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The impact of conifer plantation forestry on the ecology of peatland lakes

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A thesis submitted to the National University of Ireland, Cork, in fulfilment of the requirements for the degree of Doctor of Philosophy

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Declaration

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree. This thesis is the result of my own independent work/investigation, except where otherwise stated.

Signed

Date

Abstract

Blanket bog lakes are a characteristic feature of blanket bog habitats and harbour many rare and threatened invertebrate species. Despite their potential conservation value, however, very little is known about their physico-chemical or biological characteristics in western Europe, and their reference conditions are still unknown in Ireland. Furthermore, they are under considerable threat in Ireland from a number of sources, particularly afforestation of their catchments by exotic conifers. Plantation forestry can potentially lead to the increased input of substances including hydrogen ions (H^+), plants nutrients, dissolved organic carbon (DOC), heavy metals and sediment. The aims of this study were to investigate the effect of conifer plantation forestry on the hydrochemistry and ecology of blanket bog lakes in western Ireland.

Lake hydrochemistry, littoral Chydoridae (Cladocera) and littoral macroinvertebrate communities were compared among replicate lakes selected from three distinct catchment land use categories: i) unplanted blanket bog only present in the catchment, ii) mature (closed-canopy) conifer plantation forests only present in the catchment and iii) catchments containing mature conifer plantation forests with recently clearfelled areas. All three catchment land uses were replicated across two geologies: sandstone and granite.

Lakes with afforested catchments across both geologies had elevated concentrations of phosphorus (P), nitrogen (N), total dissolved organic carbon (TDOC), aluminium (Al) and iron (Fe), with the highest concentrations of each parameter recorded from lakes with catchment clearfelling. Dissolved oxygen concentrations were also significantly reduced in the afforested lakes, particularly the clearfell lakes.

This change in lake hydrochemistry was associated with profound changes in lake invertebrate communities. Within the chydorid communities, the dominance of *Alonopsis elongata* in the unplanted blanket bog lakes shifted to dominance by the smaller bodied *Chydorus sphaericus*, along with *Alonella nana*, *Alonella excisa* and *Alonella exigua*, in the plantation forestry-affected lakes, consistent with a shift in lake trophic. Similarly, there was marked changes in the macroinvertebrate communities, especially for the Coleoptera and Heteroptera assemblages which revealed increased taxon richness and abundance in the nutrient-enriched lakes. In terms of conservation status, despite having the greatest species-quality scores (SQS) and species richness, three of the four International Union for the Conservation of Nature (IUCN) red-listed species of Coleoptera and Odonata recorded during the study were absent from lakes subject to catchment clearfelling.

The relative strengths of bottom-up (forestry-mediated nutrient enrichment) and top-down (fish) forces in structuring littoral macroinvertebrate communities was investigated in a separate study. Nutrient enrichment was shown to be the dominant force acting on communities, with fish having a lesser influence. These results confirmed that plantation forestry poses the single greatest threat to the conservation status of blanket bog lakes in western Ireland. The findings of this study have major implications for the management of afforested peatlands. Further research is required on blanket bog lakes to prevent any further plantation forestry-mediated habitat deterioration of this rare and protected habitat.

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Chapter 1

General Introduction



Dirney's Lough, an example of an upland blanket bog lake located on the Slieve Aughty Mountains.

1.1. Irish peatland

Peat is the accumulated remains of partially decomposed plant material, and forms in active peatlands where the saturated conditions prevent the complete decomposition of organic matter from taking place (Holden et al., 2004; Montanarella et al., 2006). Although peat can form in many types of wetland habitat, a minimum depth of 30 cm is required for it to be designated as a true peatland (Joosten and Clark, 2002). Ireland is recognised as one of the main peat covered regions in the world due to an estimated 13.8 – 17% of the landscape covered by peatland (Hammond, 1981; Connolly et al., 2007). The only other countries in the world to surpass this are Canada and Finland (Doyle, 1990).

