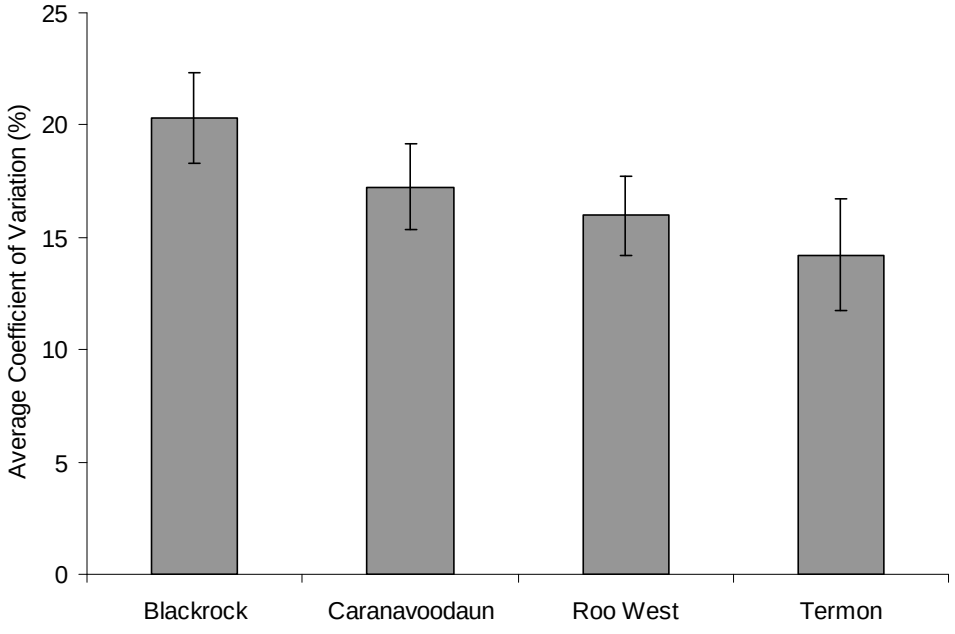


Figure 4.4: a) Seasonal variation of coefficient of variation of taxon richness (n=5). **b)** Seasonal average coefficient of variation of taxon richness during sampling season 2007/2008 per turlough (n=5 in Blackrock and Roo West; n=6 in Caranavoodaun and Termon). Error bars indicate standard error.

4.3.2 Temporal Variation in Invertebrate Community Composition and Co-occurrence of Taxa

PERMANOVA analysis revealed a significant effect of time (month of sampling) on the composition of both the whole community, and the two life-cycle groups in the four turloughs (Table 4.4). Pair-wise comparisons of the different sampling times in the four turloughs revealed significant differences in community composition for the whole community analysis among all months in all turloughs ($P<0.05$). For the permanent residents all pair-wise comparisons differed significantly except in Caranavoodaun, where no significant differences were found between December 2007 and January 2008, or January 2008 and February 2008. Pair-wise comparisons of ephemeral community structures over time showed significant difference among almost all months in all turloughs, except December 2007 and January 2008 in Roo West, and December 2007 and March 2008 in Caranavoodaun

Table 4.4: Results of PERMANOVA testing for the effect of time on community structure for the whole community and different life-cycle groups in turloughs for consecutive sampling months December 07 – April 08 (n=5 per turlough in each month; d.f., degrees of freedom; SS, sum of squares; MS, mean sum of squares).

Groups	*df*	*SS*	*MS*	*Pseudo-F*	*P(perm)*
Whole community	4,99	48377	12094	21.033	>0.001
Permanent residents	4,99	42276	10569	33.265	>0.001
Ephemeral residents	4,99	51837	12959	10.583	>0.001

Co-occurrence analyses revealed a non-random distribution of taxa over time in all four turloughs (Table 4.5). In Blackrock this was mainly caused by changes in oligochaete and dipteran species abundances (Table 4.6). Mollusc species were found only in the first sample of each season (November 2006 and December 2007) and again in April 2008. *Hydrachnidia* sp. was found in early samples of the second year's season but was not detected after a peak in March 2008. Dissimilarities of samples varied between 77.2% (November 2006 and January 2007) and 37.2% (January and February 2008) (Table 4.6). Temporal changes in macroinvertebrate taxa in Caranavoodaun were characterised by decreasing numbers of oligochaetes and an increase of trichopteran and dipteran species. Odonata and Ephemeroptera were only found in late season samples (April 2007 and May 2008), *Ostracoda* sp. only between February and April 2008, and bivalves only in May 2008. Coleopteran species abundances varied throughout the season and were highest in December

2007. Invertebrate communities found in April 2007 were more similar to May 2008 samples (54.6% dissimilarity) than to April 2008 (76.1% dissimilarity), indicating a shift in succession (Figure 4.5 & Table 4.6). In Roo West macroinvertebrate succession was marked by decreasing abundances of oligochaetes and increasing numbers of beetles, molluscs and dipterans towards the end of the inundation cycle. In this turlough *Argyroneta aquatica* disappeared simultaneously with first appearances of ostracods in March 2008, suggesting species replacement. April samples of both seasons showed dissimilarities of 59.8% caused mainly by the absence of *Omphiscola glabra* and *Hydaticus* sp. *(larva),* and presence of *Sympetrum sanguineum* in April 2007. *Hydrachnidia* sp. was present in all but April samples from both seasons, with highest numbers found in February 2008. Macroinvertebrate succession in Termon showed similarities among the two subsequent sampling seasons (Figure 4.5 & Table 4.6). During both years, abundances of oligochaetes declined while dipteran and beetle taxa increased over time. Early instar Odonata and Trichoptera species were found only at the beginning of the sampling season (November 2006 and December 2007/January 2008) and again, as late instars in high numbers, in June in both years. Ephemeroptera appeared in low numbers in April and were highly abundant in June in both seasons. Ostracods were found only later in the season (April 2007 and March 2008). In both years highest numbers of Isopoda (*Asellus aquaticu*s) occurred in June but were abundant in varying numbers throughout the hydrocycle. Dissimilarity of sampling seasons showed April samples to be most similar in their macroinvertebrate community composition (dissimilarity 42.8%). January 2007 samples showed greater similarities to February 2008 (dissimilarity 77.2%) than January 2008 (dissimilarity 92.3%) samples, also supporting a shift in successional pattern as suggested for Caranavoodaun.

Table 4.5: Summary of co-occurrence (ECOSIM) analysis of taxa over time in the studied turloughs for sampling season 2007/2008.

Turlough	*Observed C-score*	*Mean of simulated indices*	*Variance of simulated indices*	*P-value*
Blackrock	1.175	1.028	0.0003	<0.001
Caranavoodaun	0.952	0.834	0.0004	<0.001
Roo West	1.126	1.063	0.0002	<0.001
Termon	1.194	1.087	0.0004	<0.001

4.4 Discussion

4.4.1 Invertebrate Succession in Turloughs

Across four turloughs of varying hydrological regime and nutrient status over two successive years, macroinvertebrate taxon richness and community composition fluctuated both monthly and annually. An evident shift in the successional pattern of macroinvertebrate communities was identified from the MDS graph generated for the most comprehensive data set collected in Termon. The clear picture, which is also supported by the SIMPER analysis, concurs with trends seen in Caranavoodaun and Roo West. Macroinvertebrate communities in Caranavoodaun were more similar between April 2007 and May 2008 compared with April 2008, suggesting a shift in macroinvertebrate succession. As Roo West was not sampled after April 2008 this trend could not be assessed for this turlough. Nevertheless, dissimilarity of samples was highest for April comparisons and additional later season samples are expected to hold more similar macroinvertebrate communities to April 2007 assemblages. The variability in onset of flooding, owing to the comparatively late start of the rainy season in 2007/2008, most likely caused the observed change in the successional pattern in the studied turloughs. In autumn/winter 2007 flooding was observed to start about one month later compared with the proceeding flooding season, concurring with the detected shift in invertebrate succession.

Two phases of succession could be identified in turloughs during the 2007/2008 sampling season based on invertebrate taxon richness. The two successional phases were characterized by a change of the ratio of permanent/ephemeral residents towards an increase of ephemeral taxa later in the season in turloughs Caranavoodaun, Roo West and Termon. A susceptibility of this successional pattern to nutrient enrichment was, however, observed in Blackrock (mean seasonal total phosphorus 52±7.2 s.e. µg L^{-1}). Invertebrate succession in Blackrock showed similar trends compared with the other three turloughs in the beginning of the flooding season but changed towards higher abundances of passive dispersers during the last two sampling months (March and April 2008). The faunal community in Blackrock was generally dominated by taxa with high tolerances to pollutants such as oligochaetes and chironomids (BMWP score 1 and 2, respectively). Ephemeral residents found in March and April 2008 in this turlough were mainly chironomids,

which are reported as tolerant to nutrient enrichment (Hellawell, 1986; Rosenberg and Resh, 1993a). More susceptible ephemeral taxa, such as crane flies (Tipulidae; BMWP score 5) disappeared towards the end of the season.

The identified successional pattern in the four turloughs studied concurs with findings by Jocqué *et al* (2007) which also identified a two-phased hydrocycle in freshwater rock pools in Botswana. These relatively short lived pools were, however, dominated by permanent residents throughout the flooding season, but showed also an increase in ephemeral residents towards the end of the hydrocycle. In studies on relatively long-lasting temporary aquatic habitats (temporary ponds) community changes were mainly attributed to variable hatching stages of permanent residents/passive dispersers from the egg bank compared with the different time of arrival of active dispersers (Boix *et al.*, 2004; Lahr *et al.*, 1999). In both studies, succession phases based on taxonomic criteria distinguished three (Boix *et al.*, 2004) and four (Lahr *et al.*, 1999) successional stages with a trend towards higher abundances or late appearances of ephemeral insects, towards the end of the hydroperiod. Wiggins *et al.* (1980) identified four phases of invertebrate succession in intermittent woodland ponds in southern Ontario over a 17 year sampling period. Classification of successional stages was based on survival strategies of species during the dry periods. Groups 1-3 were taxa which are especially adapted to survive dry periods, while group 4 was characterized by species susceptible to desiccation, dispersing to permanent waters prior to the dry phase. Dispersal of ephemeral residents in temporary waters is not considered to be a random event, as ephemeral taxa actively select suitable habitats for reproduction, with preferences for sites with low risk of predation with the help of chemical clues or other stimuli (Berendonk, 1999; Blaustein *et al.*, 2004; Resetarits, 2001). In general, the four turloughs showed higher abundances of permanent residents such as crustaceans, molluscs or oligochaetes, which colonize newly filled ponds from dormant stages or refugia, during the first identified successional phase in both years. Aquatic insects, which depend on dispersal and migration to survive the dry period and which may need the presence of permanent taxa to prey on, dominated during the later stage of the season. While high densities of ephemeral taxa such as Ephemeroptera, Odonata or Trichoptera species were almost entirely restricted to the end of the season, the permanent community included both early and later season species.

A non-random distribution of taxa over time was identified in all four turloughs. The relative longevity of the turlough hydrocycle (normally several months compared with e.g. a few weeks in case of temporary rock pools) facilitates importance of local biotic interactions, and thus increases the possibility of species replacement (Wellborn *et al.,* 1996). While the temporal variation in some of the taxa recorded was characterized by changes in their abundance over time, other species only emerged for a specific time. *Ostracoda* which are considered passive dispersers and permanent residents of turloughs were only found in samples later in the season. Lahr *et al.* (1999) also found highest densities of ostracods later during a flooding period, corresponding with a shift towards ephemeral taxa, identifying them as relatively slow establishing crustaceans. *Sympetrum sangiuneum* (together with *Lestes dryas* and *L. sponsa* in Caranavoodaun), *Cloeon dipterum* and *C. simile* occurrences were limited to April 2007 in Roo West and Caranavoodaun, but were also found in May 2008 samples in Caranavoodaun (corresponding to a shift in successional pattern). In Termon, high numbers of Odonata and Trichoptera species were present in early season samples (early instar larvae) and only appeared again together with Ephemeroptera taxa in late season samples in both years. Early season specimens were probably the early hatched offspring of the preceding spring/summer population (Nelson and Thompson, 2004) and if early instars migrated to deeper parts of the turlough they could have been missed with the littoral zone sampling strategy used in this study. Overall, invertebrate succession in the four turloughs studied was characterised mainly by a non-random accumulation of species with some suggestions of species replacement.

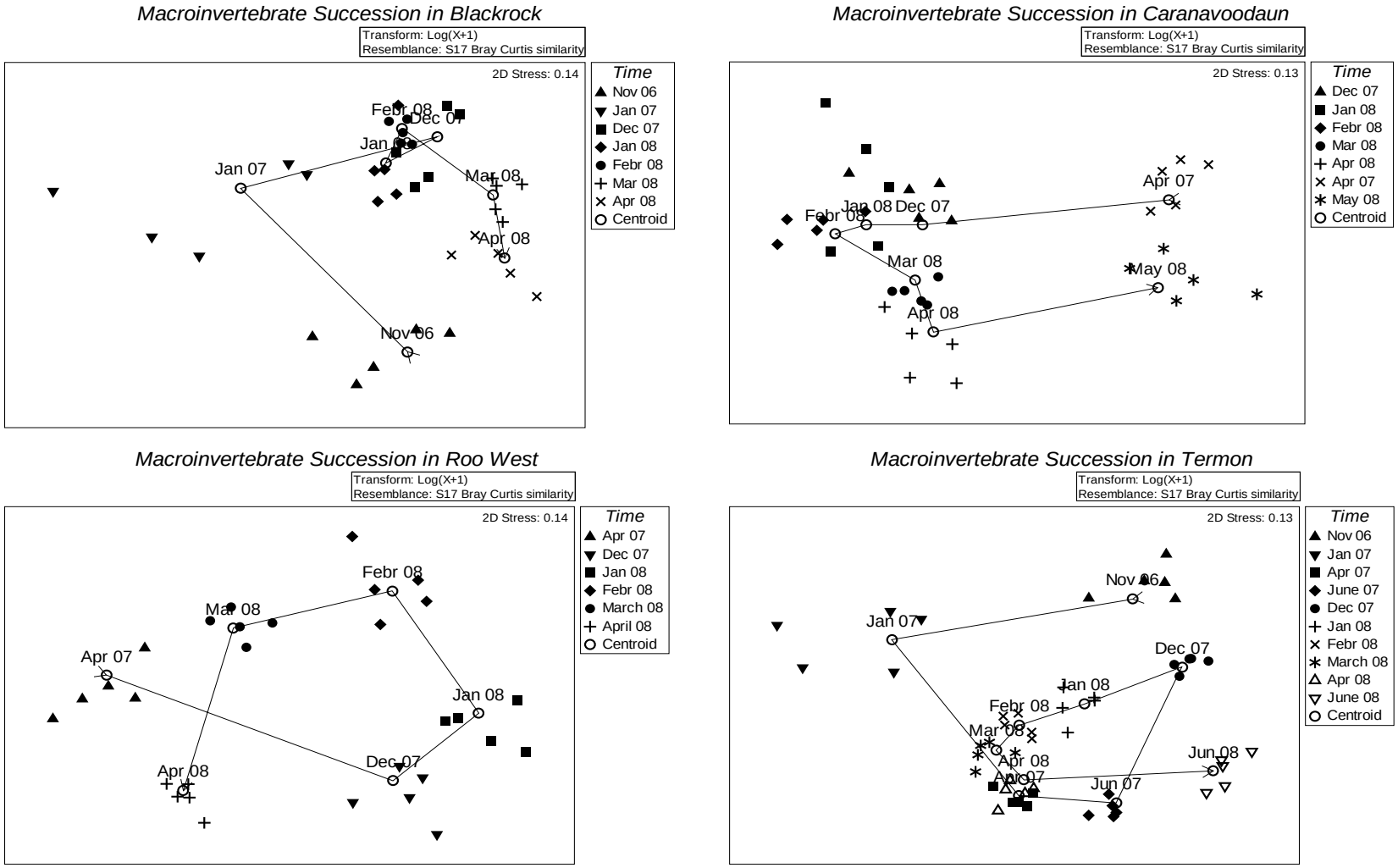


Figure 4.5: Multidimensional scaling (MDS) ordinations of macroinvertebrate communities over two successive sampling periods in four turloughs. Trajectories are indicating the chronological sequence of samples.

4.4.2 Influence of Disturbance on Invertebrate Communities

The dry phase of a turlough, as well as relatively rapid changes in water levels owing to a high areal reduction rate is an ecological disturbance (Schneider *et al.*, 1996; Sousa, 1984; White *et al.*, 1985). Thus, Blackrock, the turlough with the shortest hydroperiod and the highest areal reduction rate can be regarded as the most disturbed turlough studied. Community composition identified in this turlough concur with findings by Wiggins (1980) who found highly disturbed temporary waters to have a community structure characterised mainly by permanent residents, which are able to cope with recurring stresses. Schneider and Frost (1996) furthermore postulated that year to year changes in taxa composition are interlinked with interannual variability of hydroperiod. Thus, highly disturbed habitats will foster invertebrate community structures dominated by permanent residents after dry years, and higher abundances of ephemeral residents after relatively wet ones. The data support this assumption as macroinvertebrate assemblages of Blackrock showed generally higher proportions of permanent residents together with lower taxon richness during the first sampling season in 2006/2007, following an exceptionally dry summer when compared with samples taken during the second field season with a preceding wet summer.

Variation in taxon richness generally decreased in all turloughs towards the end of the sampling season, conforming with stabilising macroinvertebrate communities over time following major disturbance. The increase of variability in taxon richness in March/April 2008 coincided with the draining of turloughs, once more supporting the influence of disturbance on macroinvertebrate communities. Furthermore, an inverse relationship of increasing hydroperiod/decreased disturbance regime on variability in taxon richness was evident, with lowest average seasonal variability in Termon. High disturbances, caused by rapid changes in water level in Blackrock can be associated with persistent high monthly, and highest overall, seasonal variability in taxon richness. Owing to rapidly lowering water levels and likely desiccation of invertebrates during the sampling cycle, succession of invertebrates was possibly repeatedly set back towards initial colonization processes, reducing progress to stability for the invertebrate community in Blackrock. Ward and Blaustein (1994) identified flash floods in Negev Dessert pools as overriding importance for

invertebrate communities, leading to a multiple restart of colonization of pools. With increasing habitat existence, the importance of disturbance becomes less and finally, as abiotic stress decreases, biotic interactions become increasingly important (Schneider, 1999). Temporary wetlands with a relatively long hydroperiod are, therefore, expected to show a stabilization of invertebrate communities over time owing to *inter alia* increased potential of niche development (Jocqué *et al.*, 2007). In contrast, in frequently disturbed environments physical stress and species adaptations to their environment dominate the formation of the faunal matrix (Schneider *et al.*, 1996). The influence of the occurrence of droughts furthermore depends on the individual disturbance regime of wetlands (Schneider *et al.*, 1996). Thus, regularly disturbed turloughs such as Blackrock show high variability in taxon richness for the entire flooding cycle owing to constantly recurring disturbances, while variability of faunal communities in turloughs with a longer hydroperiod/low disturbance will be greater immediately after the disturbance associated with the start of the flooding season.

High disturbance, demonstrated by short hydroperiod, had an adverse influence on taxon richness. Termon, the turlough with the lowest disturbance regime, usually had highest monthly and additionally average seasonal taxon richness. Average seasonal taxon richness was lowest in Blackrock, the turlough with the shortest duration of flooding. This is in agreement with several studies on the influence of hydroperiod on macroinvertebrate taxon richness in temporary wetlands (Collinson *et al.*, 1995; Kiflawi *et al.*, 2003; Schneider *et al.*, 1996; Waterkeyn *et al.*, 2008; Williams *et al.*, 2003). The results furthermore indicate that the additional disturbance of high areal reduction rates has an adverse effect on taxon richness. Respective hydrological regimes are associated with rapid changes in water levels, which predominantly depend on the mode of filling and emptying, topographical conditions and recharge events associated with rainfall (Coxon and Drew, 1986; Tynan *et al.*, 2005). In Blackrock the change in water level can account for up to 9m in 48h, owing to its filling via surface waters and its location in an epikarstic flow system (Sheehy Skeffington *et al.*, 2006), which is reported to be associated with multimodal flood events (Tynan *et al.*, 2005). Recurring disturbances like these favour the abundance of taxa, such as chironomids, with short life cycles or high reproductive rates, which can cope with constant changes in the littoral zone

(Hershey and Lamberti, 2001), as found in Blackrock. Across the turloughs, taxon richness generally increased over time, suggesting a temporal gradient of biodiversity. The longer a habitat exists during a flooding season, the longer the exposure for colonization and emergence from resting stages, which increases the opportunity for a more diverse macroinvertebrate community (Cayrou and Céréghino, 2005; Holland *et al.*, 1998; Spencer *et al.*, 1999). This results in higher species richness and densities of macroinvertebrates following disturbance over time (Holland *et al.*, 1998).

4.5 Conclusions

Although turloughs support varied and unpredictable faunal communities, this study suggests a similarity in following general patterns observed in other ephemeral wetlands. Well adapted early season species take advantage of the habitat before the community diversifies and, in case of suitable low disturbance pressures, possible predatory species appear. The species which arrive in the late successional stage are mainly migrants and do not possess adaptations to drought. These general patterns appear vulnerable to trophic regimes and changes in hydroperiod. Climate change is expected to alter turlough hydrology and in turn lead to disruption in the observed successional patterns by changing invertebrate distribution, population dynamics and biotic interactions. This could have major implications for the long term persistence of the highly specialized fauna which is a feature of turloughs. Changes of local weather conditions associated with climate change seem to be inevitable (McElwain and Sweeney, 2007; Sweeney *et al.*, 2003) and are already starting to become evident through increased variability in rainfall patterns from year to year. Climate change will increase the number and intensity of stressors affecting turlough ecosystems. Thus, management which reduces already existing stressors, such as nutrient enrichment from land use or drainage is necessary in order to reduce anthropogenic pressures on turloughs. Effectiveness of monitoring to support conservation management needs to account for temporal variability. This includes adapting monitoring to varying onset of flooding rather than more traditionally spaced sampling. Macroinvertebrate communities observed in one particular month are likely to differ from year to year in response to rainfall patterns. Furthermore, life stages of macroinvertebrate taxa need to be considered in monitoring programmes as most univoltine ephemeral taxa emerge in spring/summer (Solimini

et al., 2006). In case sampling can only be conducted during one particular season, late season (late spring/early summer) sampling should be avoided as this could lead to an underestimation of biodiversity or misinterpretation of macroinvertebrate communities of turloughs. Taxa such as Ephemeroptera or Trichoptera generally considered sensitive to anthropogenic disturbance could have already emerged. Single season sampling could moreover overlook species with short life-cycles or egg-diapause periods. Adequate turlough sampling, thus, needs to be aligned with the starting of the turlough flooding season and suitably temporally stratified, with timing and frequency of sampling depending on the question addressed by respective sampling protocols.