There are two main peatland types in Ireland: fens and bogs. Fens are characterised as having a pH generally > 6.0, high calcium (Ca) and bicarbonate (HCO_3) concentrations, with vegetation dominated by graminoids (e.g. *Carex* spp., *Cladium* spp.) and 'brown mosses'. Bogs have a lower pH, generally < 5.0, low Ca concentrations, and chloride (Cl) and sulphate (SO_4) as the main inorganic anions, with vegetation dominated by *Sphagnum* mosses, calcifuge Cyperaceae and ericaceous shrubs (Wheeler and Proctor, 2000; Bragazza et al., 2003). Fens derive their water supply, nutrients and minerals from groundwater, while bogs depend on precipitation and aerial deposition (Gore, 1983). Irish bogs can be subdivided into raised and blanket bogs. Raised bogs, dome-shaped masses of peat which developed from fens in shallow basins, are predominantly found in the central plain of Ireland (Foss et al., 2001). Blankets bogs, which formed between 5100 and 3100 years before present (Tallis, 1998), are found mainly along the western seaboard and high

altitude regions throughout the country where annual precipitation exceeds 1,250 mm (Hammond, 1981; Renou and Farrell, 2005).

Irish blanket bogs can be further divided into three main sub-categories depending on the altitude at which they are situated: i) Lowland Atlantic Blanket Bog which is confined to altitudes < 150 m, ii) Highland Blanket Bog which occurs within the range of 150 – 300 m and iii) Mountain or Upland Blanket Bog which occurs in plateau areas all over Ireland at altitudes > 300 m (Schouten, 1984). Blanket bogs account for less than 3% of the world's peatlands (Holden, 2005). However, the combined area of blanket bogs in Ireland and the UK represents 10 – 15% of the global total of blanket bog (Foss et al., 2001; Eaton et al., 2008), and is, therefore, of international importance. Furthermore, although blanket bogs cover approximately 6% of the Irish land area, only 21% of this habitat remains in relatively intact conditions in Ireland due to peat extraction, drainage associated with agricultural reclamation, and plantation forestry (Foss et al., 2001). Similarly, much of the original blanket bog throughout the rest of Europe has been degraded by human disturbance (Chapman et al., 2003). As a result of this level of exploitation, coupled with its scarcity within the European Union, 'active' examples of this habitat have been listed for conservation under Annex I of the EU Habitats Directive (European Commission, 1992).

1.2. Blanket bog water bodies

Despite being markedly understudied in comparison with other European freshwater habitats (Maitland, 1999), standing waters form an integral part of northern latitude blanket bog habitat and range in size from small pools to larger lakes (Lindsay et al.,

1988). Blanket bog lakes provide a suitable habitat for many rare species and those with restricted distributions (Lindsay et al., 1988; Downie et al., 1996; Preston and Croft, 1997), and have a particularly species-rich aquatic invertebrate fauna. For example, three of Scotland's nationally rarest odonate species, *Aeshna caerulea* (Ström), *Somatochlora arctica* (Zetterstedt) and *Leucorrhinia dubia* (Vander Linden) inhabit blanket bog pools (Maitland, 1999). Despite being listed as water-dependent Annex I habitats of the EU Habitats Directive (European Commission, 1992), hitherto in Ireland these habitats have been inadequately studied to allow for the characterisation of their baseline physico-chemical and biological reference conditions (Curtis et al., 2009). Such reference conditions are a prerequisite to help ensure that the ecological status of these habitats is protected against any further human disturbance associated with the contiguous blanket bog habitat.

1.3. Conifer plantation forestry in Ireland

Despite the introduction of grants to encourage non-native plantations in the 1700s (O'Carroll, 1984), it was not until the 1950s that the Irish government decided to increase the rate of afforestation significantly (Renou and Farrell, 2005), since when plantation forest cover has continued to expand. The annual expansion of forest area in Ireland from 1990 to 2010 was approximately 6% (FAO, 2010). Within the EU, this is second only to Iceland which has an annual expansion of approximately 17% for the same period (FAO, 2010). Currently, plantation forests cover approximately 10% of the Irish landscape, 80% of which is comprised of exotic conifers (NFI, 2007). The majority of Ireland's plantation cover is composed of sitka spruce (*Picea sitchensis* Bongard) and lodgepole pine (*Pinus contorta* Douglas ex Louden), both of

which are planted in large monospecific stands. The ability of sitka spruce to grow in moist soil conditions (Joyce and O'Carroll, 2002), facilitated this large expansion of forest cover as the majority of the forest estate is located on peat soils (NFI, 2007). Although popular in the Nordic countries and the former Soviet Union as early as the 17th century (Paavilainen and Päivänen, 1995), peatland forestry was not widely practiced in Ireland until the 1950s, when blanket bog was seen as providing an opportunity for large-scale plantations on treeless land that was unused, apart from some extensive grazing (Renou and Farrell, 2005).