Table 4.6: Summary results from SIMPER analysis showing cumulative contribution (Cum%) of three most important contributing taxa to sample dissimilarities in % (n=5 per month in each turlough).

Blackrock			***Roo West***		
Groups Nov 06 & Jan 07			*Groups Dec 07 & Jan 08*		
Average dissimilarity = 77.16			Average dissimilarity = 53.16		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Oligochaeta sp.	33.88	Nov	*Oligochaeta* sp.	23.13	Dec
Tipulidae sp.	50.74	only Jan	*Agyroneta aquatica*	38.27	Jan
Succinea sp.	61.8	only Nov	*Ceratopogonidae* sp.	47.86	only Dec
Groups Jan 07 & Jan 08			*Groups Jan 08 & Febr 08*		
Average dissimilarity = 69.29			Average dissimilarity = 61.89		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Oligochaeta sp.	24.4	Jan 08	*Hydrachnidia* sp.	19.37	Feb
Chironomidae sp.	45.67	Jan 08	*Graptodytes bilineatus*	29.34	only Feb
Hydrachnidia sp.	58.55	Jan 08	*Tipulidae* sp.	38.27	Feb
Groups Dec 07 & Jan 08			*Groups Febr 08 & March 08*		
Average dissimilarity = 43.57			Average dissimilarity = 58.80		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Oligochaeta sp.	12.97	Dec	*Diptera Pupae*	11.06	only Mar
Velia sp.	25.86	only Dec	*Ostracoda* sp.	21.81	only Mar
Tipulidae sp.	38	Dec	*Agyroneta aquatica*	29.48	only Feb
Groups Jan 08 & Febr 08			*Groups Apr 07 & April 08*		
Average dissimilarity = 37.19			Average dissimilarity = 59.84		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Tipulidae sp.	28.4	Feb	*Omphiscola glabra*	12.04	only Apr 08
Chironomidae sp.	43.56	Feb	*Hydaticus* sp. *(larva)*	22.53	only Apr 08
Hydrachnidia sp.	58.1	Feb	*Zonitoides* sp.	29.45	only Apr 08
Groups Febr 08 & Mar 08			*Groups March 08 & April 08*		
Average dissimilarity = 52.46			Average dissimilarity = 56.09		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Hydrachnidia sp.	16.07	Only Feb	*Hydaticus* sp. *(larva)*	11.27	only Apr
Tipulidae sp.	30.55	Feb	*Omphiscola glabra*	21.22	Apr
Ostracoda sp.	44.37	only Mar	*Graptodytes bilineatus*	30	only Mar
Groups Mar 08 & Apr 08					
Average dissimilarity = 48.71					
Species	Cum.%	(Higher) presence			
Succinea sp.	16.84	only Apr			
Galba truncatula	29.07	only Apr			
Agabus sp. *(larva)*	38.08	only Mar			

Table 4.6 (Contd.): Summary results from SIMPER analysis showing cumulative contribution (Cum%) of three most important contributing taxa to sample dissimilarities in % (n=5 per month in each turlough).

Caranavoodaun			***Termon***		
Groups Dec 07 & Jan 08			*Groups Jan 07 & Febr 08*		
Average dissimilarity = 53.20			Average dissimilarity = 77,19		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Limnephilidae sp. *Instar III*	10.86	only Jan	*Oligochaeta* sp.	25,19	Feb 08
Oligochaeta sp.	20.05	Jan	*Asellus aquaticus*	40,97	only Feb 08
Berosus signaticollis	28.14	only Dec	*Chironomidae* sp.	49,53	Feb 08
Groups Jan 08 & Febr 08			*Groups Jan 07 & Apr 07*		
Average dissimilarity = 45.34			Average dissimilarity = 86,56		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Oligochaeta sp.	12.71	Feb	*Oligochaeta* sp.	17,93	Apr
Limnephilidae sp. *Instar III*	25.24	only Jan	*Chironomidae* sp.	34,83	Apr
Chironomidae sp.	32.57	Jan	*Ostracoda* sp.	46,06	only Apr
Groups Febr 08 & Mar 08			*Groups Apr 07 & June 07*		
Average dissimilarity = 57.21			Average dissimilarity = 61,05		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Ostracoda sp.	18.87	Mar	*Cloeon simile*	14,88	June
Oligochaeta sp.	30.13	Feb	*Sympetrum sanguineum*	21,64	only June
Agabus sp. *(larva)*	38.42	Mar	*Porhydrus* sp. *(larva)*	28,07	only June
Groups Mar 08 & Apr 08			*Groups Dec 07 & Jan 08*		
Average dissimilarity = 47.50			Average dissimilarity = 72,04		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Limnephilus centralis	8.56	only Apr	*Anisoptera* sp. *larvae*	18,58	Dec
Ostracoda sp.	15.48	Mar	*Galba truncatula*	29,09	only Dec
Graptodytes bilineatus	21.76	Mar	*Limnephilidae* sp. *Instar I*	38,18	only Dec
Groups Apr 08 & May 08			*Groups Jan 08 & Febr 08*		
Average dissimilarity = 74.76			Average dissimilarity = 54,24		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Sympetrum sanguineum	9.89	only May	*Tipulidae* sp.	11,64	only Feb
Pisidium/Sphaerium sp.	16.79	only Apr	*Isotomidae* sp.	23,14	Jan
Cloeon dipterum	23.1	only May	*Oligochaeta* sp.	32,50	Feb
Groups Apr 08 & Apr 07			*Groups Febr 08 & March 08*		
Average dissimilarity = 76.10			Average dissimilarity = 44,01		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Sympetrum sanguineum	12.67	only Apr 07	*Asellus aquaticus*	10,44	Feb
Anisoptera sp. *(larva)*	20.69	only Apr 07	*Ostracoda* sp.	18,95	only Mar
Culicidae sp.	28.55	only Apr 07	*Tipulidae* sp.	27,16	Feb

Table 4.6 (Contd.): Summary results from SIMPER analysis showing cumulative contribution (Cum%) of three most important contributing taxa to sample dissimilarities in % (n=5 per month in each turlough).

Caranavoodaun			***Termon***		
Groups May 08 & Apr 07			*Groups Apr 07 & Apr 08*		
Average dissimilarity = 54.63			Average dissimilarity = 42,82		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Pisidium/Sphaerium sp.	9.47	only May 08	*Hydaticus sp (larva)*	9,92	Apr 08
Anisoptera sp. *(larva)*	18.51	only Apr 07	*Oligochaeta* sp.	17,84	Apr 07
Culicidae sp.	24.12	Apr 07	*Ostracoda* sp.	24,49	Apr 07
Termon					
Groups Nov 06 & Jan 07			*Groups March 08 & Apr 08*		
Average dissimilarity = 94,48			Average dissimilarity = 50,89		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Anisoptera sp.*(larva)*	17,17	only Nov	*Hydaticus* sp. *(larva)*	12,15	only Apr
Limnephilidae sp. *Instar II*	27,23	only Nov	*Agabus* sp. *(larva)*	22,00	only Apr
Limnephilidae sp. *Instar III*	33,41	only Nov	*Chironomidae* sp.	30,39	Apr
Groups Jan 07 & Jan 08			*Groups Apr 08 & June 08*		
Average dissimilarity = 92,34			Average dissimilarity = 85,72		
Species	Cum.%	(Higher) presence	Species	Cum.%	(Higher) presence
Asellus aquaticus	16,33	only Jan 08	*Asellus aquaticus*	7,35	June
Isotomidae sp.	27,55	only Jan 08	*Sympetrum sanguineum*	14,47	only June
Oligochaeta sp.	38,57	only Jan 08	*Planorbis crista*	20,16	only June

5 Spatial Variability of Macroinvertebrates in Turloughs

5.1 Introduction

The littoral environment of freshwater ecosystems is heterogeneous (Hall *et al.*, 1992; Pickett and White, 1985; Wetzel, 2001), owing to a variety of physical, chemical and biotic interactions. This can lead to a high variability of animals in space (Downes *et al.*, 1993) and has caused concern over the meaningfulness of littoral invertebrate data collected in freshwater ecosystems (Harrison and Hildrew, 1998). Habitat heterogeneity poses a challenge to the collection of representative samples, with potentially far reaching effects on effectiveness of monitoring protocols. Ecological assessment and monitoring are based on the assumption of adequate representation of each sampling site. Understanding and evaluation of natural spatial heterogeneity in macroinvertebrate assemblages in turloughs is therefore essential for the development of adequate biomonitoring, as required under the European Water Framework Directive (WFD) (EC, 2000) and the EC Habitats Directive (EEC, 1992). Without this, it is impossible to detect anthropogenic disturbances with confidence (Johnson, 1998; Trigal *et al.*, 2006).

Macroinvertebrate spatial variation has been studied in lakes in relation to habitat and trophic status (Brodersen *et al.*, 1998; Tolonen *et al.*, 2001; White and Irvine, 2003). Results of these studies emphasized the need for habitat stratification in among-lake comparisons, especially when the purpose of monitoring is the detection of pressure gradients. Differences in macroinvertebrate communities at multiple spatial scales have been detected in oligotrophic lakes in New Zealand (Stoffels *et al.*, 2005; Weatherhead and James, 2001) and among habitats in 16 Swedish lakes (Johnson, 1998). White and Irvine (2003) found distinct clusters of macroinvertebrate samples collected from 15 visually distinct habitats in lakes of a wide range of trophic status in Ireland. The same study, furthermore, found paired samples from contrasting habitats of pebble/cobble and macrophyte-dominated mesohabitats of 21 lakes to have greater similarity within than among lakes and concluded that variation within lakes was nested in among lake variation across a range of lakes. Studies in wetlands including temporary ponds, however, have rather concentrated on the influence of hydroperiod (Brooks, 2000; Collinson *et al.*, 1995;

Solimini *et al.*, 2005) on invertebrate communities and only few studies have dealt with the implications of spatial variation for the biological assessment of ponds (Della Bella *et al.*, 2005; García-Criado *et al.*, 2005).

The spatial patterns of macroinvertebrate communities in Irish turloughs, in the context of biomonitoring, have not been examined. The littoral zone of turloughs can comprise different habitat types (i.e. grassland, limestone pavement, stone walls, reed stands) but the dominant habitat in the majority of turloughs is flooded/submerged grassland. The underlying assumption in ecological assessment programmes is that samples effectively discriminate among lakes, albeit in this case, temporary ones. Meaningful ecological surveys for the very variable and dynamic turlough environments require cost and time effective sampling.

The aim of this chapter was to determine spatial variability of turlough macroinvertebrate communities within and between-habitats. It tests the adequacy that a single grassland habitat sample collected at any location of a turlough is representative of the entire macroinvertebrate community. Spatial variation was investigated on two different spatial scales. First, two different habitats were sampled in order to examine variability of macroinvertebrates between habitats. Second, a number of replicate samples were collected in the dominant habitat type (submerged grassland) from different sites within a turlough to investigate the within-habitat variation of macroinvertebrate communities.

5.2 Methods

5.2.1 Study Sites and Macroinvertebrate Sampling

Two different habitat types comprising short, totally submerged grassland (height <10 cm) and long, emergent grassland (emerging over the water surface >30 cm) were sampled in two turloughs, Brierfield and Lisduff, in April 2007 in order to study between-habitat variability of macroinvertebrate communities in turloughs. Both habitats were sampled at 30-40 cm water depth in each turlough, with habitats in Brierfield dominated by *Glyceria fluitans* and in Lisduff by *Agrostis stolonifera*. The two habitats will subsequently be referred to as submerged and emergent grassland.

To investigate the within-habitat variability of macroinvertebrate assemblages, four grassland habitat sites were sampled in four additional turloughs in spring 2008. While the turloughs Blackrock, Roo West and Termon were sampled in April 2008, Caranavoodaun was only sampled in May 2008 owing to high water levels and, thus, inaccessibility of sampling sites. In order to see if the varying sampling times had an influence on results, Termon was sampled additionally in June 2008.

The four turloughs were selected previously from a list of twenty-two turloughs, located in counties Clare, Galway, Mayo and Roscommon which were identified as representative of the morphological and geographical range of turloughs. These turloughs represent recurrent turlough types with a range of different nutrient and hydrological regimes (Table 5.1 & Figure 5.1). Littoral macroinvertebrates were collected in both years with a 1 mm mesh size pond-net in combination with a box sampler (for details see Chapter 3 & 4). At every sampling site five replicate samples were collected, sieved and preserved in 90% industrial methylated spirits (IMS). Macroinvertebrates were later counted and identified to the lowest taxonomic level possible, typically species.

Table 5.1: Sampling sites, their nutrient status, hydrological regimes and hydroperiod of two sampling seasons 2006/07 and 2007/08 of the four turloughs studied.

Turlough	***MeanTP ± s.d. (ug/L)****	***Areal reduction rate dA/dT (m^2/Day)[1]***	***Hydroperiod (weeks) 2006/07 & 2007/08***
Blackrock	52±16	-10875	28 – 19
Caranavoodaun	11±4	-3479	32.6 – 26
Roo West	10±4	-3734	33 – 26
Termon	15±8	-1042	52 – 52

[1] calculated as the average rate of change of area between the time of maximum areal inundation and the emptying of turlough (dA= - maximum areal inundation; dT=time between max areal inundation and emptying of turlough). Data provided by Owen Naughton.
* mean of collected monthly TP concentrations during sampling season October 2006 – June 2007. Data provided by Helder Pereira.

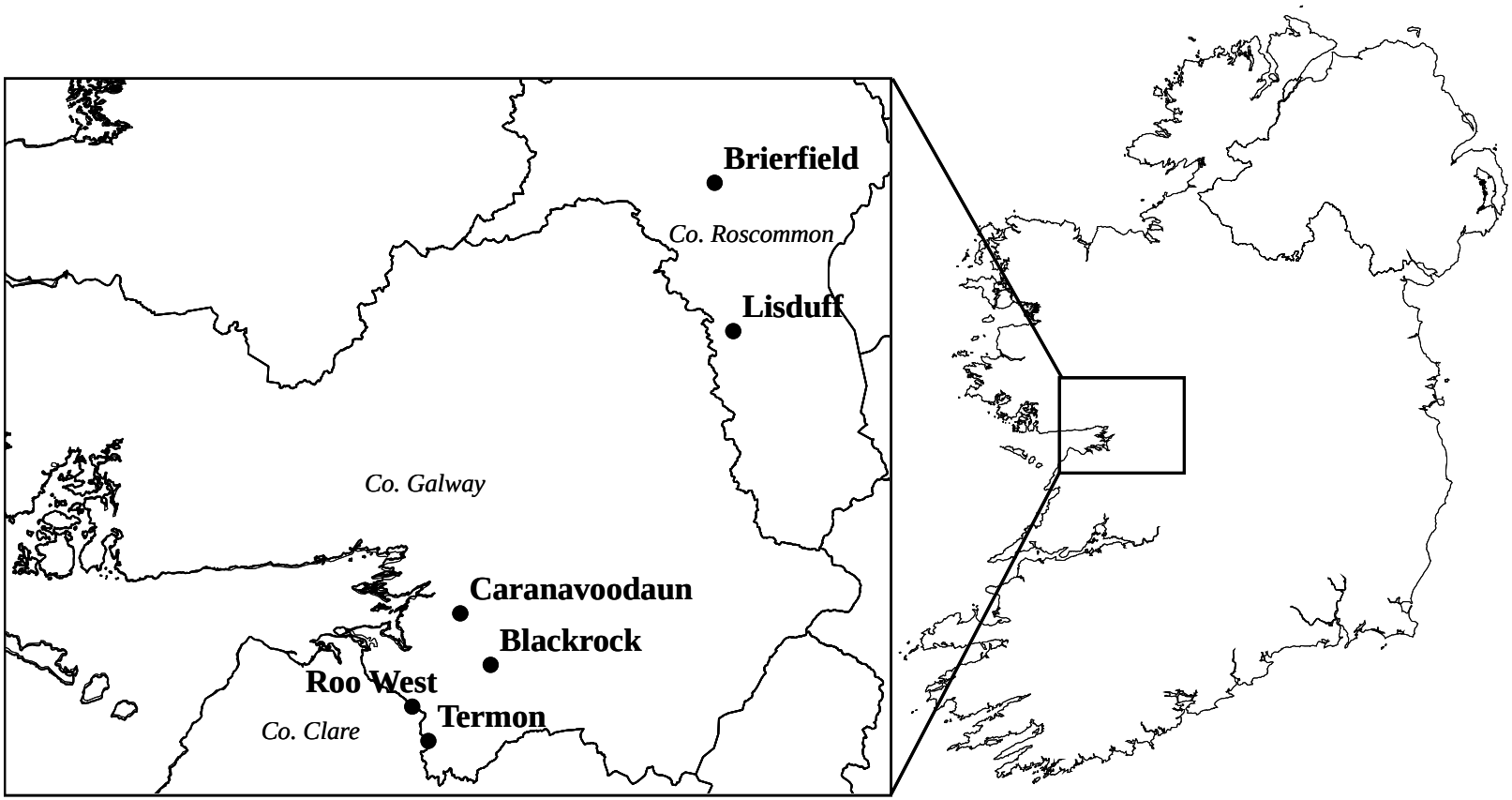


Figure 5.1: Map of Ireland showing the location of the six turloughs studied.

5.2.2 Statistical Analysis

Statistical analysis tested for between-habitat (Brierfield and Lisduff) and within-habitat differences (Blackrock, Caranavoodaun, Roo West and Termon) in macroinvertebrate community structures.

A one-way analysis of variance (ANOVA) was used to test for significant differences in taxon richness between habitats in the two turloughs Lisduff and Brierfield and between the four grassland habitat sites sampled in the four turloughs Blackrock, Caranavoodaun, Roo West and Termon. All replicate samples were included in the analysis (n=5 per habitat and per site in each turlough). The degree of variability of taxon richness within replicate samples was estimated by the coefficient of variation (CV):

$$CV = s.d. / \overline{x} * 100$$

Hierarchical Cluster Analysis and non-metric multidimensional scaling (MDS) tested for similarities of macroinvertebrate community structures across habitats and grassland sampling sites. Both ordination methods were based on log(x+1) transformed invertebrate abundance data and presence/absence data using a Bray-Curtis similarity matrix. Clusters were formed using the group average linkage method and the similarity profile (SIMPROF) permutation test was incorporated into the Cluster Analysis using 999 simulation permutations. SIMPROF tests the null hypothesis that a certain set of samples which are *a priori* unstructured do not differ from each other in multivariate space (Clarke and Gorley, 2006). Differences in community composition between habitats were, furthermore, analyzed using the similarity percentages routine SIMPER (PRIMER® 6). By decomposing Bray-Curtis similarities among all pairs of samples, within defined groups (in this case habitats in each turlough), SIMPER computes the percentage contributions of individual species to respective group differences (Clarke and Warwick, 2001).

5.3 Results

5.3.1 Between-Habitat Variability

Taxon richness did not vary significantly between habitats sampled in April 2007 in turloughs Lisduff and Brierfield (one-way ANOVA: $F_{1,9}$=1.33 and $F_{1,9}$=0.02 in Lisduff and Brierfield, respectively; P non significant in both cases) with highest average taxon richness found in submerged grassland in Lisduff (15.2±1.04 s.e.; n=5) (Table 5.2). Variability in taxon richness was highest in emergent grassland in Lisduff (C.V.=23.7%) and lowest among emergent grassland in Brierfield (C.V.=12.5%).

Table 5.2: Summary statistics of total taxa recovered from each habitat (s.g.=submerged grass; e.g.=emergent grass) in two turloughs, minimum, maximum and average taxon richness recovered from a single sample and coefficient of variation (C.V.) of taxon richness (n=5 per habitat). Samples collected in April 2007.

Turlough	*Habitat*	*Total*	*Minimum*	*Maximum*	*Average ± S.E.*	*C.V. (%)*
Lisduff	s.g.	31	12	20	15.2 ± 1.04	19.4
Lisduff	e.g.	26	9	17	13.0 ± 1.11	23.7
Brierfield	s.g.	26	11	17	13.4 ± 0.94	19.5
Brierfield	e.g.	25	11	15	13.2 ± 0.59	12.5

Hierarchical cluster analysis in combination with the SIMPROF-test detected significant differences in community structure between habitat type in Brierfield (π=4.58; P<0.001 for log(x+1) transformed abundance data) and between turloughs (π=6.72; P<0.001 for log(x+1) transformed abundance data) in both, the log(x+1) transformed total abundance and the presence/absence data set. No significant differences were found between habitats in Lisduff (Figure 5.2a) in both data sets. The results were supported by the MDS plot generated for the same macroinvertebrate abundance and presence/absence data, showing higher variability between habitats in Brierfield than in Lisduff (Figure 5.2b). Both results indicate that within turlough variability in invertebrate community composition is nested within turlough variability. As log(x+1) transformed total abundance and presence/absence data achieved similar results in both ordination methods, only hierarchical cluster dendograms and MDS graphs of the log(x+1) transformed total abundance macroinvertebrate data are subsequently presented.

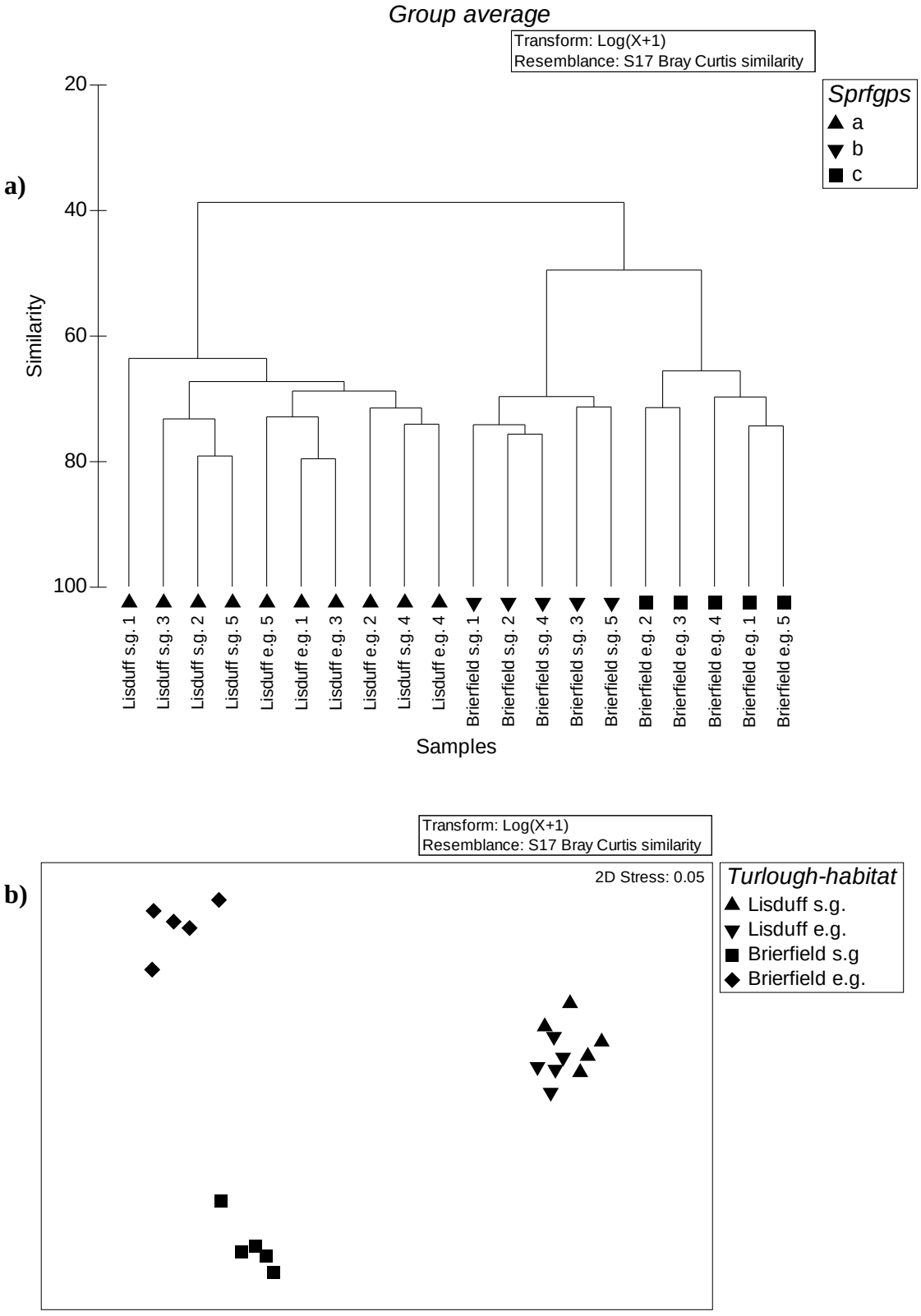


Figure 5.2: a) Hierarchical cluster analysis dendogram and b) MDS plot of macroinvertebrate species log(x+1) transformed total abundance data from submerged (s.g.) and emergent grassland habitat (e.g.) in Brierfield and Lisduff (n=5 per habitat; n=10 per turlough) (Sprfgps = SIMPROF-groups identified using SIMPROF-test).

Greater dissimilarity of macroinvertebrate community structures was identified between habitats in Brierfield (Table 5.3). While the majority of the predominant invertebrate species occurred in both habitats in differing abundances, some taxa showed preferences for one particular habitat type. For example, *Berosus signaticollis* was recovered only from submerged grassland in Lisduff, whereas *Argyroneta aquatica* was only collected from emergent grassland and *Omphiscola glabra* only from submerged grassland habitat in Brierfield.

Table 5.3: Summary results from SIMPER analysis showing cumulative contribution (Cum%) of contributing taxa to habitat (submerged grassland=s.g.; emergent grassland=e.g.) dissimilarities (in %) (only first 10 contributing species are presented) (n=5 per habitat).

Lisduff submerged grass & Lisduff emergent grass			*Brierfield submerged grass & Brierfield emergent grass*		
Average dissimilarity = 33.47			Average dissimilarity = 50.44		
Species	Cum.%	higher presence	Species	Cum.%	higher presence
Graptodytes bilineatus	9.36	s.g.	*Agyroneta aquatica*	9.89	only e.g.
Limnephilus centralis	15.11	s.g.	*Agabus* sp. *(larvae)*	17.75	s.g.
Berosus signaticollis	20.36	only s.g.	*Omphiscola glabra*	25.28	only s.g.
Oligochaeta sp.	25.05	e.g.	*Ostracoda* sp.	31.74	s.g.
Hydrachnidia sp.	29.29	e.g.	*Halticinae* sp.	38.16	e.g.
Polycelis nigra/tenuis	33.52	s.g.	*Graptodytes bilineatus*	43.76	s.g.
Sympetrum sanguineum	37.49	s.g.	*Dryops* sp. *(larvae)*	49.06	e.g.
Asellus aquaticus	41.3	s.g.	*Culicidae* sp.	53.97	s.g.
Chironomidae sp.	44.9	e.g.	*Chironomidae* sp.	58.09	s.g.
Culicidae sp.	48.36	s.g.	*Rhantus* sp. *(larvae)*	62.18	e.g.

5.3.2 Within-Habitat Variability

Average taxon richness in grassland habitat samples (n=20 per turlough) sampled between April and June 2008 varied among turloughs (Table 5.4). Highest average taxon richness was found in Caranavoodaun (18.7±0.5 s.e.) sampled in May 2008 and Termon (26±0.97 s.e.) in June 2008, suggesting an increase of taxon richness over time of flooding.

Table 5.4: Summary statistics of total, minimum, maximum and average taxon richness found in four grassland sites in four turloughs (n=20 in each turlough).

Turlough	***Total***	***Minimum***	***Maximum***	***Average ± S.E.***
Blackrock	17	4	10	6.8 ± 0.57
Caranavoodaun	48	15	24	18.7 ± 0.5
Roo West	29	8	15	11.4 ± 0.31
Termon (April)	48	9	17	13.1 ± 0.28
Termon (June)	57	21	33	26 ± 0.97

No significant difference in taxon richness was found among the four grassland habitat sites in Caranavoodaun (May 2008), Roo West (April 2008) and Termon (April 2008). However, taxon richness varied significantly among sampling sites in Blackrock and Termon collected in June 2008 (Table 5.5).

Table 5.5: One-way ANOVA results examining the differences in taxon richness among sites in the four turloughs studied (n=5 per site; n=20 per turlough and sampling month).

Turlough	***SS***	***df***	***MS***	***F***	***P***	***Post hoc***
Blackrock	37.4	3	12.5	7.55	0.002	1,3 * 4
Caranavoodaun	28.6	3	9.5	1.23	0.332	
Roo West	11.4	3	3.8	1.63	0.223	
Termon (April 08)	8.9	3	3.0	0.48	0.702	
Termon (June 08)	108.4	3	36.1	5.58	0.008	2,3 * 4

Variability in taxon richness among replicate samples was highest in site one in Blackrock (C.V.=25%) and lowest in site one in Termon in June 2008 (C.V.=5.9%) indicating a negative correlation of variability with increasing hydroperiod (Figure 5.3). The average coefficient of variation per turlough was also highest in Blackrock and lowest in Termon in June 2008 (C.V.=9.2%). The decrease in variability in Termon from 13% in April 2008 to 9.2% two months later, furthermore, concurs with a stabilisation of the invertebrate community over time.

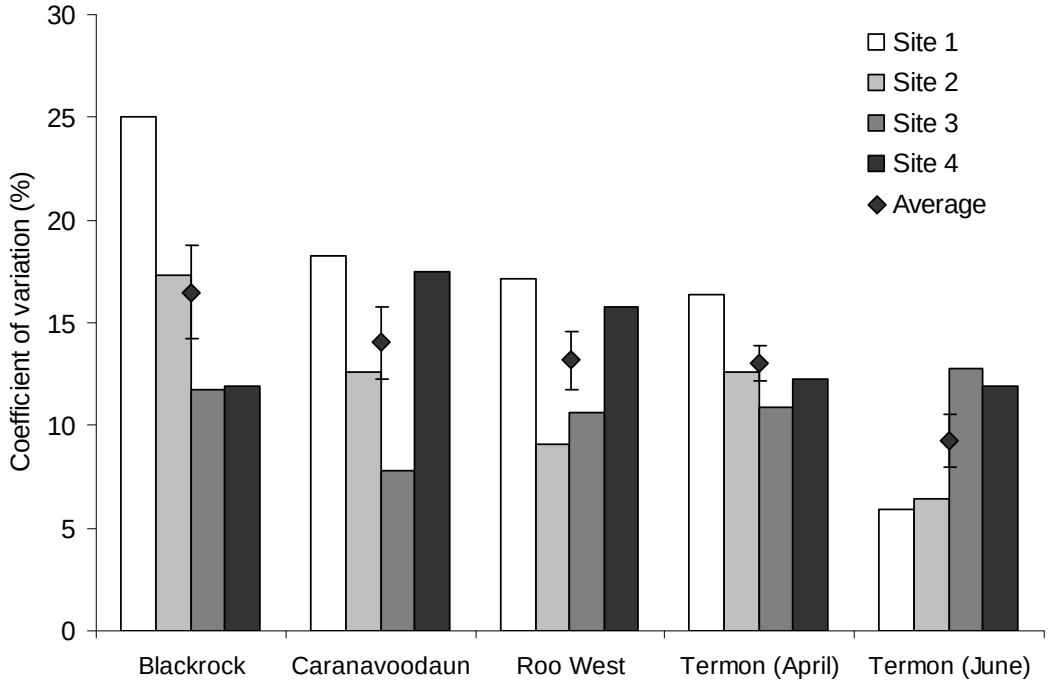
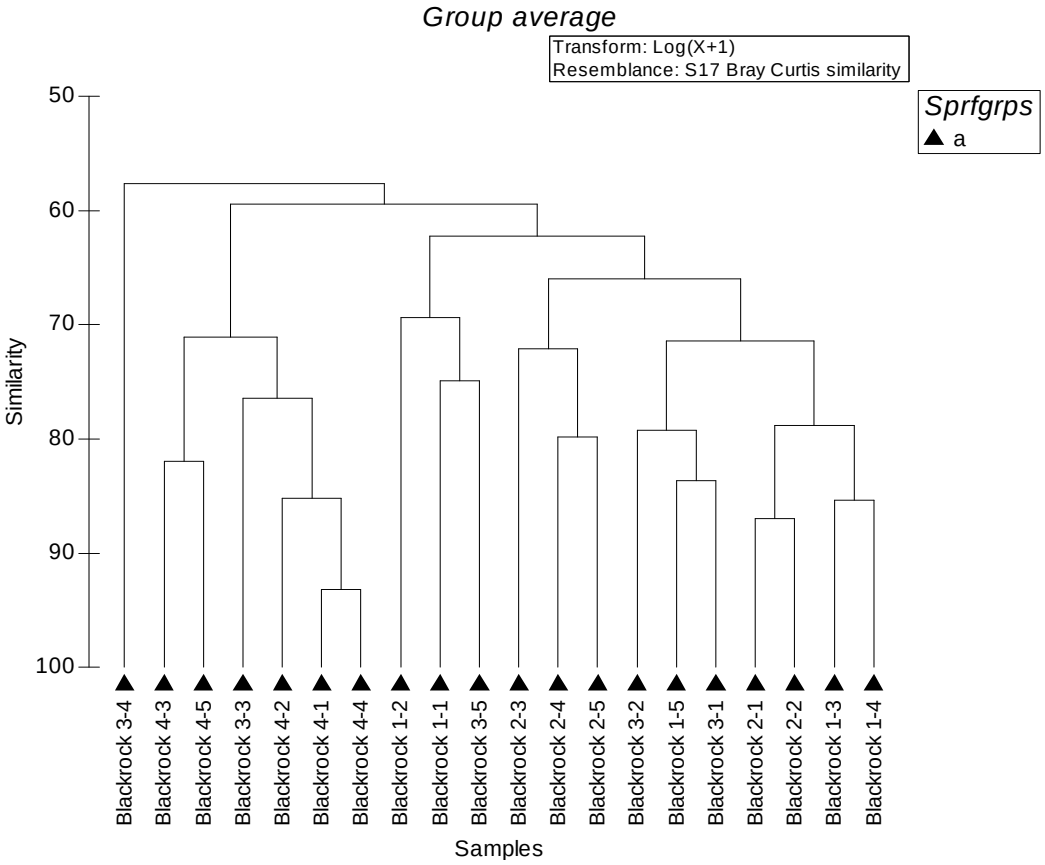


Figure 5.3: Coefficient of variation (C.V.) of replicate samples per site per turlough and average C.V. per turlough ± s.e. (n=5 per site; n=20 per average in each turlough). Turlough order is ranked according to hydroperiod.

The SIMPROF test, which was incorporated in the hierarchical cluster analysis, identified no significant differences among samples from different grassland sampling sites in turloughs sampled in April 2008 (Figures 5.4a, 5.6a & 5.7a) using both, log(x+1) transformed total abundance and presence/absence data. These results were supported by those from the non-metric multidimensional scaling (MDS) equally using both data sets (Figures 5.4b, 5.6b & 5.7b). However, samples collected

at different grassland sites in Caranavoodaun in May 2008 and Termon in June 2008 separated samples into two significantly different groups identified by the SIMPROF test employing log(x+1) transformed abundance data (Caranavoodaun: π=1.64, P<0.01; Termon: π=0.7, P<0.01) (Figure 5.5a & 5.8a). The clustering of sites was also apparent in the respective MDS plots (Figure 5.5b & 5.8b). No significant difference was found among grassland sampling sites in the same turloughs using presence/absence data, highlighting the importance of macroinvertebrate abundance for the separation of sites. The MDS plot generated using log(x+1) transformed abundance data of all grassland habitat macroinvertebrate samples collected in each turlough (n=20 per turlough) revealed that invertebrate community structures within the turloughs were, nevertheless, highly distinct. Samples clustered closely together with no overlap among turloughs (Figure 5.9). Similar results were obtained using the presence/absence data set. Significant differences among turloughs were identified using the SIMPROF-test (cluster diagram not shown here). The MDS plot revealed a closer clustering of turloughs sampled in the same month (April 2008) compared with later samples collected in May 2008 and June 2008, indicating a spatio-temporal interaction in invertebrate community structure (Figure 5.9).

a)



b)

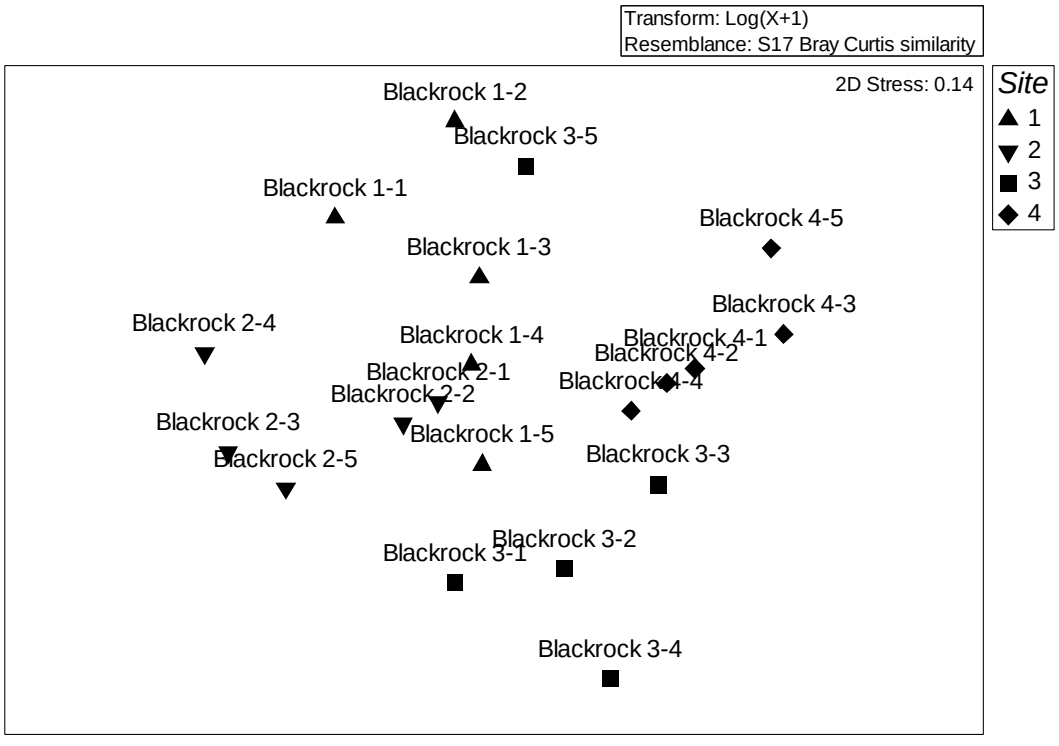


Figure 5.4: a) Hierarchical cluster analysis dendogram and **b)** MDS plot of macroinvertebrate species log(x+1) transformed total abundance data from Blackrock sampled in April 2008 (n=5 per site).

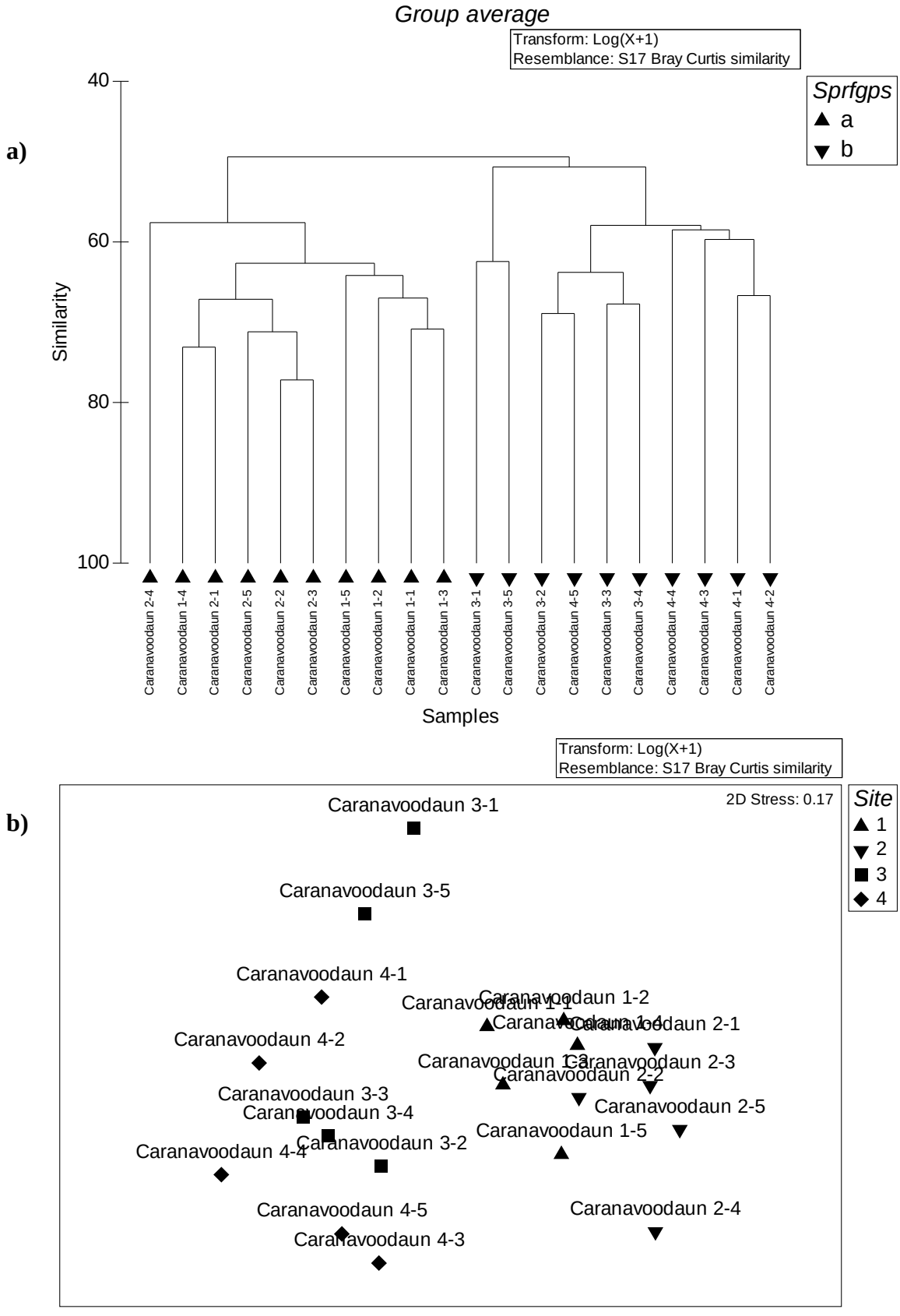


Figure 5.5: a) Hierarchical cluster analysis dendogram and **b)** MDS plot of macroinvertebrate species log(x+1) transformed total abundance data from Caranavoodaun sampled in May 2008 (n=5 per site).

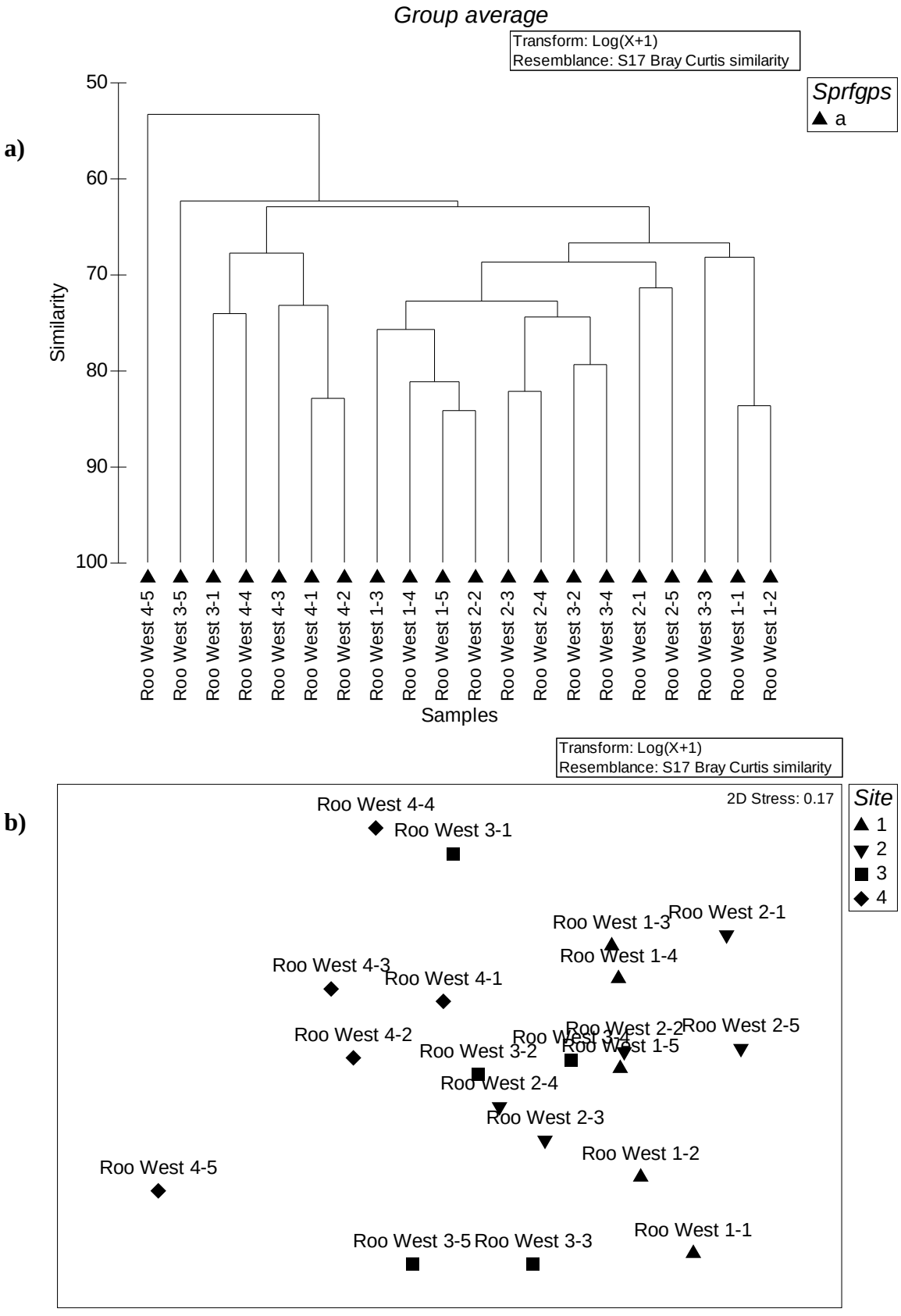


Figure 5.6: a) Hierarchical cluster analysis dendogram and **b)** MDS plot of macroinvertebrate species log(x+1) transformed total abundance data from Roo West sampled in April 2008 (n=5 per site).