1.4. Effects of plantation forestry on the hydrochemistry of surface waters

The effect of forestry on standing waters is less frequently studied than for running waters (Laird and Cumming, 2001; Northcote and Hartman, 2004). Many studies on streams have shown that conifer plantation forestry practices, especially clearfelling, have the potential to affect the hydrochemical and ecological state of lakes by increasing catchment loadings of plant nutrients, heavy metals, both dissolved and particulate organic matter, major ions, as well as increasing acidity (Kortelainen and Saukkonen, 1998; Binkley et al., 1999; Pühr et al., 2000; Neal et al., 2001; Vuorenmaa et al., 2002; Cummins and Farrell, 2003a, 2003b; Harriman et al., 2003; Neal et al., 2004a, 2004b; Feller, 2005; Kreutzweiser et al., 2008; Ågren et al., 2010; Ågren and Löfgren, 2012). The potential hydrochemical and ecological impacts of conifer plantation forestry on Irish surface waters is even higher due to the majority of plantation forests having been planted on peat soils, which is known to pose the greatest risk to receiving waters (Hutton et al., 2008). Blanket bog soils are

inherently nutrient-deficient and require fertilisers to yield a commercially viable tree crop (Smethurst, 2010). However, the ability of peat soils to retain these applied fertilisers is extremely poor (Cuttle, 1983). Plantation forestry on organic-rich peatland soils is, therefore, regularly associated with leaching of phosphorus (P), nitrogen (N) and dissolved organic carbon (DOC) to receiving surface waters (Cummins and Farrell, 2003a, b; Renou and Farrell, 2007; Hutton et al., 2008).

1.5. Ecological impacts of plantation forestry on surface waters

The impact of plantation forestry operations on aquatic biota has also been studied more in lotic rather than lentic systems. The majority of stream-based studies have focused on the impacts of forestry-driven stream acidification and associated aluminium (Al) toxicity, as exotic conifers are recognised as being efficient scavengers of atmospheric pollutants (e.g. sulphur (S) and N compounds) (Reynolds et al., 1994). The main finding of such studies is a major shift in benthic macroinvertebrate communities associated with the loss of acid-sensitive species of Ephemeroptera, Plecoptera and Trichoptera (Ormerod et al., 1993, 2004; Ormerod and Durance, 2009; Feeley et al., 2011). Other studies have also documented changes in benthic macroinvertebrate and periphyton communities (Kiffney et al., 2003; Nislow and Lowe, 2006), as well as microbial decomposition rates (Benfield et al., 2001), due to the reduced riparian shading and increased nutrient availability post-clearfell. Increased sediment runoff to streams has also been shown to affect stream invertebrates (Death et al., 2003). In contrast, studies investigating the impact of forestry on lake biota have revealed a wide range of results, the majority showing slight and short lived changes in algal, zooplankton, zoobenthos or fish communities

(Paterson et al., 1998; Rask et al., 1998; Patoine et al., 2000; Planas et al., 2000; Scrimgeour et al., 2000; Laird and Cumming, 2001, Laird et al., 2001; Bredeisen et al., 2002). The few studies to document significant changes are those which have investigated chrysophyte and diatom communities (Lott et al., 1994; Koster et al., 2005).

1.6. Global stressors of lake habitat quality

Globally, there are numerous stressors which affect the functioning of lake ecosystems. These include eutrophication, acidification, contamination by heavy metals and organochlorines, and introductions of exotic species (Brönmark and Hansson, 2002). Of these, it is generally accepted that eutrophication is one of the most pervasive problems associated with lake water quality globally (Vadeboncoeur et al., 2003). Inputs of N, and particularly P, into receiving waters are recognised as one of the main causes of eutrophication of freshwater ecosystems (Carpenter et al., 1998; Smith et al., 1999; Conley et al., 2009). Since the seminal studies by Vollenweider (1968) and Schindler (1974), there have been many studies investigating the impact of eutrophication on all of the main biological compartments of lake ecosystems.

Eutrophication results in a shift from benthic to pelagic dominance of lake primary production as a result of increased phytoplankton biomass attenuating light within the water column (Vadeboncoeur et al., 2003). Phytoplankton communities can also shift towards a larger-bodied community due to the heavy grazing by *Daphnia* spp. and other large zooplankton on small, readily ingestible phytoplankton (Kalff and Knoechel, 1978; Leibold, 1989; Watson et al., 1992; Mazumder, 1994).