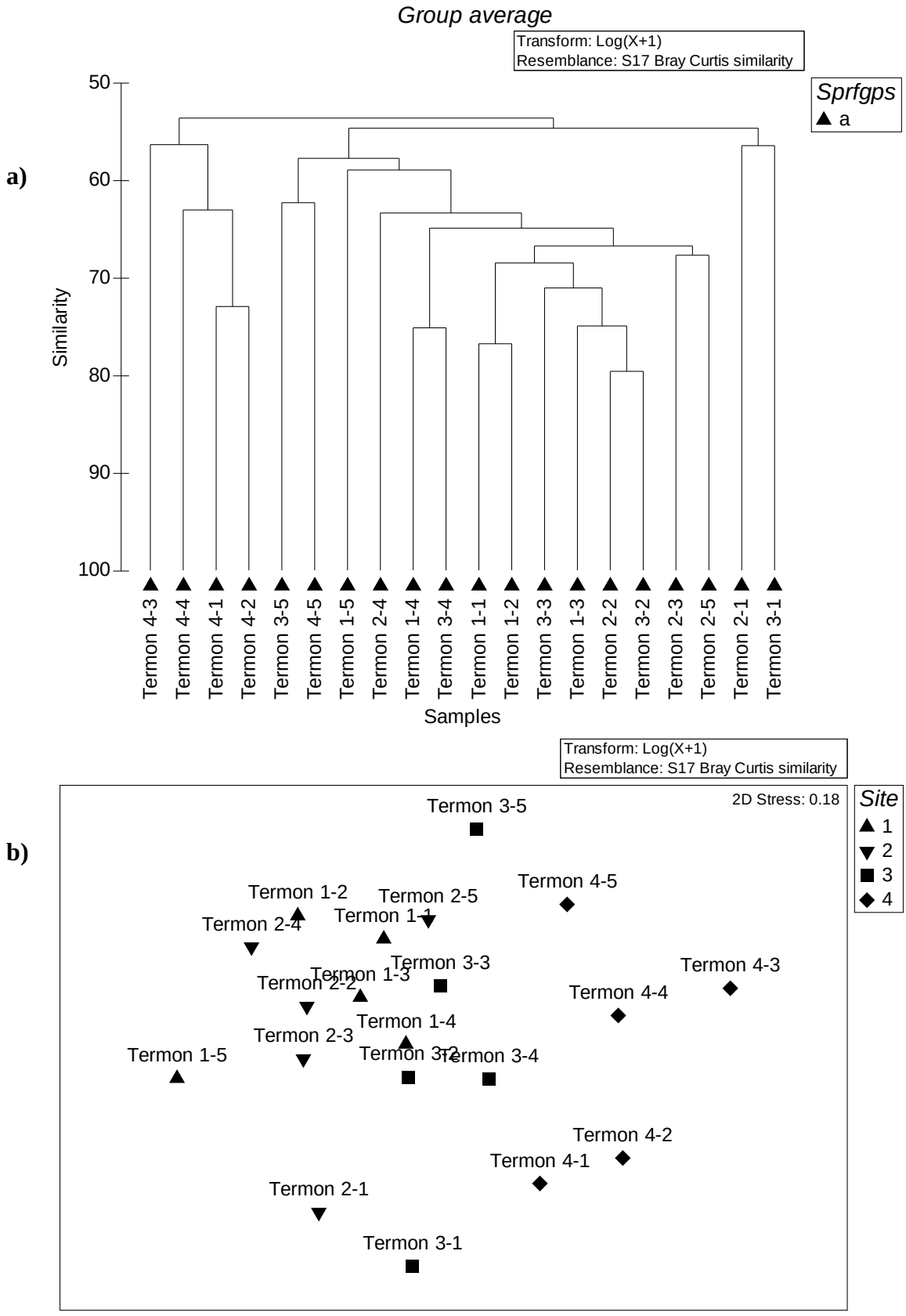


Figure 5.7: a) Hierarchical cluster analysis dendogram and **b)** MDS plot of macroinvertebrate species log(x+1) transformed total abundance data from Termon sampled in April 2008 (n=5 per site).

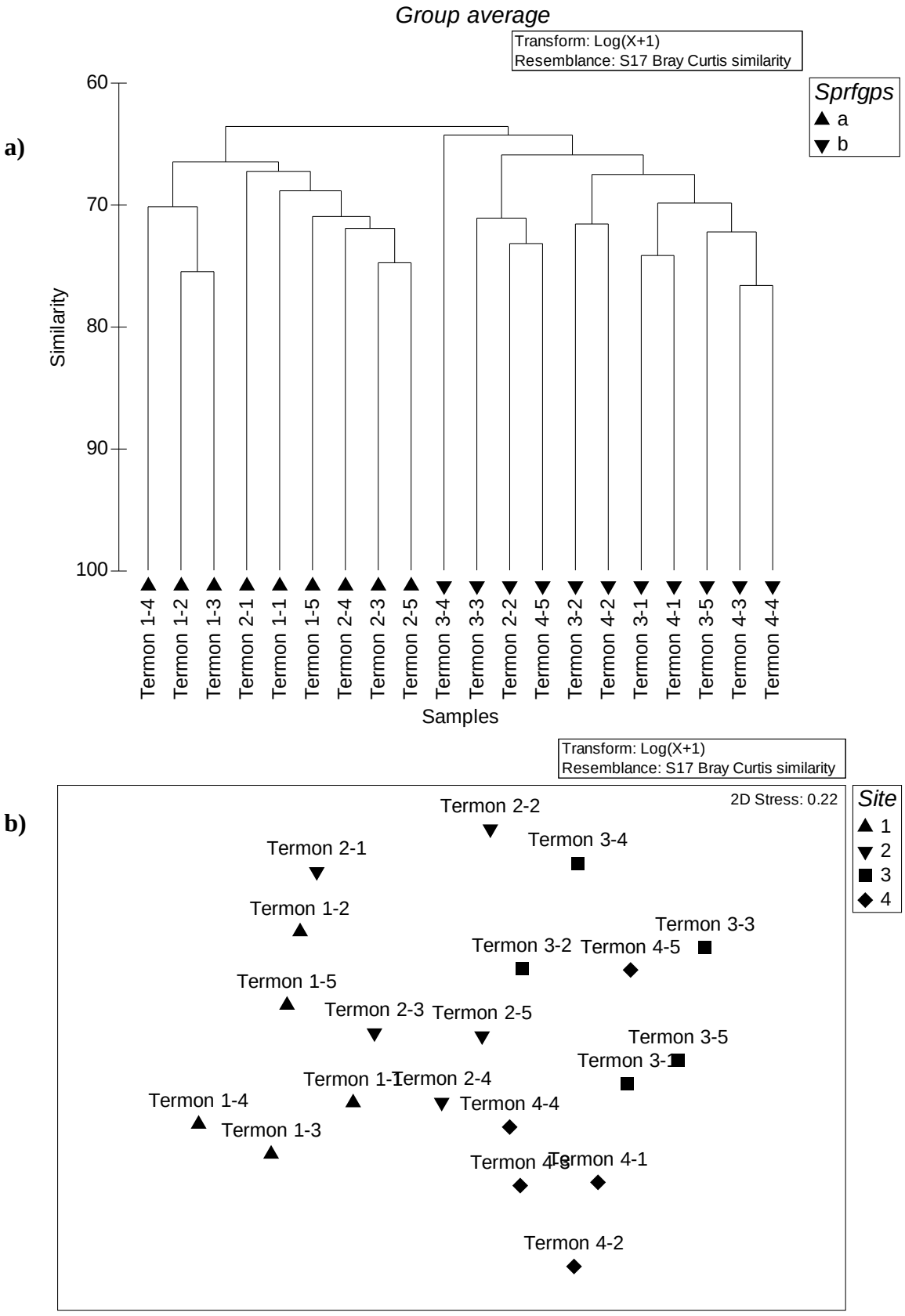


Figure 5.8: a) Hierarchical cluster analysis dendogram and **b)** MDS plot of macroinvertebrate species log(x+1) transformed total abundance data from Termon sampled in June 2008 (n=5 per site).

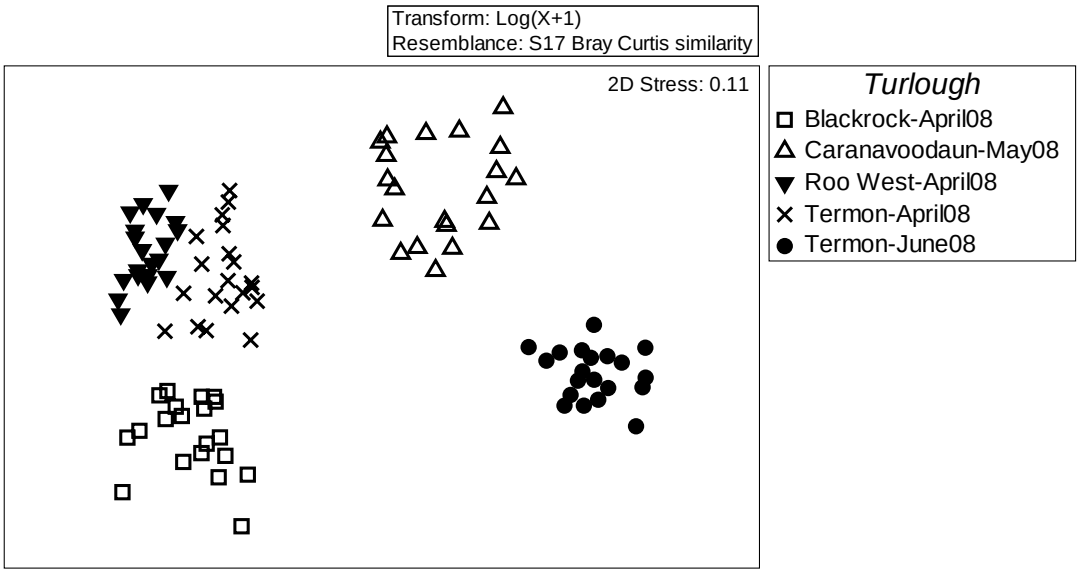


Figure 5.9: MDS plot of macroinvertebrate species log(x+1) transformed abundance data of 4 turloughs sampled in April 2008 till June 2008 (n=20 in each turlough).

5.4 Discussion

5.4.1 Between-Habitat Variability

Several authors have identified habitat structure as affecting invertebrate community organization and composition in lentic freshwater systems (Heino, 2000; Hinden *et al.*, 2005; Stoffels *et al.*, 2005; Tolonen *et al.*, 2001; White *et al.*, 2003). Habitat structure was found by Tolonen *et al*. (2001) to have a stronger effect on the distribution of macroinvertebrate communities than trophic status. However, White and Irvine (2003) found physical, chemical and other environmental variables to have a greater effect in structuring macroinvertebrate communities than habitat in lakes, with overall community variation greater among than within lakes. The results of this study are in agreement with the latter findings and indicate that, despite different habitats having an influence on invertebrate assemblages of turloughs, congruence of invertebrate assemblages is greater within than among turloughs. Significant differences between macroinvertebrate community structures of different habitats were only found in Brierfield. The stronger invertebrate variability between habitats in this turlough could be a result of the location of the different habitat sampling sites. In Brierfield the two sampling sites were situated further apart from each other compared with the situation in Lisduff. Taxon richness, however, did not

differ significantly between habitats and most prevalent invertebrate species were represented in both habitats, although differing in abundance.

Some taxa such as the nationally notable B species *Berosus signaticollis* and the UK RDB category one (vulnerable) species *Omphiscola glabra* did show preferences for the submerged grassland habitat in Lisduff and Brierfield, respectively. Thus, habitat heterogeneity within the littoral zone of turloughs is nevertheless important and should be considered for conservation assessment. Sampling of all available habitats in a turlough is likely to generate a more thorough evaluation of turlough biodiversity. Della Bella *et al.* (2005) also found habitat specific preferences of species of conservation concern in a study of temporary ponds in Italy and suggested sampling of all available mesohabitats for conservation purposes in temporary ponds.

5.4.2 Within-Habitat Variability

The results of this study indicate that grassland habitat samples collected in any location of a turlough can provide a reliable metric of the macroinvertebrate community of the turlough as a whole. This supports applicability of sampling a single location for monitoring where purpose is to provide an estimation of general status of a site. This was demonstrated by the clear separation of turlough replicate grassland samples collected in spring 2008 using MDS and the SIMPROF-test (incorporated in the cluster analysis). This is in agreement with results by Irvine *et al.* (2001a) who found differences among macroinvertebrate communities within lakes to be generally smaller than among lakes. Turloughs sampled in April 2008, furthermore, showed no significant differences among sampling sites, emphasizing the adequacy of single or pooled grassland habitat samples from any location in a turlough for the representation of the aquatic macroinvertebrate community of turloughs.

Turloughs are very dynamic and naturally variable systems and specific sets of microhabitats in the dominant submerged grassland habitat might, thus, prevail for a limited amount of time only. Exclusive specialization of turlough invertebrates in microhabitats would consequently pose a threat to the survival of specialists in a rapidly changing wetland environment (Batzer *et al.*, 2004). Turlough invertebrates

have to endure high habitat variability frequently and are therefore likely to adapt to this challenge by habitat generalization, enabling them to cope with changing habitat conditions. For habitat generalists, habitat size or location becomes less important, and environmental variability may, therefore, not be expected to negatively affect many invertebrate taxa of temporary wetlands (Williams, 1996).

The separation of macroinvertebrate communities into two significantly different groups using log(x+1) transformed total abundance data in turloughs sampled in May and June 2008 suggests a spatio-temporal interaction in turloughs. Results from the presence/absence data set highlight the importance of changes in macroinvertebrate abundance over time for the separation of communities. Spatial variation within submerged grassland habitat in turloughs increases over time possibly owing to seasonal changes in life cycle and abundance of invertebrates. The longer availability of a habitat offers the possibility of niche-building and continued colonisation, reflected in a change in invertebrate community structure (Dvořaki and Bestz, 1982; Jocqué *et al.*, 2007), even within one habitat type. Furthermore, as habitat duration increases so does local diversity and, thus, community structure (Holland and Jenkins, 1998). An increase in ephemeral species later in the season as reported by several authors (Boix *et al.*, 2004; Lahr *et al.*, 1999; Schneider, 1999), and in a separate study on temporal dynamics of macroinvertebrate communities in turloughs reported in Chapter 4, possibly also contributes to the observed spatio-temporal trend. Habitat selection of ephemeral residents may not be a random event and sites with low predator densities are preferably selected for oviposition by active dispersers with the help of chemical clues or other stimuli (Blaustein *et al.*, 2004; Resetarits, 2001) possibly leading to the observed increased patchiness of invertebrate species. The spatial differences in grassland habitat sites from late season samples do not, however, weaken turlough invertebrate community distinctiveness. The clear clustering of grassland replicate samples of individual turloughs in the MDS plot and results from the SIMPROF-test (incorporate in the cluster analysis) identified turloughs to hold discrete invertebrate communities despite their inherent natural spatial variation. The results furthermore highlight that differences in benthic communities among turloughs cannot be explained on the basis of habitat structures alone. As turloughs generally possess highly individual characters owing to differences in hydrological, nutrient, soil or geographical

regime, it is likely that such variation promotes the variable macroinvertebrate communities of turloughs.

Variability in community composition is a natural feature of the littoral zone (White *et al.*, 2003). Albeit that between-habitat variability was excluded by sampling one distinct habitat type (submerged grassland) in each turlough, within-habitat variability in invertebrate community structures of turloughs could still be detected. Taxon richness varied significantly among sampling sites in only two of the studied turloughs but considerable variability in taxon richness was also apparent among replicate samples from each sampling site and within each turlough. An increase in taxon richness over time was furthermore discovered in Termon, which is in agreement with studies on successional progress in invertebrate communities (Cayrou and Céréghino, 2005; Jocqué *et al.*, 2007) and results from Chapter 4. Variability in community structure was also evident from the results of the MDS and cluster analysis as replicate samples never showed exactly matching community structures, even when no significant differences among replicate samples within a turlough were detected.

5.5 Conclusions

The Water Framework Directive requires the assessment of water bodies on the basis of a wide suite of variables, including benthic invertebrates (EC, 2000). Their meaningful use as monitoring tools in turlough management programmes depends on the ability of assessment tools to discriminate natural spatial (and temporal) variation in invertebrate community structure from alterations caused by anthropogenic disturbance (Trigal *et al.*, 2007; White *et al.*, 2003). The results of this study suggest that despite inherent spatial heterogeneity of the littoral zone of turloughs, macroinvertebrate samples can be used as reliable indicators of change, even across a range of habitat structures. The dominant and easily identifiable turlough habitat submerged grassland seems, moreover, highly suitable for routine, standardised (among) turlough monitoring especially for the detection of pressure gradients. A standardised stratified sampling approach furthermore reduces natural "noise" in biotic monitoring and facilitates cost and time effective collection and processing of samples. A recommendation from this work would therefore be to apply a standardised sampling approach for routine turlough sampling with

macroinvertebrate samples collected from the easily identifiable submerged grassland habitat, rather then attempting to collect samples from an extensive range of habitats. This routine sampling would not be a comprehensive conservation assessment, however, but a pressure response method and, thus, fulfil the requirements of the WFD (EC, 2000). Yet, a sampling regime incorporating all available habitats in a turlough seems more appropriate for a full assessment of conservation value of turloughs as required under the EC Habitats Directive (EEC, 1992), providing a more comprehensive picture of turlough biodiversity and enhanced likelihood for detection of local and nationally rare taxa.

6 Macroinvertebrate and Cladoceran Zooplankton Communities of Turloughs and their Usefulness as Bioindicators

6.1 Introduction

Turloughs appear in a wide range of hydrological, geomorphological and trophic states throughout the West of Ireland. While the general pattern is to flood in autumn and empty in summer, hydroperiod can vary greatly among turloughs (Sheehy Skeffington *et al.*, 2006) depending on fluctuations in the local groundwater table (Reynolds, 1982; Reynolds *et al.*, 1998). Soil type, vegetation and nutrient status determine, further, each turlough's unique hydromorphological regime which, in turn, has a direct influence on the faunal and floral communities (Goodwillie and Reynolds, 2003; Regan, 2005; Sheehy Skeffington *et al.*, 2006).

Zooplankton represents an important part of lentic water food webs. They are the primary consumers of phytoplankton and are themselves an important food source for invertebrate and vertebrate predators (Irvine *et al.*, 2001a). Zooplankton communities have been reported as sensitive to various types of water quality changes including eutrophication (Brett, 1989; Moss *et al.*, 1991; Sládeček, 1983). The Chydoridae are a family of the Anomopoda which are primarily littoral dwellers. They have been described as potential tools to assess the status of ecological quality of freshwaters, including turloughs (de Eyto *et al.*, 2002; de Eyto *et al.*, 2003; Duigan and Kovach, 1991). Several authors (Ali *et al.*, 1987; Duigan, 1988; Grainger, 1966, 1976, 1979, 1989; Reynolds, 1985a) reported high entomostracan densities (mainly chydorids and copepods) in turloughs. Most entomostracans possess resting stages enabling them to live in temporary environments. However, single turlough sites are often dominated by one or two zooplankton species only (Duigan *et al.*, 1991; Reynolds and Marnell, 1999). The glacial relict species *Eurycercus glacialis* is largely restricted to temporary habitats characteristic of turloughs (Sheehy Skeffington *et al.*, 2006). It has been reported to occur with a mix of common forms such as *Daphnia pulex* and *Chydorus sphaericus* and species which are more restricted in their occurrence such as *Eurycercus lamellatus* (Reynolds, 1997, 2000).

Benthic invertebrates inhabit the bottom substrate of freshwater habitats for at least part of their life (Rosenberg and Resh, 1993b). Owing to their ubiquitous occurrence, long life cycles, sedentary nature, diversity, sensitivity to changes in their environment and their importance in freshwater food chains there is a long tradition in using benthic macroinvertebrates in the assessment of running waters (Hellawell, 1986; Rosenberg and Resh, 1993a). Assessment of standing waters has traditionally mainly relied on water chemistry measures and chlorophyll *a* and, to a lesser extent, invertebrates of the profundal (Brodersen and Lindegaard, 1999; Langdon *et al.*, 2006). This tradition is now challenged under the European Water Framework Directive (2000/60/EC) (WDF) (EC, 2005) as it specifically requires the inclusion of benthic invertebrates in the assessment of surface waters.

Hydroperiod, habitat complexity and nutrient status can contribute to differences in invertebrate community structures of temporary wetlands. Several studies showed that an increase in hydroperiod had a positive effect on the presence of invertebrate taxa in temporary wetlands (Collinson *et al.*, 1995; Della Bella *et al.*, 2005; Duigan, 1988; Schneider and Frost, 1996; Tavernini *et al.*, 2005) with long duration wetlands supporting colonizers lacking adaptations to drought (Schneider *et al.*, 1996). The influence of habitat structure on aquatic invertebrate communities has been documented by several authors (Heino, 2000; Tolonen *et al.*, 2001; White and Irvine, 2003) and habitat heterogeneity and diversity has been attributed to increasing invertebrate diversity and abundance (Brönmark, 1985; Tolonen *et al.*, 2003). Studies on invertebrate community responses to nutrient enrichment in lentic environments are quite recent and have so far focused mainly on lake invertebrate communities (Brauns *et al.*, 2007; Brodersen *et al.*, 1998; Brodersen *et al.*, 1999; Pinel-Alloul *et al.*, 1996; Tolonen *et al.*, 2001; White, 2000).

The objective of this study was to assess macroinvertebrate and cladoceran zooplankton community structures of a range of turloughs and to investigate the effect of differences in hydrological, morphological and trophic regimes on their invertebrate biodiversity, taxonomic and community structure.

6.2 Material and Methods

6.2.1 Study Sites

Twenty-two turloughs, located in counties Clare, Galway, Mayo and Roscommon, were selected for study as representative of the hydrological conditions and geographical range of turloughs in Ireland, based on existing hydrogeological (Drew, 1990; Southern Water Global, 1998; Tynan *et al.*, 2005) and hydromorphological data (Coxon, 1986) (for details on the selection process see Chapter 2.1; Table 6.1 & Figure 6.1).

Table 6.1: List of turloughs studied, their ID, TP concentrations per sampling month, number of habitats sampled in each sampling month and respective hydroperiods.

Turlough	***ID***	***TP (µg L^{-1})*** [1]		***Nr of habitats sampled***		***Hydroperiod (days)*** [2]
		Nov 06	***Apr 07***	***Nov 06***	***Apr 07***	
Ardkill	1	34	98	2	1	296
Ballindereen	2	7	5	3	2	239
Blackrock	3	56	--	1	--	196
Brierfield	4	14	15	1	2	331
Caherglassaun	5	46	38	1	1	365
Caranavoodaun	6	12	11	1	1	228
Carrowreagh	7	56	36	1	1	220
Coolcam	8	9	27	1	1	365
Croaghill	9	11	14	1	1	365
Garryland	10	21	12	1	1	221
Kilglassan	11	16	18	1	1	365
Knockaunroe	12	1	3	2	2	231
Lisduff	13	5	8	1	2	256
Lough Aleenaun	14	23	31	1	1	194
Lough Coy	15	62	25	1	1	365
Lough Gealain	16	5	2	2	2	230
Rathnalulleagh	17	62	43	1	2	214
Roo West	18	4	8	1	1	231
Skealoghan	19	14	20	1	1	252
Termon	20	4	11	2	1	365
Tullynafrankagh	21	16	18	4	2	365
Turloughmore	22	36	--	1	--	139

[1] Data provided by Helder Pereira
[2] Data provided by Owen Naughton

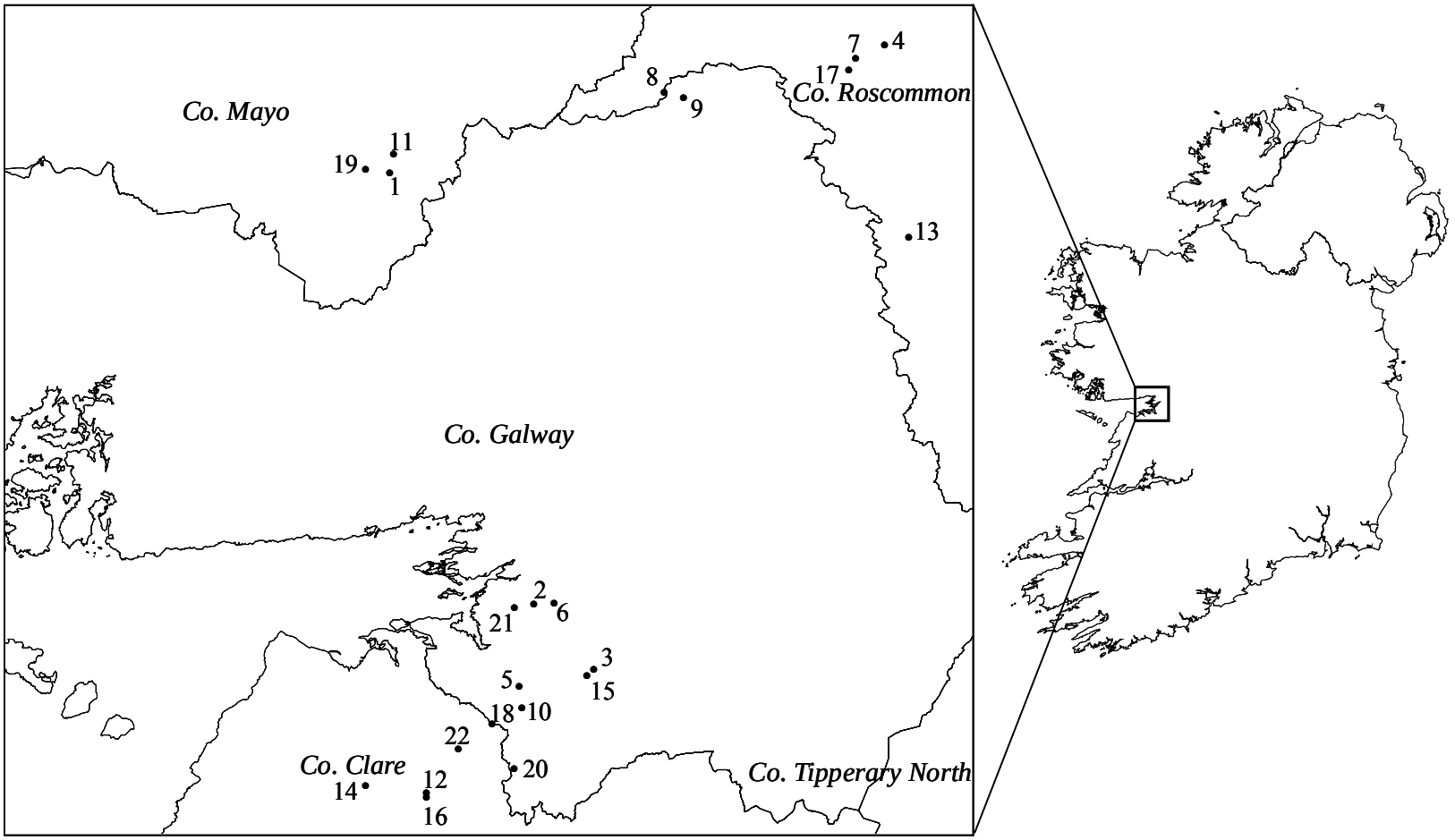


Figure 6.1: Map of Ireland showing the location of twenty-two turloughs studied (numbers refer to turlough IDs as indicated in Table 6.1).

6.2.2 Macroinvertebrate Sampling

At each turlough macroinvertebrate samples were collected using sweeps with a standard FBA pond net with 1 mm mesh size. Sampling within the accessible area of each turlough was carried out proportional to habitat availability, modified after Biggs *et al.* (1998). The sweep net samples comprised a 3 minute sampling time, which was subdivided proportionally to each habitat's availability. Samples were sieved using a 500 μm sieve on site and preserved in 90% industrial methylated spirits (IMS) for later sorting and identification in the laboratory. Number of habitats sampled and their proportions were recorded. Where samples had a very high abundance of macroinvertebrates they were split prior to sorting and taxonomic identification following methods by Donohue (2008). All individuals were identified to the lowest practicable level, typically species. Sampling was carried out in November 2006 (autumn sampling) about one month after flooding of turloughs had started and again before water receded in April 2007 (spring sampling). However, during spring only twenty turloughs were sampled, as Turloughmore and Blackrock had already dried out.

6.2.3 Zooplankton and Chydorid Sampling

In April 2007 open water cladoceran zooplankton as well as separate chydorid samples were collected from twenty turloughs. Open water cladoceran zooplankton samples were collected using a zooplankton net with 60 μm mesh size. At every turlough three cladoceran zooplankton samples were collected with horizontal hauls of the zooplankton net from the shore at three random locations. Samples were subsequently pooled, washed into collection bottles and preserved with 90% IMS for later identification in the laboratory.

At all twenty turloughs, separate sampling for chydorids was carried out with the use of a perspex tube (diameter 5.5 cm, volume 2276 cm^2) after Irvine *et al.* (1989). All available habitats in each turlough were sampled proportional to their abundance in accessible areas as described for the collection of macroinvertebrate sweep net samples in section 6.2.2. For every chydorid sample a total of 25 L was collected by rapidly lowering the perspex tube to the substratum, sealing the end with a rubber ball and collecting the content in a container. The sample was subsequently sieved

through a sieve of 60 μm mesh size, washed into collection bottles and preserved in situ in 90% IMS. Separate samples of cladoceran zooplankton and chydorids were identified and enumerated in the laboratory. Where subsampling of samples was necessary no less than 20% of each sample was analysed following methods by de Eyto *et al.* (2003).

6.2.4 Statistical Analysis

6.2.4.1 Relating Macroinvertebrate, Zooplankton and Chydorid Taxon Richness and Abundances to Environmental Variables

Relationships of macroinvertebrate taxon richness and log-transformed abundance to log-transformed TP concentrations and number of habitats sampled were assessed using Pearson product-moment correlations. Spearman rank-order correlation investigated the influence of hydroperiod on macroinvertebrate taxon richness and abundances, respectively. Average values for samples from 22 turloughs (22 sampled in November 2006 and 20 sampled in April 2007) were included in the analysis. Total abundance recorded in Turloughmore was excluded from the analysis owing to its extreme outlier character.

Relationships of cladoceran zooplankton and log-transformed chydorid taxon richness and respective log-transformed abundances, to macroinvertebrate taxon richness and log-transformed TP were investigated using Pearson product-moment correlations. Correlation of cladoceran zooplankton and chydorid taxon richness and abundances with hydroperiod of turloughs was, furthermore, investigated using Spearman rank-order correlation. TP concentrations recovered from Ardkill were excluded from the analysis owing to a strong outlier character.

Data normality was verified using the Shapiro Wilk test and homogeneity of variance checked with the Leven's test before choosing parametric or nonparametric statistical analysis.

6.2.4.2 Relating Macroinvertebrate Taxonomic Structure to Environmental Variables

Spearman rank-order correlation tested the relationships between environmental variables (TP, hydroperiod and number of habitats sampled) and the respective abundances of Amphipoda, Aranea, Bivalvia, Coleoptera, Diptera, Ephemeroptera, Gastropoda, Heteroptera, Hirudinea, Hydrachnidia, Isopoda, Lepidoptera, Odonata, Oligochaeta, Ostracoda, Plecoptera, Trichoptera and Turbellaria in the two different seasons.

To identify the similarities of communities in each sampling season the similarity percentage routine SIMPER (PRIMER® 6) was carried out. This method decomposes Bray-Curtis similarities among all pairs of samples, within *a priori* defined groups (in this case individual turloughs), into percentage contributions from each species to the respective similarities (Clarke and Warwick, 2001). Dissimilarities of seasonal turlough samples of each individual turlough were computed using the same method, in order to investigate changes in the macroinvertebrate community of each turlough with sampling season.

Cluster Analysis and Multi-Dimensional Scaling (MDS) ordination on log(x+1) transformed total abundance macroinvertebrate data assessed similarity of samples. Cluster Analysis and MDS were based on a Bray-Curtis similarity matrix, with clusters formed using the average group linkage method. The similarity profile (SIMPROF) permutation test, which tests for statistically robust clusters of *a priori* undefined groups (Clarke and Gorley, 2006) was incorporated into the Cluster Analysis.

Canonical Correspondence Analysis (CCA) was performed to examine the ability of the environmental variables TP, season, number of habitats sampled and hydroperiod to explain the variability present in the macroinvertebrate community (CANOCO Version 4.5). CCA is a non-linear eigenvector ordination technique in which the axes are constrained to be linear combinations of the measured environmental variables. The ordination was performed on log(x+1) transformed macroinvertebrate abundance data using automatic forward selection of the environmental variables to obtain the conditional effects for each variable and down-weighting of rare species. When selecting the down-weighting option in

CANOCO version 4.5, species with a total frequency less than 20% of the maximum recorded total frequency are weighted in proportion to their frequency, divided by 20% of the maximum recorded total frequency (ter Braak and Šmilauer, 2002). Treating each variable as the sole predictor variable in a first step, all environmental variables were ranked on the basis of the variance they explained separately, thus representing marginal effects. The explanatory effect of each variable was evaluated for its significance using Monte Carlo permutation tests with 999 permutations.

To asses the similarity of macroinvertebrate sample ordinations of different seasons, turlough samples were ranked according to their arrangement in the 2D CCA ordination created using the log(x+1) transformed abundance macroinvertebrate data. Turlough ranks of each season were correlated using Spearman rank-order correlation.

6.3 Results

6.3.1 Relating Macroinvertebrate, Zooplankton and Chydorid Taxon Richness and Abundances to Environmental Variables

Pearson product-moment correlation detected a positive correlation of macroinvertebrate taxon richness with number of habitats sampled ($R=0.435$; $P<0.05$; $n=22$). A positive correlation was also found for macroinvertebrate taxon richness with hydroperiod of turloughs (Spearman rank-order correlation; $R=0.666$; $P<0.001$; $n=22$).

A significant positive correlation was found between log-transformed TP and both log-transformed cladoceran zooplankton and chydorid abundance, respectively ($R=0.529$; $P<0.05$; and $R=0.498$; $P<0.05$, respectively; $n=19$ in both cases), using Pearson product-moment correlation. A negative correlation was found between cladoceran zooplankton taxon richness and log-transformed TP (Pearson product-moment correlation; $R=-0.506$; $P<0.05$). Spearman rank-order correlation indicated a positive relationship of both cladoceran zooplankton and chydorid abundance with turlough hydroperiod ($R=0.556$; $P<0.05$ and $R=0.489$; $P<0.05$, respectively; $n=20$ in both cases).

6.3.2 Relating Macroinvertebrate Taxonomic Structure to Environmental Variables

Spearman rank correlations of macroinvertebrate orders with environmental variables TP, hydroperiod and number of habitats sampled showed increases, of Ostracoda and Diptera and decreases of Aranea, Odonata and Trichoptera with nutrient enrichment. Significant positive correlations were found between hydroperiod and Gastropoda, Heteroptera and Trichoptera, respectively, while abundances of Ostracoda were negatively correlated with increasing hydroperiod of turloughs. The increase of the number of habitats sampled was correlated positively with Aranea, Odonata, Trichoptera and Plecoptera abundances, but negatively with Ostracoda abundances. Significant relationships are summarized in Table 6.2 a) and b).

Table 6.2: Spearman rank-order correlations of macroinvertebrate orders significantly correlated with environmental variables TP, hydroperiod and number of habitats sampled in **a)** November 2006 and **b)** April 2007. Significant relationships between variables are highlighted (significance level indicated as *=P<0.05 and **=P<0.01; n=42 in all cases).

a)

	TP	***Hydroperiod***	***Nr. of habitats sampled***
Aranea	-0.258	0.304	0.632**
Gastropoda	-0.366	0.470*	0.286
Heteroptera	0.243	0.529*	-0.118
Odonata	-0.322	0.087	0.534*
Ostracoda	0.496*	-0.484*	-0.408
Trichoptera	-0.684**	0.457*	0.428*

b)

	TP	***Nr. of habitats sampled***
Aranea	-0.457*	0.575**
Diptera	0.463*	-0.246
Odonata	-0.444*	0.046
Ostracoda	0.511*	-0.524*
Plecoptera	0.244	0.454*

The similarity percentage routine SIMPER identified overall similarity of turloughs sampled in November 2006 to be 27.6% and in April 2007 32.3%. Turlough macroinvertebrate communities differed between sampling months by 76.4%, suggesting a strong seasonal influence on macroinvertebrate community structure. Macroinvertebrate species composition and contributions to overall turlough similarities in each sampling month differed among sampling seasons. While macroinvertebrates identified to contribute strongly to overall turlough similarity in November 2006 were *Ostracoda* sp.*, Galba truncatula* and *Agabus* sp. *larvae* (17.6%, 12.4% and 12.1% contribution to overall similarity of samples, respectively), macroinvertebrates playing a major part in overall similarity among turloughs in April 2007 were *Chironomidae* sp., *Agabus* sp. *larvae*, *Diptera pupae* and *Oligochaeta* sp. (17.7%, 14.9%, 8.6% and 8.5% contribution to overall similarity of samples, respectively) (Table 6.3). Taxa contributing to overall turlough similarities occurring in both months were generally those classified as permanent residents, or early larval stages of macroinvertebrates classified as ephemeral resident of temporary waters after Williams (1987) and Lahr (1997). Differences in contributing taxa among sampling months were largely owing to ephemeral taxa, thus, indicating a seasonal effect on turlough macroinvertebrate community structure.

Table 6.3: Summary results from SIMPER analysis cumulative contribution (Cum%) of macroinvertebrate taxa to sample similarities (in %) (cut-off level 90% similarity).

November 2006: Average similarity: 27.64%		*April 2007: Average similarity: 32.31%*	
Species	Cum.%	Species	Cum.%
Ostracoda sp.	17.55	*Chironomidae* sp.	17.72
Galba truncatula	29.96	*Agabus* sp. *(larvae)*	32.61
Agabus sp. *(larvae)*	42.04	*Diptera* sp. *Pupae*	41.19
Oligochaeta sp.	49.36	*Oligochaeta* sp.	49.73
Radix balthica	53.68	*Ostracoda* sp.	56.55
Hydrachnidia sp.	57.49	*Cloeon dipterum*	60.56
Phacopteryx brevipennis	60.74	*Rhantus* sp. *(larvae)*	63.68
Limnephilus lunatus	63.8	*Sympetrum sanguineum*	66.74
Limnephilidae sp. *Instar III*	66.81	*Hydrachnidia* sp.	69.67
Rhantus sp. *(larvae)*	69.62	*Cloeon simile*	72.27
Chironomidae sp.	72.28	*Radix balthica*	74.76
Ilybius sp. *(larvae)*	74.86	*Hydroporus palustris*	76.9
Succinea sp.	77.41	*Porhydrus lineatus*	78.98
Limnephilidae sp. *Instar II*	79.69	*Asellus aquaticus*	81.03
Limnephilus auricula	81.44	*Hygrotus inaequalis*	82.72
Pisidium/Sphaerium sp.	82.95	*Ilybius* sp. *(larvae)*	84.37
Agyroneta aquatica	84.3	*Galba truncatula*	85.77
Limnephilus marmoratus	85.49	*Dryops* sp. *(larvae)*	87.04
Hydaticus sp. *(larvae)*	86.62	*Corixinae Instar I & II*	88.27
Asellus aquaticus	87.7	*Succinea* sp.	89.27
Tipulidae sp.	88.72	*Lestes* sp.	90.16
Dryops sp. *(larvae)*	89.69		
Culicidae sp.	90.64		

Comparisons of individual turlough macroinvertebrate communities collected in November 2006 and April 2007 using SIMPER supported importance of seasonality of macroinvertebrates in turloughs. Generally, higher abundances of permanent taxa were detected in November 2006, while ephemeral macroinvertebrate taxa were more abundant or restricted to spring samples (Table 6.4).

Table 6.4: Summary results from SIMPER analysis at individual turlough level showing cumulative contribution (Cum%) of macroinvertebrate taxa to sample dissimilarities (in %)(first ten contributing taxa).

Ardkill			***Knockaunroe***		
Average dissimilarity: 69.04%			Average dissimilarity: 80.51%		
Species	Cum.%	(higher) presence	Species	Cum.%	(higher) presence
Chironomidae sp.	8.31	only Apr 07	*Oligochaeta* sp.	8.99	only Nov 06
Agabus sp. *(larvae)*	16.19	only Apr 07	*Cloeon simile*	17.58	only Apr 07
Radix balthica	21.42	Nov 06	*Chironomidae* sp.	24.18	only Apr 07
Hydroporus palustris	26.27	Apr 07	*Limnephilus lunatus*	30.61	only Nov 06
Oligochaeta sp.	30.74	Apr 07	*Limnephilidae* sp. *Instar III*	37.03	only Nov 06
Haliplus fulvus	35.01	only Nov 06	*Limnephilidae* sp. *Instar II*	43.46	only Nov 06
Haliplus sp. *ruficollis group (females)*	39.03	only Nov 06	*Diptera* sp. *Pupae*	49.31	only Apr 07
Planorbis crista	42.39	only Nov 06	*Anisoptera* sp. *(larvae)*	54.05	Apr 07
Ostracoda sp.	45.01	Apr 07	*Hydroporus palustris*	58.41	only Apr 07
Hygrotus sp. *(larvae)*	47.61	only Apr 07	*Hygrotus inaequalis*	62.33	only Apr 07
Ballindereen			***Lisduff***		
Average dissimilarity: 72.26%			Average dissimilarity: 56.04%		
Species	Cum.%	(higher) presence	Species	Cum.%	(higher) presence
Ostracoda sp.	8.81	Nov 06	*Limnephilus auricula*	6.6	only Nov 06
Vallonia pulchella	16.54	Nov 06	*Pisidium/Sphaerium* sp.	13.16	only Nov 06
Limnephilus lunatus	22.18	Nov 06	*Valvata cristata*	18.81	only Nov 06
Phacopteryx brevipennis	27.11	Nov 06	*Limnephilus centralis*	24.3	only Apr 07
Lymnaea fusca	31.91	Nov 06	*Limnephilus lunatus*	29.39	Nov 06
Limnephilus auricula	36.35	Nov 06	*Agabus* sp. *(larvae)*	34.39	Apr 07
Limnephilus decipiens	40.55	Nov 06	*Sympetrum sanguineum*	38.95	only Apr 07
Asellus aquaticus	44.72	Apr 07	*Limnephilus marmoratus*	43.37	Nov 06
Diptera sp. *Pupae*	48.32	Apr 07	*Galba truncatula*	46.99	Nov 06
Cloeon dipterum	51.92	Apr 07	*Lestes* sp.	50.45	only Apr 07
Brierfield			***Lough Aleenaun***		
Average dissimilarity: 57.24%			Average dissimilarity: 57.57%		
Species	Cum.%	(higher) presence	Species	Cum.%	(higher) presence
Phacopteryx brevipennis	9.51	only Nov 06	*Oligochaeta* sp.	8.88	Apr 07
Succinea sp.	17.87	only Nov 06	*Radix balthica*	15.87	Apr 07
Omphiscola glabra	24.53	only Apr 07	*Chironomidae* sp.	22.66	Nov 06
Galba truncatula	30.53	Nov 06	*Pisidium/Sphaerium* sp.	28.65	only Nov 06
Limnephilus auricula	35.64	only Nov 06	*Helophorus brevipalpis*	34.23	only Apr 07
Culicidae sp.	40.04	only Apr 07	*Ceratopogonidae* sp.	39.81	only Apr 07
Rhantus sp. *(larvae)*	44	only Nov 06	*Haliplus* sp. *(larvae)*	44.66	only Nov 06
Euconulus alderi	47.69	Nov 06	*Cloeon dipterum*	49.43	only Apr 07
Ostracoda sp.	51.32	Nov 06	*Coroxinae Instar I & II*	54.2	only Apr 07
Pisidium/Sphaerium sp.	54.72	only Nov 06	*Planorbis leucostoma*	58.42	only Apr 07

Table 6.4 (Contd.): Summary results from SIMPER analysis at individual turlough level showing cumulative contribution (Cum%) of macroinvertebrate taxa to sample dissimilarities (in %)(first ten contributing taxa).