Pelagic zooplankton communities also respond to eutrophication by undergoing a reduction in species richness, particularly for cladoceran species (Jeppesen et al., 2000). A similar reduction in size of the littoral zooplankton (Chydoridae, Cladocera) has been noted, with the smaller-bodied *Chydorus sphaericus* (O. F. Müller) usually increasing in abundance with increasing lake trophicity (Hofmann, 1996; Vijverberg and Boersma, 1997; Brodersen et al., 1998a; de Eyto et al., 2003). Pelagic zooplankton biomass usually increases with increasing trophicity for all the major groups; however, there is usually a marked decrease in mean body size of *Daphnia* spp. and other smaller cladocerans (Jeppesen et al., 2000). For benthic macroinvertebrates, many studies have revealed a reduction in species richness, while the abundances of Chironomidae, tubificid oligochaetes and crustaceans usually increase (Brodersen et al., 1998b; Tolonen et al., 2001; Brauns et al., 2007). There has been much research investigating the impact of eutrophication on lake macrophyte communities. Submerged macrophyte coverage and species richness both generally decrease with increasing trophic conditions (Moss et al., 2003; James et al., 2005; Søndergaard et al., 2010). Eutrophication has also been shown to cause significant changes in fish communities, which at least in Europe, typically follows the sequence of dominance from salmonids-coregonids-percids-cyprinids with increasing lake trophicity (Nümann, 1972; Persson et al., 1991; Jeppesen et al., 2000).

1.7. Study objectives

Despite the fact that the rate of peatland afforestation has declined in the previous two decades (Black et al., 2009), many of these blanket bog plantations are now reaching harvestable age and concerns are mounting as to the potential impacts of

leachate on receiving aquatic systems as a result of clearfell harvesting. As Irish forests guidelines have only been in existence since 1991, much of the current harvestable crop was established pre-guidelines and is, therefore, lacking in measures such as buffer zones adjacent to surface waters, installation of drains and sediment traps, which were created to provide best management practices to minimise adverse impacts of forestry operations on surface waters. The aims of this present study, therefore, were to determine the influence of conifer plantation forestry operations on the hydrochemistry and ecology of blanket bog lakes in western Ireland.

Chapter 2 describes baseline physico-chemical and biological data for two types of blanket bog lake in western Ireland. The hydrochemistry, littoral Chydoridae (Cladocera), littoral macroinvertebrate and macrophyte communities were surveyed from a group of 13 study lakes located on lowland (Atlantic) blanket bog in coastal regions and on upland blanket bog in inland regions distant from the sea.

Chapter 3 examines the effect of conifer plantation forestry on the hydrochemistry of blanket bog lakes. The hydrochemistry of 26 lakes was assessed, 13 of which were studied in chapter 1, from three distinct catchment land use categories: i) unplanted blanket bog only present in the catchment, ii) mature (closed-canopy) conifer plantation forests only present in the catchment and iii) catchments containing mature conifer plantation forests with recently clearfelled areas. All three catchment land uses were replicated across two geologies: sedimentary (sandstone) and igneous (granite). To further investigate potential differences in the biochemical lability of TDOC emanating from afforested catchments, water samples were

collected and compared from three separate streams from a nearby recently clearfelled site (Glennamong): i) a stream draining from the clearfelled site, ii) a stream draining from the mature plantation and iii) a stream draining from nearby undisturbed blanket bog.

Chapter 4 details how forestry-mediated hydrochemical change affects the littoral chydorid communities of blanket bog lakes. This was examined by comparing the littoral chydorid communities and lake hydrochemistry from the same 26 lakes studied in chapter 3.

Chapter 5 documents the impact of conifer plantation forestry on the conservation value of blanket bog lakes. The aquatic Coleoptera, Heteroptera and Odonata assemblages were used to compare the conservation values of the same 26 lakes studied in the previous two chapters (3 & 4).

Chapter 6 describes an investigation into the relative influences of both plantation forestry-mediated bottom-up (resources) and top-down (fish) forces on littoral macroinvertebrate community structure of blanket bog lakes. This study was carried out on six lakes which were selected in a paired design (fish present/absent) across three bands of forestry-mediated nutrient status: i) low nutrients, ii) medium nutrients and iii) high nutrients. Three of the fishless lakes were a subset of the 26 studied in previous chapters, while the three lakes containing fish populations were newly selected lakes for this study.