Caherglassaun			***Lough Coy***		
Average dissimilarity: 78.45%			Average dissimilarity: 81.75%		
Species	Cum.%	(higher) presence	Species	Cum.%	(higher) presence
Planorbis contortus	8.73	only Apr 07	*Ostracoda* sp.	9.05	Apr 07
Agabus sp. *(larvae)*	16.82	Apr 07	*Cloeon dipterum*	17.8	only Apr 07
Chironomidae sp.	24.72	only Apr 07	*Hydroporus palustris*	24.33	only Apr 07
Asellus aquaticus	31	only Apr 07	*Galba truncatula*	30.19	only Nov 06
Ostracoda sp.	36.98	Nov 06	*Chironomidae* sp.	34.76	only Apr 07
Diptera sp. *Pupae*	42.91	only Apr 07	*Valvata macrostoma*	39.32	only Apr 07
Hydaticus sp. *(larvae)*	48.29	only Nov 06	*Gammarus lacustris*	43.42	Apr 07
Haliplus sp. *ruficollis group (females)*	53.04	only Nov 06	*Oligochaeta* sp.	47.52	only Apr 07
Ilybius sp. *(larvae)*	57.5	only Nov 06	*Sigara dorsalis*	51.35	Apr 07
Rhantus sp. *(larvae)*	61.64	only Nov 06	*Sigara concinna*	55	Apr 07
Caranavoodaun			***Lough Gealain***		
Average dissimilarity: 56.91%			Average dissimilarity: 79.42%		
Species	Cum.%	(higher) presence	Species	Cum.%	(higher) presence
Limnephilidae sp. *Instar II*	7.11	only Nov 06	*Cloeon simile*	11.7	only Apr 07
Sympetrum sanguineum	13.79	only Apr 07	*Porhydrus lineatus*	20.02	only Apr 07
Limnephilidae sp. *Instar III*	19.77	only Nov 06	*Chironomidae* sp.	25.41	only Apr 07
Limnephilus lunatus	25.52	only Nov 06	*Limnephilidae* sp. *Instar III*	30.79	only Nov 06
Ostracoda sp.	31.04	only Nov 06	*Phacopteryx brevipennis*	36.18	only Nov 06
Leste dryas	36.31	only Apr 07	*Graptodytes bilineatus*	40.82	only Nov 06
Radix balthica	41.47	Nov 06	*Diptera* sp. *Pupae*	45.46	only Apr 07
Hydaticus sp. *(larva)*	46.07	only Nov 06	*Omphiscola glabra*	50.1	only Nov 06
Anisoptera sp. *larvae*	50.29	Apr 07	*Limnephilidae* sp. *Instar II*	54.74	only Nov 06
Berosus signaticollis	54.06	Apr 07	*Agyroneta aquatica*	58.42	only Apr 07
Carrowreagh			***Rathnalulleagh***		
Average dissimilarity: 66.42%			Average dissimilarity: 60.29%		
Species	Cum.%	(higher) presence		Cum.%	(higher) presence
Chironomidae sp.	9.25	Apr 07	*Ostracoda* sp.	13.9	only Nov 06
Phacopteryx brevipennis	17.41	only Nov 06	*Diptera* sp. *Pupae*	21.33	only Apr 07
Hydaticus sp. *(larvae)*	25.46	only Nov 06	*Planorbis planorbis*	28.77	only Apr 07
Galba truncatula	33.17	only Nov 06	*Tipulidae* sp.	35.61	only Apr 07
Rhantus sp. *(larvae)*	40.63	only Nov 06	*Nemoura cinerea*	42.46	only Apr 07
Ilybius sp. *(larvae)*	47.49	only Nov 06	*Corixa iberica*	47.75	only Apr 07
Succinea sp.	54.17	only Nov 06	*Galba truncatula*	52.62	Nov 06
Oligochaeta sp.	60.32	Apr 07	*Rhantus* sp. *(larvae)*	56.81	only Apr 07
Ostracoda sp.	65.71	Nov 06	*Cloeon dipterum*	61.01	only Apr 07
Limnephilus decipiens	70.64	only Nov 06	*Succinea* sp.	65.21	only Apr 07

Table 6.4 (Contd.): Summary results from SIMPER analysis at individual turlough level showing cumulative contribution (Cum%) of macroinvertebrate taxa to sample dissimilarities (in %)(first ten contributing taxa).

Coolcam			***Roo West***		
Average dissimilarity: 71.27%			Average dissimilarity: 56.33%		
Species	Cum.%	(higher) presence	Species	Cum.%	(higher) presence
Limnephilus lunatus	7.5	only Nov 06	*Ostracoda* sp.	10.82	only Nov 06
Limnephilidae sp. *Instar II*	13.6	only Nov 06	*Sympetrum sanguineum*	20.34	only Apr 07
Limnephilidae sp. *Instar III*	19.26	only Nov 06	*Cloeon dipterum*	28.03	only Apr 07
Cloeon simile	24.76	only Apr 07	*Planorbis planorbis*	35.71	only Apr 07
Limnephilus marmoratus	30.26	only Nov 06	*Diptera* sp. *Pupae*	42.3	only Apr 07
Gammarus sp. *juveniles*	34.86	only Apr 07	*Lymnaea fusca*	48.88	only Nov 06
Lymnaea fusca	39.02	only Nov 06	*Galba truncatula*	53.7	only Nov 06
Porhydrus lineatus	42.94	only Apr 07	*Chironomidae* sp.	57.41	Nov 06
Limnephilus auricula	46.76	only Nov 06	*Agabus* sp. *(larvae)*	60.83	Nov 06
Agabus sp. *(larvae)*	50.53	Apr 07	*Cloeon simile*	64.12	only Apr 07
Croaghill			***Skealoghan***		
Average dissimilarity: 67.07%			Average dissimilarity: 69.09%		
Species	Cum.%	(higher) presence	Species	Cum.%	(higher) presence
Agabus sp. *(larvae)*	10.52	only Apr 07	*Sympetrum sanguineum*	4.31	only Apr 07
Lestes sp.	17.89	only Apr 07	*Lymnaea fusca*	8.59	only Apr 07
Planorbis crista	24.75	only Nov 06	*Notonectidae* sp. *(larvae)*	12.37	only Apr 07
Valvata cristata	30.77	only Nov 06	*Triaenodes bicolor*	15.96	only Apr 07
Lestes dryas	36.57	only Apr 07	*Limnephilidae* sp. *Instar II*	19.53	only Nov 06
Galba truncatula	42.15	only Nov 06	*Corixinae Instar I & II*	22.95	only Apr 07
Limnephilidae sp. *Instar II*	47.72	only Nov 06	*Helophorus brevipalpis*	26.3	only Apr 07
Phacopteryx brevipennis	53.3	Nov 06	*Asellus aquaticus*	29.58	only Apr 07
Limnephilidae sp. *Instar III*	58.33	only Nov 06	*Oligochaeta* sp.	32.83	only Nov 06
Chironomidae sp.	63.04	only Apr 07	*Cloeon dipterum*	35.73	Apr 07
Garryland			***Termon***		
Average dissimilarity: 49.16%			Average dissimilarity: 87.77%		
Species	Cum.%	(higher) presence	Species	Cum.%	(higher) presence
Chironomidae sp.	8.79	only Apr 07	*Limnephilidae* sp. *Instar II*	5.37	only Nov 06
Planorbis planorbis	16.63	only Apr 07	*Bithynia tentaculata*	9.94	only Nov 06
Asellus meridianus	23.87	Apr 07	*Limnephilus lunatus*	14.47	only Nov 06
Hydrachnidia sp.	30.13	only Apr 07	*Pisidium/Sphaerium* sp.	18.98	only Nov 06
Hygrotus quinquelineatus	36.1	Apr 07	*Chironomidae* Sp.	23.42	April 07
Hygrobia hermanni	41.95	only Apr 07	*Bithynia leachi*	27.69	only Nov 06
Oligochaeta sp.	47.39	Nov 06	*Ostracoda* sp.	31.7	only Apr 07
Diptera sp. *Pupae*	52.03	Apr 07	*Galba truncatula*	35.66	only Nov 06
Zygoptera sp. *(larvae)*	55.96	only Apr 07	*Anisoptera* sp. *(larvae)*	39.63	only Nov 06
Helobdella stagnalis	59.71	only Nov 06	*Limnephilidae* sp. *Instar III*	43.32	only Nov 06

Table 6.4 (Contd.): Summary results from SIMPER analysis at individual turlough level showing cumulative contribution (Cum%) of macroinvertebrate taxa to sample dissimilarities (in %)(first ten contributing taxa).

Kilglassan			***Tullynafrankagh***		
Average dissimilarity: 81.44%			Average dissimilarity: 69.46%		
Species	Cum.%	(higher) presence	Species	Cum.%	(higher) presence
Agabus sp. *(larvae)*	7.21	only Apr 07	*Culicidae* sp.	4.81	only Nov 06
Cloeon dipterum	12.31	only Apr 07	*Limnephilidae* sp. *Instar II*	9.19	only Nov 06
Sympetrum sanguineum	16.37	only Apr 07	*Chironomidae* sp.	13.55	only Apr 07
Oligochaeta sp.	20.24	Apr 07	*Limnephilus lunatus*	17.78	only Nov 06
Corixinae Instar I & II	23.98	only Apr 07	*Bithynia leachi*	21.75	only Nov 06
Chironomidae sp.	27.62	only Apr 07	*Laccobius biguttatus*	25.25	only Nov 06
Radix balthica	30.98	Nov 06	*Polycelis nigra/tenuis*	28.41	Nov 06
Zygoptera sp. *(larvae)*	34.29	only Apr 07	*Agyroneta aquatica*	31.55	Nov 06
Cloeon simile	37.47	only Apr 07	*Limnephilus marmoratus*	34.65	Nov 06
Asellus aquaticus	40.5	only Apr 07	*Sympetrum sanguineum*	37.61	only Apr 07

Hierarchical cluster analysis revealed a tendency of similar groupings of turloughs, clustering the majority of turloughs in similar significant groups identified with the similarity profile test (SIMPROF) in both sampling months. SIMPROF identified eight and five significantly different groups of turloughs in November 2006 and April 2007, respectively. Cluster Analysis identified turloughs sampled in April 2007 to be overall more similar to each other compared with November 2006 samples (last cluster at 23.8% similarity and 18.4%, respectively) corresponding with results from the SIMPER analysis (Figure 6.2 a) & b)). Non-metric multidimensional scaling results revealed a strong influence of season on macroinvertebrate structure, concurring with findings of the SIMPER and cluster analysis (Figure 6.3).

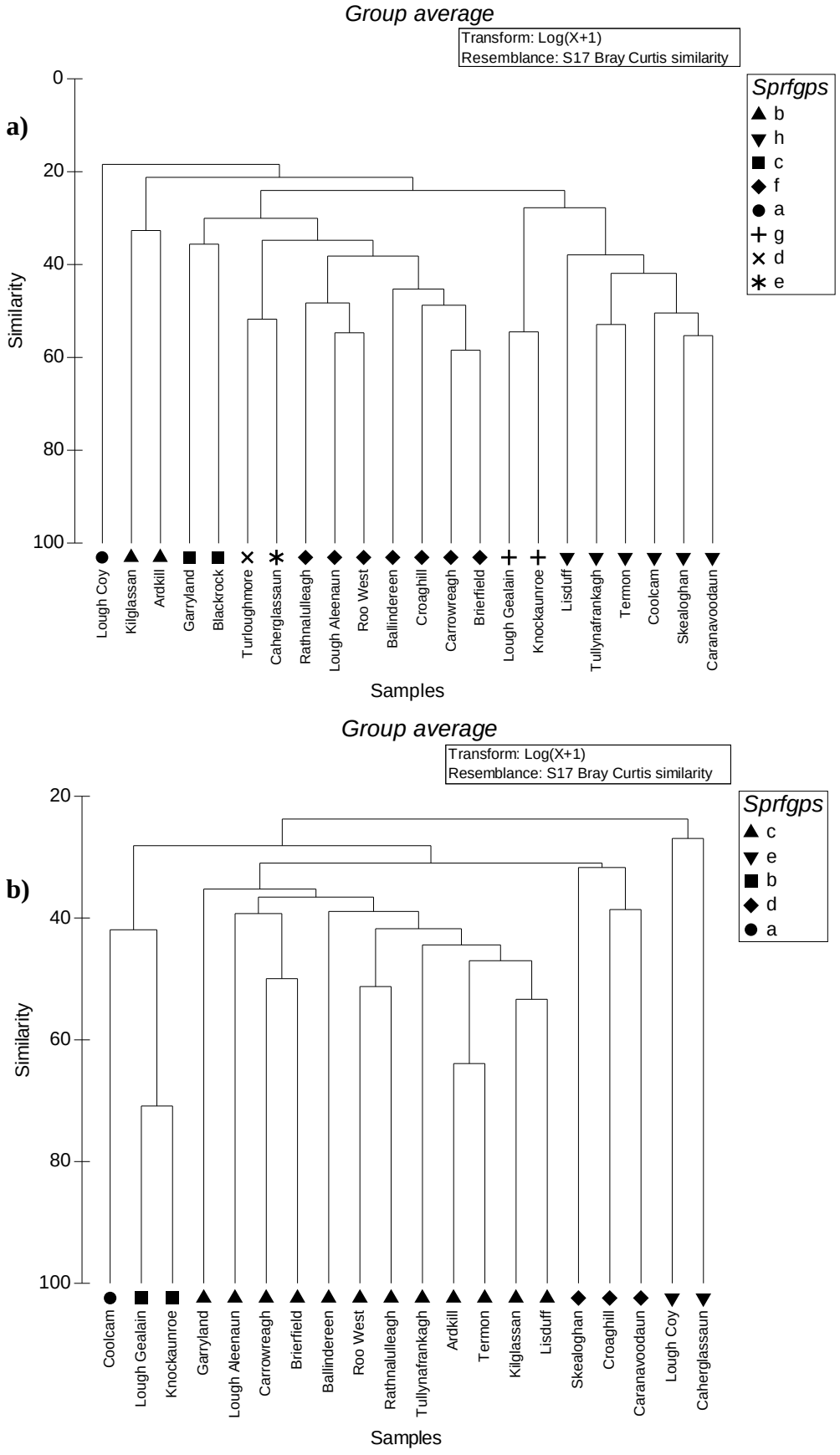


Figure 6.2: a) Hierarchical cluster analysis dendogram of macroinvertebrate species log(x+1) transformed total abundance data of 22 turloughs sampled in November 2006 and **b)** 20 turloughs sampled in April 2007.

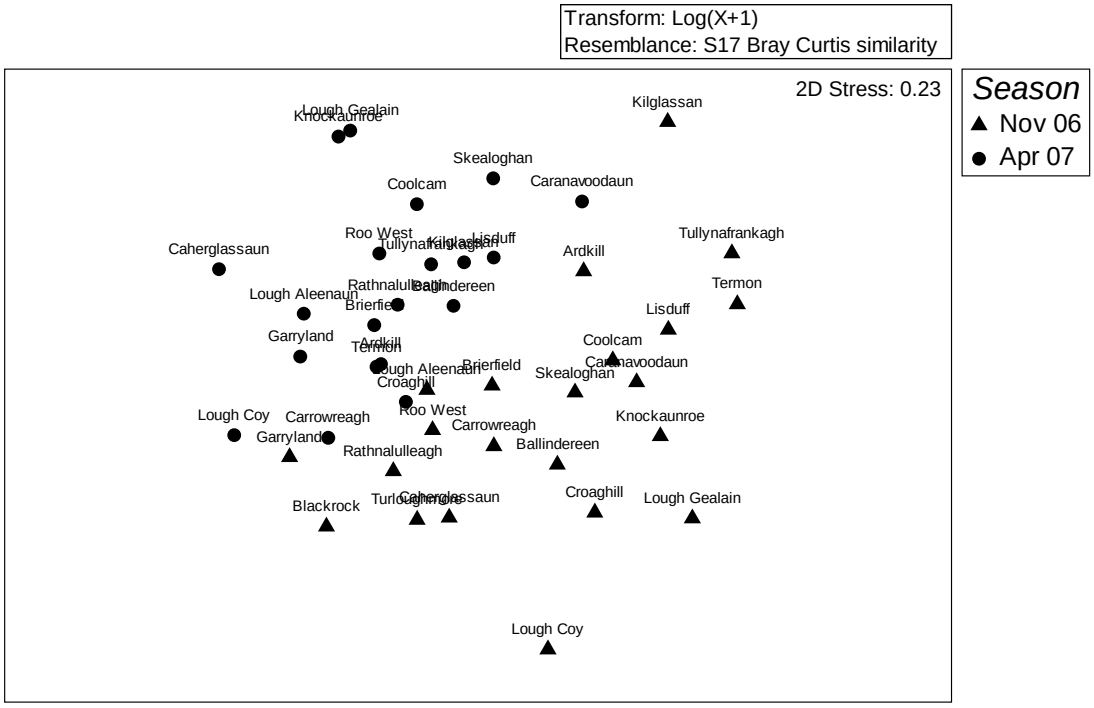


Figure 6.3: MDS plot of macroinvertebrate species log(x+1) transformed total abundance data collected in November 2006 (n=22) and April 2007 (n=20).

The four environmental variables could explain 60% of the total variability (inertia) in the macroinvertebrate community matrix, with axes 1 and 2 of the ordination explaining 72% of the variance present in the biological data using canonical correspondence analysis (CCA) (Table 6.5). Monte Carlo permutation tests indicated that the environmental variables season, number of habitats sampled and TP were significant in explaining some of the variation in the macroinvertebrate log(x+1) abundance data (all $P<0.01$), whereas hydroperiod did not improve significantly the explanation of the variability in the biological data set ($P=0.126$; $F=1.22$). The length and direction of the arrows in the 2D CCA ordination indicate the gradients and the relative importance of the environmental variables in explaining the variation in the biological community (Figure 6.4).

Table 6.5: Summary statistics of CCA ordination on macroinvertebrate log(x+1) abundances data, using automatic forward selection of four environmental variables (n=42).

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.275	0.156	0.104	0.068	
Species-environment correlations	0.908	0.872	0.865	0.826	
Cumulative percentage variance					
of species data	8.4	13.1	16.3	18.4	
of species-environment relation	45.7	71.5	88.7	100	
Total inertia					0.603

The results of the automatic forward selection of the four environmental variables are summarized in Table 6.6. The marginal effects (the percentage variance explained by each environmental variable when used as sole predictor) indicated that season explained the most variation in the biological data set. The conditional effects show the environmental variables in order of their inclusion in the model, together with the additional variance each variable explains at the time it was included (Lambda-A), its significance (P-value) and its test statistic (F-value).

Table 6.6: Summary of automatic forward selection in CCA ordination using log(x+1) transformed macroinvertebrate abundance data and four environmental variables (n=42).

Marginal Effects		Conditional Effects			
Variable	Lambda1	Variable	Lambda A	P	F
Season	0.26	Season	0.26	0.001	3.38
Nr habitats	0.15	Nr habitats	0.13	0.006	1.88
TP	0.15	TP	0.12	0.004	1.65
Hydroperiod	0.10	Hydroperiod	0.09	0.126	1.22

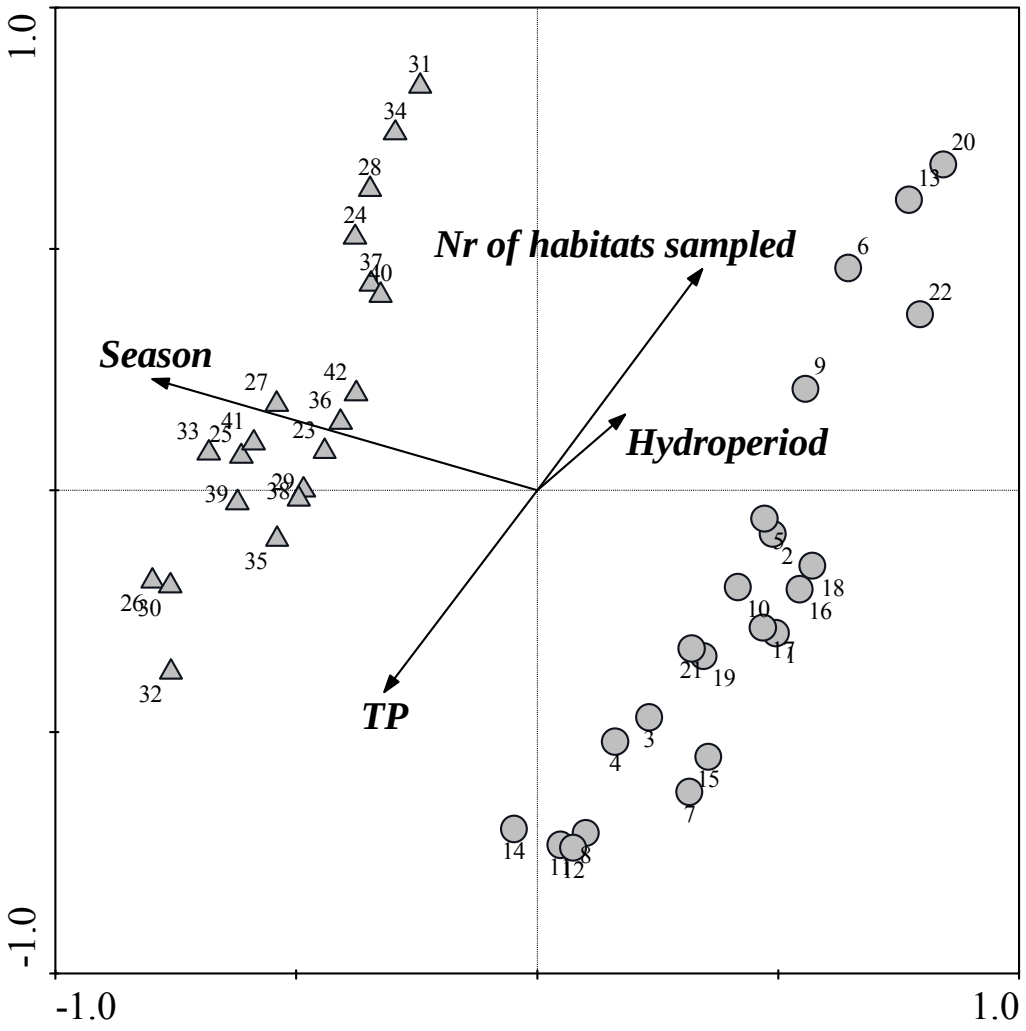


Figure 6.4: Axes 1 and 2 of the CCA ordination generated using automatic forward selection of four environmental variables and log(x+1) transformed macroinvertebrates abundances data (n=42). Circles are representing macroinvertebrate samples collected in November 2006, triangles those collected in April 2007.

Spearman rank-order correlation of turlough sample ranks of the two sampling seasons according to their arrangement in the CCA ordination (Figure 6.4) showed that the alignment of turlough samples to each other was similar among seasons ($R=0.732$; $P<0.001$; $n=42$), concurring with trends seen in cluster dendograms.

6.3.3 *Relating Zooplankton Taxonomic Structure to Nutrient Enrichment*

Combining the two sampling strategies for open water cladoceran zooplankton and chydorids a total of 29 cladoceran zooplankton species were found in the 20 turloughs sampled in April 2007. Recorded taxa varied from common species such as *Chydorus sphaericus* or *Daphnia pulex*, to rare species such as *Alona rectangular* or *Alonopsis elongata* which only occurred in Croaghill and Lough Gealain, respectively. While some taxa such as *Alona rectangula*, *A. rustica*, *Alonella excisa* and *Alonopsis elongate* only occurred in turloughs with low to medium TP concentrations, the more common *Chydorus sphaericus* and *Daphnia pulex* were found across the whole range of TP concentrations (Table 6.7).

Table 6.7: Summary of cladoceran zooplankton taxa (presence indicated with 1) found in 20 turloughs in April 2007 combining records from open water zooplankton and chydorid sampling protocols. Order of turloughs is ranked according to total phosphorus (TP) concentrations.

	Lough Gealain	Knockaunroe	Ballindereen	Roo West	Lisduff	Caranavoodaun	Termon	Garryland	Croaghill	Brierfield	Tullynafrankagh	Kilglassan	Skealoghan	Lough Coy	Coolcam	Lough Aleenaun	Carrowreagh	Caherglassaun	Rathmalulleagh	Ardkill
Acroperus angustatus			1	1																1
Acroperus harpae			1												1					1
Alona affinis	1	1	1	1		1	1	1	1			1	1		1	1	1	1		1
Alona excisa			1			1							1							
Alona guttata			1			1	1	1												1
Alona intermedia			1						1											
Alona quadrangularis								1		1			1	1						
Alona rectangula									1											
Alona rustica			1	1		1			1											
Alonella excisa	1	1	1	1	1	1		1	1			1	1	1						
Alonella nana		1				1														
Alonopsis elongata	1																			
Chydorus globosus	1				1						1									
Chydorus latus							1						1		1		1	1		
Chydorus ovalis										1										
Chydorus piger									1											
Chydorus sphaericus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Daphnia pulex	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Eurycercus glacialis						1			1				1							
Eurycercus lamellatus	1	1	1	1	1		1			1	1	1	1	1	1	1		1		1
Graptoleberis testudinaria		1	1	1		1			1	1		1	1	1		1		1		
Lathurona rectirostris	1	1	1	1	1	1	1			1		1	1							1
Leydigia leydigi							1									1				
Peracantha truncata																			1	
Pleuroxus laevis	1			1		1		1		1	1		1							
Pleuroxus trigonellus				1				1				1	1							
Polyphemus pediculus	1							1												
Rhynchotalona rostrata																				1
Simocephalus vetulus	1	1	1	1	1		1				1	1	1		1	1	1	1		1
TP µg L-1	2	3	5	8	8	11	11	12	14	15	18	18	20	25	27	31	36	38	43	98

6.4 Discussion

6.4.1 Macroinvertebrate Community Composition and its Relationship to Environmental Variables

6.4.1.1 Season

Non-metric multidimensional scaling (MDS), SIMPER and Canonical Correspondence Analysis (CCA) revealed a strong influence of sampling season on macroinvertebrate community structure of turloughs. Seasonal differences in macroinvertebrate community assemblages are most likely owing to differences in life-cycle stages of different taxa, with ephemeral taxa more abundant later in the season (Boix *et al.*, 2004; Jocqué *et al.*, 2007). Differences in community structures among the different sampling months were identified by SIMPER mainly as a result of increases or appearances of ephemeral taxa in April 2007 samples. Trichoptera (predominantly early instar stages) were, however, mainly collected in November 2006 samples. The comparatively low representation of Trichoptera larvae in later season samples, albeit being characterised as an ephemeral macroinvertebrate species, could be partly owing to the sampling regime used. Samples were collected in the same location of the accessible, wadable littoral zone of each turlough in each month moving along a transect with the turlough shore line with increasing or decreasing water level. Trichopteran larvae could have migrated to deeper parts of the turlough and, thus, been omitted with the sampling strategy used. The alternative possibility is an early emergence of Trichoptera larvae from turloughs before the collection of samples in April 2007.

Cluster Analysis and SIMPER estimated overall similarity of turlough macroinvertebrate communities to be higher in April 2007 than in November 2006. This suggests a stabilisation of the macroinvertebrate community of turloughs over time which is in agreement with results from the study on temporal dynamics of macroinvertebrates in turloughs reported in Chapter 4. Moving further away from a disturbance, in this case the occurrence of the dry phase and, thus, habitat loss for aquatic invertebrates in turloughs, the greater the possibility of niche building and stabilisation of the faunal communities will be (Jocqué *et al.*, 2007). Significantly, different groups of turloughs clustering together identified using the SIMPROF-test

decreased from eight in November 2006 to five in April 2007, supporting the higher resemblance of macroinvertebrate community structures in later season samples.

Despite differences in overall turlough similarities among sampling months, certain macroinvertebrate taxa were identified to occur in all of the sampled turloughs, accounting for about one third (27.6% and 32.3% overall similarity of turloughs in November 2006 and April 2007, respectively) of the community. This macroinvertebrate 'core group' comprises taxa which were previously described as characteristic turlough species such as the molluscs *Lymnaea fusca*, *Radix balthica* and *Galba truncatula* (Byrne *et al.*, 1989; Donaldson *et al.*, 1979), the beetles *Porhydrus lineatus*, *Hydroporus palustris*, larvae of the genus *Agabus* sp. and *Dryops* sp. (Bilton, 1988), the damselfly *Lestes* sp. and dragonfly *Sympetrum sanguineum* (Nelson and Thompson, 2004), the mayfly *Cloeon dipterum*, caddis-fly species of the family *Limnephilidae*, *Ostracoda* sp. and the amphipod *Asellus aquaticus* (Reynolds, 1982, 1985b, 1996; Reynolds, 1997; Reynolds, 2003). Even though some of the macroinvertebrate taxa identified as the 'core group' are common inhabitants of ponds (Lansbury, 1965; Reynolds, 2000), they all possess special adaptations to the ephemeral turlough environment either through the formation of resting stages or resistance to desiccation, or through migration to permanent water bodies as aerial adults (Reynolds, 1982, 1996; Sheehy Skeffington *et al.*, 2006).

6.4.1.2 Nutrient Enrichment

CCA identified total phosphorus (TP) concentrations as important in structuring the macroinvertebrate community of turloughs. Other studies have emphasized the importance of trophic conditions in determining the structure of macroinvertebrate assemblages (Brauns *et al.*, 2007; Brodersen *et al.*, 1998; Heino, 2000; Langdon *et al.*, 2006; Rasmussen, 1988; Tolonen *et al.*, 2001; Tolonen *et al.*, 2005; White *et al.*, 2003). Brauns *et al.* (2007) found macroinvertebrate community composition between oligotrophic and hypertrophic lakes to differ significantly from each other while communities from mesotrophic lakes were less distinct. The same study, furthermore, identified the effects of trophic state on macroinvertebrate assemblages to be nested within habitat type and partly substituted by biotic interactions and small-scale habitat complexity. Indicators of nutrient enrichment, chlorophyll *a* and

Secchi depth were identified as important in contributing to structuring the macroinvertebrate community in a study on 39 Danish lakes of differing trophic state using CCA (Brodersen *et al.*, 1998). Although Tolonen *et al.* (2001) identified habitat structure to be more important than trophic state in structuring macroinvertebrate communities in lakes, their results were from lakes within a limited range of nutrient concentrations (TP among all studied habitats: 3-26 μg L^{-1}). White and Irvine (2003), in contrast, found physical, chemical and other environmental conditions to have a greater effect than substrata on structuring macroinvertebrate assemblages in a study across systems comprising a wider trophic range. In this study nutrient concentrations were shown also to be important in structuring macroinvertebrate communities of turloughs, with similar importance to habitat heterogeneity. The interrelatedness of nutrient trophic state and habitat structure, however, can make the separation of the two effects on macroinvertebrate community structure often difficult (Brauns *et al.*, 2007; Brodersen *et al.*, 1998; Solimini *et al.*, 2006).

Occurrences of macroinvertebrate orders Aranea, Odonata and Trichoptera showed a significant negative correlation with increasing nutrient concentration of turloughs, while Diptera and Ostracoda abundances increased significantly with nutrient state. Aquatic macroinvertebrates such as Odonata or Trichoptera larvae are widely recognised as characterizing habitat quality since they are sensitive indicators of environmental stressors, such as altered hydrology and nutrient enrichment (Moore, 1980; Nelson *et al.*, 2004; Resh and Jackson, 1996). While decreases in species richness were reported to occur as a response to nutrient enrichment of freshwaters (Brodersen *et al.*, 1998; Rasmussen, 1988), some taxa may benefit from these extreme conditions owing to reduced biotic-interactions. Ostracoda have previously been reported as tolerant to a wide range of environmental conditions and certain species have been identified to proliferate in extreme environments, with increasing abundances in more productive systems (Külköylüoğlu *et al.*, 2007; Wetzel, 2001; Yılmaz and Külköylüoğlu, 2006). The positive correlation of Diptera with increased trophic state of turloughs is in agreement with previous reports by Hellawell (1986) and Rosenberg and Resh (1993a) and their traditional use as indicators of pollution.

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6.4.1.3 Habitat

CCA identified the number of habitats sampled to have a strong relationship with macroinvertebrate community structure. Habitats sampled varied from submerged grassland (dominant habitat type in most turloughs) limestone pavement and stone walls, submerged shrub flora to thick stands of sedges or reeds. The importance of habitat heterogeneity for macroinvertebrates is well known (Heino, 2000; Hinden *et al.*, 2005; Stoffels *et al.*, 2005; Tolonen *et al.*, 2001; Tolonen *et al.*, 2003; van den Berg *et al.*, 1997; White *et al.*, 2003), with distinct invertebrate communities often associated with particular habitat types. In a study on two eutrophic lakes van den Berg (1997) identified vegetation type as a major factor in determining macroinvertebrate community composition. Cheruvelil *et al.* (2000) found plant architecture to have a significant influence on macroinvertebrate abundance, with dissected-leaf macrophytes supporting higher numbers of macroinvertebrates than broad-leafed vegetation.

Habitat heterogeneity also significantly influenced macroinvertebrate taxon richness in turloughs. Habitat diversity has previously been identified to have a positive effect on macroinvertebrate taxon richness (Brönmark, 1985; Jeppesen *et al.*, 2000; Tolonen *et al.*, 2003). Increasing numbers of habitats provide more potential niches (Heino, 2000) favouring coexistence of potential competitors. Submerged vegetation can also provide shelter from predation by fish (if present). Tolonen *et al.* (2003) found Odonata, Corixidae, Dytiscidae, Ephemeroptera and Sialidae taxa in lower abundances in macrophyte-poor regions compared with areas of thick macrophyte stands and postulated their depletion by fish because of the greater visibility of these larger macroinvertebrates in visibly unprotected areas. The loss of submerged vegetation not only causes an increase in predation pressure but also a decrease in important food resources for many macroinvertebrates such as epiphytic algae associated with macrophyte habitats (Jones *et al.*, 1998).

The number of available habitats varied in some of the studied turloughs among seasons, owing to changes in water levels and consequently available habitats in the littoral zone. Thus, the seasonal changes in the macroinvertebrate community may also be influenced by seasonal differences of habitat availability in turloughs (Solimini *et al.*, 2006). Pieczyńska (1998) found invertebrate littoral fauna to be

regulated by seasonal changes in species composition and abundance of submerged vegetation. Seasonal changes in habitat preference of macroinvertebrate taxa in accordance with life-cycle stages may affect community composition (Solimini *et al.*, 2006). A positive correlation was found between Plecoptera taxa (only *Nemoura cinerea*), which were generally seldom detected, and the number of habitats sampled. Plecoptera are widely credited as bioindicators in rivers, including of acidification, sedimentation, nutrient enrichment and loss of riparian structures (Camargo *et al.*, 2004; Küry, 1995; Quinn and Hickey, 1990; Resh *et al.*, 1996a). However, Plecoptera are not common inhabitants of standing waters and especially not temporary ponds (Williams, 1997), but *Nemoura cinerea*, a stonefly species very abundant and widespread in Britain and Ireland has been previously reported from turloughs (Byrne, 1981) and Pant-y-Llyn, a seasonal lake in Wales (Blackstock *et al.*, 1993). The positive relationship between Aranea occurrences with more structurally complex habitats probably reflects modes of feeding or movement (e.g. net or web building) (Warren, 1989). Significantly greater abundances of Odonata and Trichoptera taxa in turloughs with higher habitat heterogeneity could be attributed to refuges from predation by fish (if present) (Gilinsky, 1984) or perches for feeding (Brooks and Lewington, 1997; Nelson *et al.*, 2004; Warren, 1989).

6.4.1.4 Hydroperiod

The importance of hydroperiod on the biodiversity of temporary waters has been reported by a number of authors (Batzer *et al.*, 2004; Brooks, 2000; Collinson *et al.*, 1995; Schneider, 1999) identifying habitat loss during dry periods as severe disturbance for the macroinvertebrate community (De Meester *et al.*, 2005; Holland and Jenkins, 1998; Schneider *et al.*, 1996; Sousa, 1984). In this study, turlough macroinvertebrate taxon richness increased significantly with increasing hydroperiod of turloughs. Results from CCA, however, suggest that hydroperiod had a low influence on community composition of macroinvertebrates compared with the other environmental variables measured, and did not describe any additional variation in the biological community after including it in the model (marginal effect: $\lambda 1 = 0.10$; conditional effect: $\lambda A = 0.09$, $P = 0.126$, $F = 1.22$). The effect of hydroperiod on community compositions could be expected to be reflected in higher abundances of ephemeral taxa in more permanent turloughs, because in turloughs with longer habitat permanence there is a greater possibility of colonization. Thus,

effects of hydroperiod are directly linked to macroinvertebrate life-stages. The strongly dominating seasonal effect on macroinvertebrate community structure seems most likely to have an overriding effect on hydroperiod, which nevertheless has an important effect on shaping macroinvertebrate diversity of turloughs. The interrelatedness of macroinvertebrate life-strategies and hydroperiod was also evident from the significant positive correlation of Trichoptera and Heteroptera abundances with hydroperiod. Both macroinvertebrate groups are ephemeral residents of temporary waters and need more permanent habitats in order to complete their life-cycles before water recedes (Lahr, 1997; Lahr *et al.*, 1999; Williams, 1987). The association of higher abundances of Gastropoda in turloughs with longer hydroperiods concurs with their limited mobility (Follner and Henle, 2006). Despite possessing adaptations to drought (Williams, 2006), the limited mobility of molluscs seems to permit greater survival in longer inundated sites.

6.4.2 Zooplankton Community Structure and its Relationship to Environmental Variables

The cladocerans found in this study are generally well known in turlough conditions. *Acroperus harpae*, *Alona affinis*, *Alonella excisa*, *Chydorus sphaericus*, *Eurycercus lamellatus*, *Graptoleberis testudinaria* and *Simocephalus vetulus* were previously recorded in Knockaunroe and Lough Gealain (Reynolds, 1985a). Reynolds *et al.* (2004) detected 15 taxa belonging to four families in a survey on 28 turloughs early in the season, with *Chydorus sphaericus* occurring in all but one of the sampled turloughs, sometimes as the only species present. This almost ubiquitous distribution of *C. sphaericus* is in agreement with the results of this study, which identified *C. sphaericus* together with *Daphnia pulex* as the most common zooplankton species. *C. sphaericus* dominated almost a third of 66 studied shallow European lakes, generally those demonstrating low diversity, in a study by de Eyto *et al.* (2003). *C. sphaericus* can colonize new environments quickly as it is characterised by the ability to utilize various food sources more efficiently than more littoral, detritus feeding species such as *Alona affinis* (de Eyto and Irvine, 2001). It is tolerant of a wide range of environmental conditions (Fryer, 1993) and possibly the most ubiquitous chydorid species in Ireland (Duigan, 1992).

Eurycercus glacialis was first recorded in Ireland by Duigan and Frey (1987b) in 1985 in four sites close to Gort, Co. Galway, while investigating thirty-eight sites in the karstic limestone region between Ballyvaughan, Gort and Corofin, Cos. Galway and Clare. So far it has been recorded from eighteen turloughs (Duigan *et al.*, 1987b; Reynolds *et al.*, 1999) of which seventeen were considered to lack vertebrate predators. It is assumed that *E. glacialis*, as well as other cladoceran species forming resting eggs, would be able to occur with vertebrate predators such as newts or fish if the populations' diapauses commence before juvenile predators will be large enough to prey on the large entomostracan (Reynolds, 2000). This study detected *E. glacialis* in three of the twenty turloughs, all of which also contained larger predatory invertebrate species of the order Odonata and/or predatory flatworms. Reynolds (2000) reported the simultaneous occurrence of both entomostracans and predators in some turloughs and assumed the rather large size of the cladoceran larvae would make them unsuitable as prey for the coexisting carnivorous cladoceran *Polyphemus pediculus*. Furthermore, he attributed habitat complexity to permit the occurrence of predatory leeches, flatworms and Odonata larvae and *E. glacialis* in several of the study sites in the Gort-Kinvara area. Reynolds *et al.* (2004) described *E. glacialis* as an indicator of turlough conditions rather than water quality, as its occurrence is limited to turloughs whose hydrology is unimpacted by major drainage.

Cladoceran zooplankton and chydorid abundances increased significantly with increasing permanence of turloughs. This is in agreement with Duigan (1988) who concluded that turloughs which contain permanent still or flowing water throughout the year have higher invertebrate abundance and greater taxon richness than those drying out for a certain amount of time. This study, however, did not find any correlation between hydroperiod of turloughs and cladoceran zooplankton diversity. Cladoceran zooplankton and chydorid abundances were both positively related to trophic state of turloughs. The abundance and biomass of zooplankton is usually positively related to nutrient concentrations (Karjalainen *et al.*, 1999; McCauley and Kalff, 1981; Tolonen *et al.*, 2005) owing to the positive relationship of phytoplankton abundance with nutrient enrichment and, thus, higher food availability for zooplankton in nutrient rich waters (Canfield and Jones, 1996). The diversity of zooplankton has been found to be highest in complex vegetated habitats

(Van den Brink et al., 1994). The number of habitats sampled did not, however, have any association with chydorid species richness, which is in agreement with Tolonen *et al.* (2005) who did not find any relationship with zooplankton taxon richness and environmental variables, including habitat. Chydorid species richness did not differ among rocky and macrophyte sampling sites in the 66 European shallow lakes sampled by de Eyto *et al.* (2003). The lack of correlation of taxon richness with habitat heterogeneity is nevertheless surprising as it is generally considered that areas with higher spatial heterogeneity posses higher species richness (Rasmussen, 1988; Rundle and Ormerod, 1991).

Some zooplankton species showed marked preferences for certain turlough types. Presence of *Alonopsis elongata* in only one turlough, the turlough with lowest nutrient concentrations, suggests a low tolerance of this species to eutrophication. This is in agreement with other studies identifying its distribution as limited to colder, oligotrophic water bodies (de Eyto *et al.*, 2003; Fryer, 1993; Irvine *et al.*, 2001b). *Alona rustica* and *Alonella excisa* have been reported to show negative correlations with nutrient trophic state of lakes (de Eyto *et al.*, 2002; de Eyto *et al.*, 2003) and were predominantly found in turloughs with low to medium trophic state. Cladoceran zooplankton taxon richness significantly decreased with increasing trophic state of turloughs, which concurs with findings by other authors linking high nutrient status to a shift from diverse zooplankton assemblages to monospecific communities of predominantly *C. sphaericus* in eutrophic waters (de Eyto, 2001; Duigan and Murray, 1987a). This effect was, however, not congruent for macroinvertebrate taxon richness, indicating that the link between littoral macroinvertebrates and zooplankton is not direct but rather that conditions in the turloughs affect both, but in different ways. As zooplankton as well as macroinvertebrates are second order consumers, tangible links are unlikely, which was reflected in a lack of correlation between neither cladoceran nor chydorid taxon richness and macroinvertebrate taxon richness.

6.5 Conclusions

Season explained the most variability in the macroinvertebrate community data set emphasizing the importance of temporal variability in assemblage structure for the sampling of macroinvertebrates for monitoring purposes. Life-cycle attributes (e.g. reproduction, hatching and emergence periods) need to be carefully considered when deciding on sampling strategies for conservation purposes (Cayrou and Céréghino, 2005). The similar grouping of turloughs in the two different sampling seasons, however, indicates that despite considerable temporal variation in macroinvertebrate community composition, macroinvertebrate communities are nevertheless comparable among turloughs when sampled at the same time. Sampling for monitoring of ecological status of turloughs should always be carried out within limited time spans in order to reduce variation owing to phenology and colonisation, thus, discriminating meaningful results from the background noise of temporal variation. Variable associations of the macroinvertebrate as well as the zooplankton communities to environmental variables were found, with some macroinvertebrate orders and zooplankton species showing significant relationships with chemical descriptors of nutrient enrichment. Despite the importance of habitat heterogeneity on macroinvertebrate community structure single habitat sampling showed similar results when compared with a more labour intensive multi-habitat sampling approach. While seasonal as well as spatial variations can be marked among littoral macroinvertebrate assemblages, the results of this study suggest that littoral shoreline samples of benthic macroinvertebrates can be a meaningful descriptor of turlough ecological status. The complexity of benthic macroinvertebrate communities and possible difficulties associated with temporal and spatial variation may, however, make their use for routine monitoring programmes of the variable turlough environment difficult. Yet, some chydorid species offer an alternative biotic element for monitoring of turloughs as their identification is less complex and this group includes a number of possibly useful indicators of ecological change.