Chapter 7 synthesises the findings of each individual section of the research. Overall conclusions from all aspects of the study on the effects of conifer plantation forestry on the hydrochemistry and ecology of blanket bog lakes are discussed. Recommendations for areas of further research, conservationists, policy makers and forestry practitioners are also presented.

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Chapter 2

Variation in the physico-chemical and biological characteristics between upland and lowland (Atlantic) blanket bog lakes in western Ireland



An example of an upland blanket bog lake (**top**) and a lowland blanket bog lake (**bottom**). The top picture was taken during late spring, while the bottom picture was taken during winter.

2.1. Summary

Small shallow lakes are a characteristic feature of blanket bog habitats. The biotic assemblages of these lakes can be particularly species rich, especially in terms of the aquatic invertebrate fauna. Despite their potential conservation value, relatively little is known about their physico-chemical or biological characteristics in northern Europe in comparison with other freshwater habitats, and their undisturbed reference conditions are still unknown in Ireland. Upland and lowland blanket bog lakes were surveyed, across both sedimentary (sandstone) and igneous (granite) geologies, to compare baseline physico-chemical and biological conditions for blanket bog lakes in western Ireland. A comprehensive data set of water chemistry, littoral Chydoridae, littoral macroinvertebrate and aquatic macrophyte taxa were collected from all lakes over a 12-month period beginning in March 2009. The main difference in lake hydrochemistry was that the lowland lakes, situated at lower altitude and in closer proximity to the coast than the upland lakes, had significantly higher conductivity and major ion (sodium [Na], chloride [Cl], magnesium [Mg], potassium [K] and sulphate [SO₄]) concentrations due to the greater influence of atmospheric (sea spray) deposition. The upland lakes were also significantly cooler and had higher concentrations of total phosphorus (TP). Differences were also evident between the upland and lowland lakes in the chydorid, littoral macroinvertebrate and macrophyte communities, primarily due to the marine-driven hydrochemical variation and differences in benthic substrate. The chemical effect of marine deposition appeared to have a much greater impact on lake hydrochemistry and biology than either underlying geology or altitude. This is the first study of its kind to be carried out on blanket bog lakes in Ireland. More information is needed

on the biology of such lakes, together with research on anthropogenic drivers of biotic communities, if significant loss of biodiversity associated with agriculture, peat extraction, burning, wind farm developments and conifer afforestation is to be prevented.

2.2. Introduction

Blanket bog has a restricted distribution in Europe, being confined to regions of high precipitation excess, usually in upland areas or in lowland areas where geomorphic conditions maintain saturation (Holden et al., 2004). A high percentage of extant European blanket bog is found in Ireland, with an estimated area of 773,860 – 1,063,499 ha of blanket bog present (NPWS, 2007). Much of the original blanket bog in Europe, however, including Ireland, has been altered and degraded by human disturbance (Chapman et al., 2003). The high level of exploitation and disturbance of this restricted habitat has led it to being protected under Annex I of the EU Habitats Directive (European Commission, 1992).

Small lakes are a characteristic feature of northern latitude blanket bog habitat and range in size from small pools to lakes with a mineral benthic substrate (Lindsay et al., 1988); these latter can have clear water and well-developed macrophyte communities, which distinguishes them from the former, which tend to be dystrophic in nature. Blanket bog lakes provide a habitat for many rare species and those with restricted distributions (Downie et al., 1996; Preston and Croft, 1997). Their aquatic invertebrate fauna can be particularly species rich, especially in terms of Odonata, Coleoptera and Heteroptera (Downie et al., 1998; Towers, 2004). In Scotland, three of the nationally rarest odonate species, *Aeshna caerulea* (Ström), *Somatochlora arctica* (Zetterstedt) and *Leucorrhinia dubia* (Vander Linden) inhabit blanket bog pools (Maitland, 1999). Other than a few studies, which were mainly non habitat-specific (Gorham, 1957; Bowman, 1986, 1991; Aherne et al., 2002; Burton and Aherne, 2012), relatively little information exists on the physico-

chemical and biological characteristics of blanket bog lakes in Ireland, despite their potential international conservation importance.