7 Discussion

7.1 Research Aims

The overall aim of this study was to investigate the effects of season, habitat, hydroperiod and water chemistry on the distribution of turlough aquatic invertebrate communities. Twenty-two turloughs, selected as representative of geographical distribution and hydrological conditions were included in the study. A comparative study of eight turloughs representing a nutrient gradient determined macroinvertebrate community distinctiveness in a stratified sampling design and related assemblage structures to environmental variables. Assessment of macroinvertebrate temporal and spatial variation was the objective of separate studies conducted in a subset of four turloughs, varying in hydrological and nutrient regimes. The influence of disturbance and habitat characteristics on macroinvertebrate community dynamics was tested. Across twenty-two turloughs macroinvertebrates and cladoceran zooplankton communities were analysed and their relation to varying trophic, hydrological and morphological regimes identified.

7.2 Importance of Season, Habitat, Nutrients and Hydroperiod for Turlough Invertebrate Distinctiveness and Community Structures and Implications for Monitoring

Components of this study indicated the importance of season, habitat, nutrient status and hydroperiod for invertebrate distinctiveness and community composition, with important implications for monitoring programmes (see summary in Figure 7.1).

7.2.1 Season

A strong influence of season on macroinvertebrate biodiversity and community structure was found. Trends identified in the detailed study on successional patterns in macroinvertebrate communities conducted in four turloughs (Chapter 4) were verified by an independent data set of twenty-two turloughs using a multi-habitat sampling approach. Both studies identified season to be important for structuring macroinvertebrate assemblages of turloughs. Two phases of succession were identified, which were primarily characterised by an increase or appearance of ephemeral taxa later in the season. The importance of season for macroinvertebrate communities was confirmed in a wider study on twenty-two turloughs. Differences

in macroinvertebrate community composition among sampling months reflected life-stages of macroinvertebrates. Early season species were identified as those possessing resting/dormant stages, or resistance to desiccation allowing them to take advantage of the ephemeral nature of the turlough environment before the community diversifies. Macroinvertebrate species which arrive in the late successional stage are considered ephemeral residents of turloughs, depending largely on migration or aerial dispersal as they do not possess adaptations to drought. These results concur with other studies on macroinvertebrate succession in temporary freshwater environments (Boix *et al.*, 2004; Jocqué *et al.*, 2007; Lahr, 1997; Lahr *et al.*, 1999; Wiggins, 1980). Changes in life cycle and abundance and an increase of ephemeral taxa later in the season contributed, subsequently, to an increase in spatial variation in macroinvertebrate community structure as reported in Chapter 5. The increase of ephemeral taxa later in the season and their possibly non-random habitat selection could, furthermore, lead to increased patchiness of macroinvertebrate distribution (Blaustein *et al.*, 2004; Resetarits, 2001). Not only seasonal variation as a result of succession was found important for structuring processes of the turlough macroinvertebrate communities. Macroinvertebrate taxon richness and community structures varied interannually. The later onset of flooding during sampling season 2007/2008 of about one month compared with the previous year could explain the observed shift of equally one month in the successional pattern. Sampling for monitoring of turloughs should account for seasonal and interannual variability of turlough macroinvertebrate communities. Monitoring programmes relying on single annual samples could lead to an underestimation of turlough biodiversity, and negatively influence quality scores if taxa such as Ephemeroptera, Odonata or Trichoptera are included as indicator taxa of anthropogenic disturbances. These animals can emerge before water recedes in spring or early summer. Single season sampling could moreover overlook short-lived or egg-diapausing macroinvertebrate taxa. The highly variable turlough environment requires a flexible and adaptable sampling programme, to allow for interannual variability of macroinvertebrate communities. Variable starts of the flooding cycle should be taken as an orientation rather than sticking to a fixed sampling-month regime. Thus, adequate turlough sampling needs to be aligned with the start of the turlough flooding season and temporary stratified according to the

needs of respective monitoring programmes. Timing and frequency of sampling should depend on particular questions dealt with by respective sampling protocols.

7.2.2 Habitat

The number of habitats sampled explained a significant amount of variance in the macroinvertebrate total abundance data of twenty-two turloughs. Habitat heterogeneity has been recognised as important for structuring macroinvertebrate communities in lentic freshwaters (Heino, 2000; Hinden *et al.*, 2005; Stoffels *et al.*, 2005; Tolonen *et al.*, 2001; Tolonen *et al.*, 2003; van den Berg *et al.*, 1997; White and Irvine, 2003), with various macrophyte communities or sediment types associated with distinct macroinvertebrate assemblages (Brauns *et al.*, 2007; Cheruvelil *et al.*, 2000; Hinden *et al.*, 2005; Pieczyńska *et al.*, 1998; Tolonen *et al.*, 2001; van den Berg *et al.*, 1997). The positive influence of habitat heterogeneity on macroinvertebrate taxon richness is in agreement with previous studies (Brönmark, 1985; Jeppesen *et al.*, 2000; Tolonen *et al.*, 2003). Increasing number of habitats leads to an increase in potential refugia from predation by fish (Tolonen *et al.*, 2003) and may support the coexistence of competing taxa (Heino, 2000). Seasonal changes of habitat availability reported in this study could have contributed to seasonal faunal differences. Changes in habitat preferences of certain taxa as a result of different life-cycle stages are also reported to affect community structures (Pieczyńska *et al.*, 1998; Solimini *et al.*, 2006).

Differences in macroinvertebrate assemblages among turlough habitats were identified in Chapter 5. This study found certain macroinvertebrate taxa of conservation concern to be associated with particular habitats. For a comprehensive conservation assessment, a sampling regime incorporating all available habitats in a turlough seems necessary, as this would provide a more comprehensive picture of turlough biodiversity. Several parts of this study, however, identified variation *within* turlough macroinvertebrate communities to be less than *among* turlough variability. This adds weight to the usefulness of macroinvertebrates as reliable indicators of change even across a range of habitat types despite inherent spatial variation in littoral zones. Similar results were found by White and Irvine (2003) in a study on twenty-one Irish lakes. Whether one or multiple habitats should be sampled for monitoring purposes should consequently depend on the objective of

respective sampling protocols. If the aim of a sampling programme is the detection of a pressure response, routine standardised among turlough sampling of the most dominant turlough habitat submerged grassland seems highly appropriate. This stratified sampling approach would reduce inherent spatial 'noise' and, furthermore, facilitate cost and time effective monitoring of turloughs. Reduction of inherent variability would strengthen the possibility of detecting anthropogenic disturbances in turlough littoral zones. The results of this study emphasize the suitability of a single or pooled submerged grassland macroinvertebrate sample for routine turlough monitoring as required under the WFD (EC, 2000). For a comprehensive survey of turlough macroinvertebrate biodiversity as required for conservation assessment under the EC Habitats Directive (EEC, 1992), sampling all available habitats in a turlough would, however, be favoured. This thorough sampling approach would enhance the possibility of the detection of local and internationally rare taxa.

7.2.3 Nutrients

The importance of trophic conditions for structuring macroinvertebrate assemblages in freshwater environments has been widely acknowledged (Brauns *et al.*, 2007; Brodersen *et al.*, 1998; Heino, 2000; Langdon *et al.*, 2006; Rasmussen, 1988; Tolonen *et al.*, 2001; Tolonen *et al.*, 2005; White *et al.*, 2003). This study identified total phosphorus (TP) concentrations as important in structuring macroinvertebrate communities of turloughs. Brauns *et al.* (2007) found distinct macroinvertebrate assemblages in oligotrophic and hypertrophic lakes while communities in mesotrophic lakes were less distinct, with effects of trophic state nested within habitat type. The importance of nutrient enrichment on the structuring of macroinvertebrate communities was identified by Brodersen *et al.* (1998) in a study on 39 Danish lakes. Canonical Correspondence Analysis (CCA) results showed turlough nutrient status to be similarly important as habitat heterogeneity for macroinvertebrate communities in turloughs. Separating the effects of habitat structure on macroinvertebrate assemblages from those of nutrient trophic state can be difficult as these are often interrelated (Brauns *et al.*, 2007; Brodersen *et al.*, 1998; Solimini *et al.*, 2006). Taxonomic groups responded to increased nutrient concentrations with higher abundances of Diptera and Ostracoda, while orders Aranea, Odonata and Trichoptera showed a significant negative correlation with nutrient state. These findings correspond to those from various other studies

(e.g. Hellawell, 1986; Moore, 1980; Nelson and Thompson, 2004; Resh and Jackson, 1996; Yılmaz and Külköylüoğlu, 2006), emphasizing the potential of respective macroinvertebrate orders as indicators for nutrient trophic state. Certain cladoceran zooplankton taxa also showed associations with nutrient state of turloughs. Low tolerance of *Alonopsis elongata* to eutrophication has been previously reported (de Eyto *et al.*, 2003; Fryer, 1993; Irvine *et al.*, 2001b) and agrees with it being found in only one of the studied turloughs, which had low nutrient status. Other species such as *Alona rustica* and *Alonella excisa* were predominantly detected in turloughs of low to medium trophic state, concurring with de Eyto *et al*. (2002; 2003). Decrease of biodiversity owing to eutrophication of waters has been previously reported (Brodersen *et al.*, 1998; de Eyto, 2001; Duigan and Murray, 1987) and was reflected in the decrease of cladoceran zooplankton taxon richness with nutrient concentrations across the turloughs. The increase of zooplankton abundance with trophic state of turloughs originates from the positive relationship of phytoplankton abundance with nutrient enrichment and, thus, higher food availability for zooplankton in nutrient rich waters (Canfield and Jones, 1996), and agrees with several other studies (Karjalainen *et al.*, 1999; McCauley and Kalff, 1981; Tolonen *et al.*, 2005). No evidence was, however, found for the influence of nutrient concentrations on macroinvertebrate taxon richness and abundance, which is in agreement with Reynolds (2000), who found nutrient concentrations to be unimportant in determining faunal community diversity in turloughs.

Chapter 4 identified an influence of nutrient enrichment on successional patterns of macroinvertebrates in turloughs. This was characterised by a general dominance of taxa considered tolerant to pollution in turloughs with high trophic state (mainly oligochaetes and chironomids) (Brodersen *et al.*, 1998; Hellawell, 1986; Pinel-Alloul *et al.*, 1996), and a trend of more susceptible ephemeral residents (if present) disappearing towards the end of the season owing to their inability to endure prolonged exposure to high nutrient concentrations. Climate change will possibly increase the number of stressors affecting turlough ecosystems. Thus, priority should be given to the reduction of already existing pressures such as nutrient enrichment. While the spatial and temporal variability of the comparatively complex macroinvertebrate communities could be challenging for routine turlough sampling,

some chydorid taxa have the potential to be used as relatively straightforward elements for monitoring ecological change of turloughs.

7.2.4 Hydroperiod

The temporary nature of the turlough environment poses a challenge to its faunal communities. Different macroinvertebrate taxa have adapted in various ways to the repeating occurrence of drought in turloughs in order to mature, reproduce or disperse before the end of the wet cycle. Adaptations include the production of resting eggs and resistance to desiccation by permanent residents of turloughs, migration of adults to permanent waters, or survival over a dry period as terrestrial adults by ephemeral residents (Lahr *et al.*, 1999; Williams, 1987). The occurrence of uncommon invertebrate taxa in temporary ponds has been previously reported (Collinson *et al.*, 1995; Della Bella *et al.*, 2005; Williams, 1987) and concurs with findings of invertebrate species and assemblages of restricted distribution and high conservation value in this study. Several rare invertebrate taxa and assemblages were detected such as the characteristic 'edge moss dwelling' beetle community or the glacial relict species *Eurycercus glacialis* many of which are reported as sensitive to anthropogenic disturbances such as nutrient enrichment (Bilton, 1988; Shirt, 1987). The loss of water during the periodically occurring dry phase of turloughs may support not only very distinct and adapted invertebrate communities but also confer specific advantages to particular rare species including an absence of fish. The rather large size of *E. glacialis* was postulated to make it particularly vulnerable to visual predators, thus, restricting it to temporary habitats (Duigan and Frey, 1987). The rare damselfly *Lestes dryas* is also considered to benefit from the absence of larger predatory invertebrates and fish in many turloughs (Nelson *et al.*, 2004).

The importance of hydroperiod and, thus, habitat permanence for the diversity of macroinvertebrate communities in temporary wetlands has been reported by several authors (Collinson *et al.*, 1995; Kiflawi *et al.*, 2003; Schneider and Frost, 1996; Waterkeyn *et al.*, 2008; Williams *et al.*, 2003). The dry phase of a turlough can be defined as a natural disturbance for the faunal communities of turloughs and the associated hydroperiod length was found to have severe effects on successional patterns of turlough macroinvertebrates. Macroinvertebrate communities of

turloughs with a short hydroperiod and, thus, high disturbance were identified to be characterised mainly by permanent residents possessing adaptations to the recurring stress of drought. Wiggins (1980) found the same to be true for faunal communities of temporary pools. Interannual variability of taxa composition was furthermore found to be related to interannual differences in hydroperiod (Schneider *et al.*, 1996). Faunal communities of highly disturbed turlough environments were detected to support invertebrate community assemblages characterised mainly by permanent residents after dry years, and greater numbers of ephemeral residents after relatively wet ones. Variability in taxon richness was negatively correlated with increasing habitat permanence, favouring more stable communities in turloughs with long habitat permanence. Complying with stabilising macroinvertebrate assemblages, variability in taxon richness decreased over time following major disturbance by drought. With increasing habitat persistence influence of disturbance becomes less and, finally, biotic interactions become more important (Schneider, 1999). Across the studied turloughs taxon richness, moreover, increased over time. This temporal gradient of biodiversity reflects a longer exposure for colonization and emergence from resting stages (Cayrou and Céréghino, 2005; Holland and Jenkins, 1998; Spencer *et al.*, 1999). CCA results suggested that hydroperiod had, however, a low influence on community structures of macroinvertebrates relative to effects of season, nutrient concentrations and number of habitats sampled. The effect of hydroperiod on community structure was nevertheless evident in the positive correlation of ephemeral macroinvertebrate orders Heteroptera and Trichoptera with increasing habitat permanence. Thus, effects of hydroperiod are directly linked to macroinvertebrate life-stages and the strong identified seasonal effect had likely an overriding effect in the CCA analysis.

Possible effects of hydroperiod and its variability among turloughs and years for macroinvertebrate assemblages of turloughs pose a challenge for the development of monitoring protocols under the EC WFD (EC, 2000) and the EC Habitats Directive (EEC, 1992). The highly dynamic nature of turloughs might negate the development of a classification of turloughs and, thus, associated estimation of type-specific reference conditions as is required for lakes and rivers. Turlough monitoring protocols need a more flexible approach, and geared towards flooding regimes and the variable hydrocycles.

7.2.5 Macroinvertebrate Distinctiveness

The highly individual character of turlough macroinvertebrate communities was a recurrent theme throughout this study. Replicate macroinvertebrate turlough samples repeatedly formed highly distinct clusters and certain macroinvertebrate taxa showed associations to certain morphological (e.g. Odonata in well-vegetated habitats of Caranavoodaun) or water chemical characteristics (e.g. Diptera and Gastropoda in nutrient rich waters of Caherglassaun) of turloughs. Turlough macroinvertebrate distinctiveness could be a result of the generally high individual features of these temporary habitats. Turloughs like other temporary habitats (Collinson *et al.*, 1995; Williams, 1996; Williams *et al.*, 2003) generally posses very individual physico-chemical characters and hydromorphological regimes which contribute to the uniqueness of the habitats. However, similar results have been reported for lakes (White and Irvine, 2003), suggesting that spatial variation *within* lentic freshwaters is nested in *among* lake/turlough variation. The conclusion from Chapter 3 that a single submerged grassland sample would be sufficient in describing the macroinvertebrate community of a turlough was tested in a more comprehensive spatial study as reported in Chapter 5. Results emphasized the highly individual character of turlough macroinvertebrate assemblages, leading to the conclusion that a single submerged grassland habitat sample collected *at any location* in the littoral zone of a turlough is representative for the macroinvertebrate community as a whole. Similar groupings of eight turloughs sampled in April 2007 using a multi-habitat and a single-habitat sampling approach, furthermore, support this assumption and emphasize the usefulness of macroinvertebrates as reliable indicators of change despite inherent heterogeneity in the littoral zone of turloughs. It is, however, a matter of the scale of interest, with conclusions affected by the extent of the dominating interest. Turloughs may represent quite widespread, but often unappreciated phenomena of spatial patterns of freshwaters, and maybe all ecosystems.

7.3 Conclusions

- Turlough macroinvertebrate communities are highly distinct and conducive to simple and cost-effective routine monitoring regimes. A single submerged grassland habitat sample located in any location of a turlough can provide a reliable metric of the macroinvertebrate community. This stratified sampling approach would reduce inherent spatial 'noise' and is, thus, suited for the detection of pressure gradients.

- The number of habitats sampled should depend on the questions addressed by sampling objectives. When sampling for more holistic purposes, signal precision should be sacrificed in order to obtain a more comprehensive survey of turlough biodiversity by adopting a multi-habitat sampling approach.

- Season had a significant influence on macroinvertebrate community structure with permanent taxa characterising early season, and ephemeral species increasing in late season samples. Macroinvertebrate community structure and biodiversity varied among months and years. Single samples collected late in the season could lead to an underestimation of turlough biodiversity and reduce quality scores if based on emerged taxa. Turlough sampling should be responsive to variable commencements of flooding. Timing and frequency of sampling should be appropriately stratified depending on monitoring objectives.

- Macroinvertebrate community structure varied with increased nutrient state of the turloughs. Total phosphorus concentrations explained a significant amount of variance in the biological data set and a change in abundance of taxonomic groups with nutrient enrichment was detected. Macroinvertebrate successional pattern seem vulnerable to nutrient enrichment with communities characterised by permanent residents in turloughs, with higher trophic state. Some macroinvertebrate orders and chydorid taxa have the potential to be used as biotic elements for monitoring of ecological change of turloughs.

- Disturbance, defined as the dry phase of a turlough and rapid changes in turlough water levels, markedly influenced macroinvertebrate succession and community structures. High disturbance regimes generally supported lower biodiversity and communities characterised by taxa possessing adaptations to drought.

- Turloughs are inherently variable systems which might negate the development of simple type-specific reference conditions as required for lakes under the WFD. Turlough sampling regimes need a flexible approach and should be geared towards the start of the flooding season and variable hydrocycles.

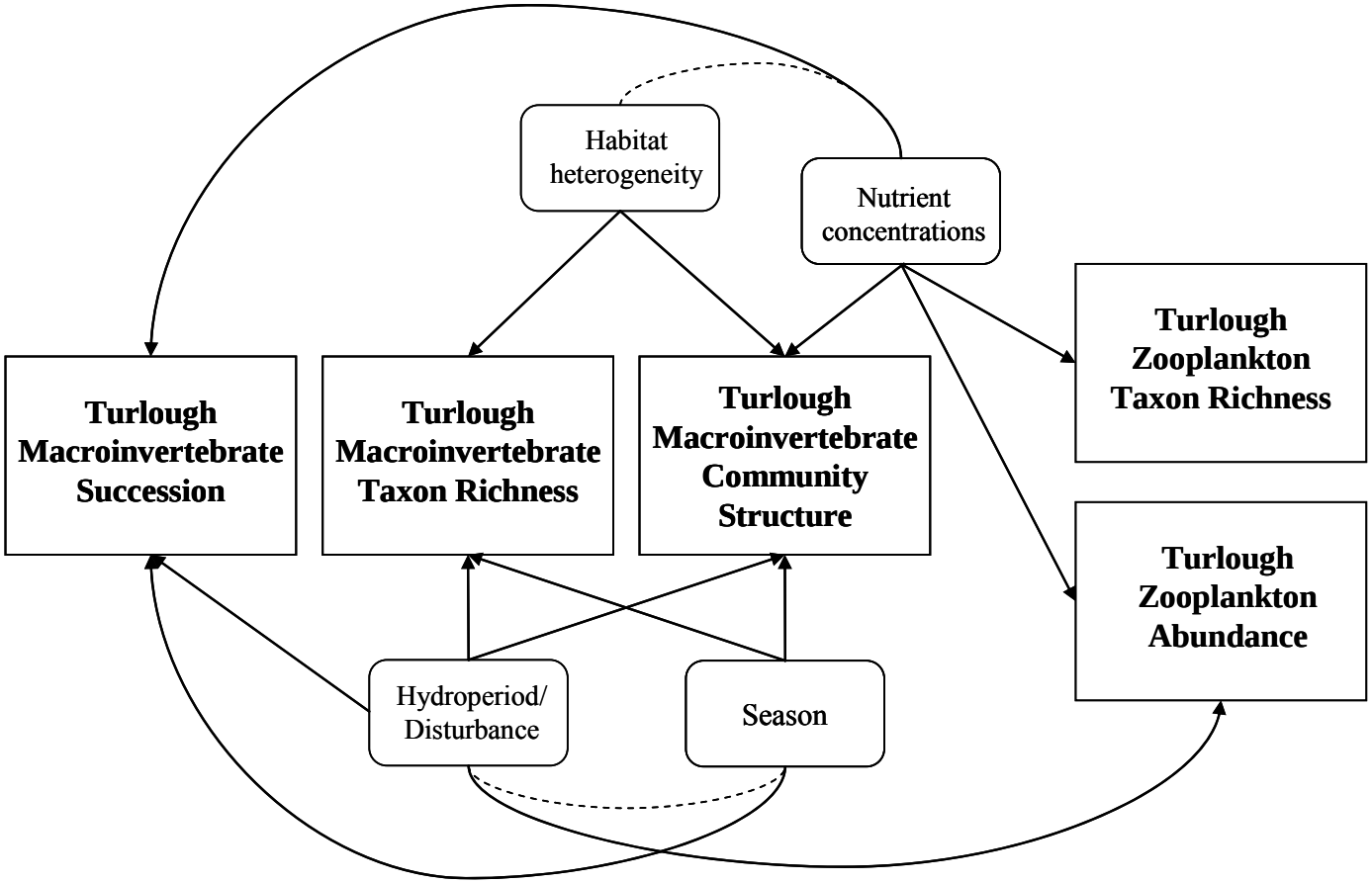

Figure 7.1: Conceptual model of the turlough aquatic invertebrate community, summarizing major findings of this study. Arrows indicate a direct effect on the invertebrate community; dashed lines indicate interactions between factors.

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