As for the blanket bog habitat itself, blanket bog lakes are particularly vulnerable to environmental degradation. Drainage and fertilisation associated with agricultural reclamation, peat extraction, overgrazing by sheep, burning, wind farm developments and extensive, large-scale conifer afforestation can all result in deleterious changes to the peat soil (Holden et al., 2004; NPWS, 2007). Such changes can impact upon the physico-chemical conditions of these blanket bog lakes.

The physico-chemical and biological conditions of blanket bog lakes will be determined to a great extent by the *Sphagnum* peat itself, which constitutes almost the entire catchment soil type. The geomorphic setting, including altitude, latitude, proximity to the coast and underlying geology of individual lakes within the habitat range of blanket bog may also influence conditions to some degree. Reference conditions should, therefore, be described for lakes encompassing the natural range of physico-chemical factors for this habitat.

In Ireland, determining the ecological status of blanket bog lakes is currently hindered by the lack of baseline physico-chemical and biological reference conditions for such habitat types (Curtis et al., 2009). Reference conditions can be defined as the point where “the values of the physico-chemical, hydromorphological and biological quality element should correspond to totally or nearly totally undisturbed conditions” (Wallin et al., 2003). One of the requirements of the EU Water Framework Directive (European Commission, 2000), is that member states comply with any standards or objectives implemented for Natura 2000 protected sites which are water-dependent (Curtis et al., 2009). Considering the water-dependent Annex I habitats listed in the EU Habitats Directive (European

Commission, 1992), Irish blanket bog lakes may be classified as one of three habitat types: oligotrophic waters containing very few minerals of sandy plains (*Littorelletalia uniflorae*) [3110], oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or *Isoëto-Nanojuncetea* [3130] or natural dystrophic lakes and ponds [3160]. Assigning lakes to a particular habitat type in the Habitats Directive can be challenging and subjective (Evans, 2006; Irvine, 2009). Considering the paucity of baseline data for such habitat types in Ireland, the possibility of producing a clearer delineation for these habitat types in Ireland is unlikely without further research.

Blanket bogs are found at lower altitude, coastal areas and higher altitude, inland areas of western Ireland (NPWS, 2007). The aim of this study was to compare baseline physico-chemical and biological characteristics between lakes located on lowland (Atlantic) blanket bog in coastal regions and on upland blanket bog in regions distant from the sea, in western Ireland.

2.3. Materials and methods

2.3.1. Study sites

Potential study lakes in areas of upland and lowland blanket bog throughout the south-west, mid-west and west of Ireland were identified using ArcGIS (ESRI ArcMap v.9.3). Thirteen lakes were selected for study, based on their similar size (≤ 4 ha) and catchment land use (blanket bog comprised 100% of the catchment). Six of the lakes were located on upland blanket bog and seven were located on lowland blanket bog (Fig. 2.1; Table 2.1). The upland blanket bog lakes were located in the south-west and mid-west of Ireland and underlain by sedimentary (sandstone) geology. The lowland blanket bog lakes were all located in the west of Ireland and underlain by igneous (granite) geology (Fig. 2.1; Table 2.1).

The plant species surrounding the study lakes were typical blanket bog species (Fossitt, 2000). These included purple moor-grass (*Molinia caerulea* (Linnaeus)), cross-leaved heath (*Erica tetralix* Linnaeus), deergrass (*Scirpus cespitosus* Linnaeus), common cottongrass (*Eriophorum angustifolium* Roth), bog asphodel (*Narthecium ossifragum* (Linnaeus) Hudson) and white beak-sedge (*Rhynchospora alba* (Linnaeus) Vahl).

Although these lakes were small and oligotrophic in nature, fish were nonetheless observed in several lakes that had connections to downstream running waters. Due to the inaccessibility of the lakes, conventional sampling techniques (gill and fyke netting) were infeasible. Instead, populations were assessed using baited rod and line surveys with a standardised sample effort across all lakes. This technique has been shown to provide suitable estimates of fish relative abundance

(Haggarty and King, 2006). Sampling in this manner was carried out in all lakes in June and September 2009. Fish populations were present in seven of the study lakes, three of the upland lakes and four of the lowland lakes. Eel (*Anguilla anguilla* (Linnaeus)), brown trout (*Salmo trutta* Linnaeus) and three-spined stickleback (*Gasterosteus aculeatus* Linnaeus) were the most common. One study lake contained a small population of perch (*Perca fluviatilis* Linnaeus) (Table 2.1). Fish populations in all lakes were extremely low.

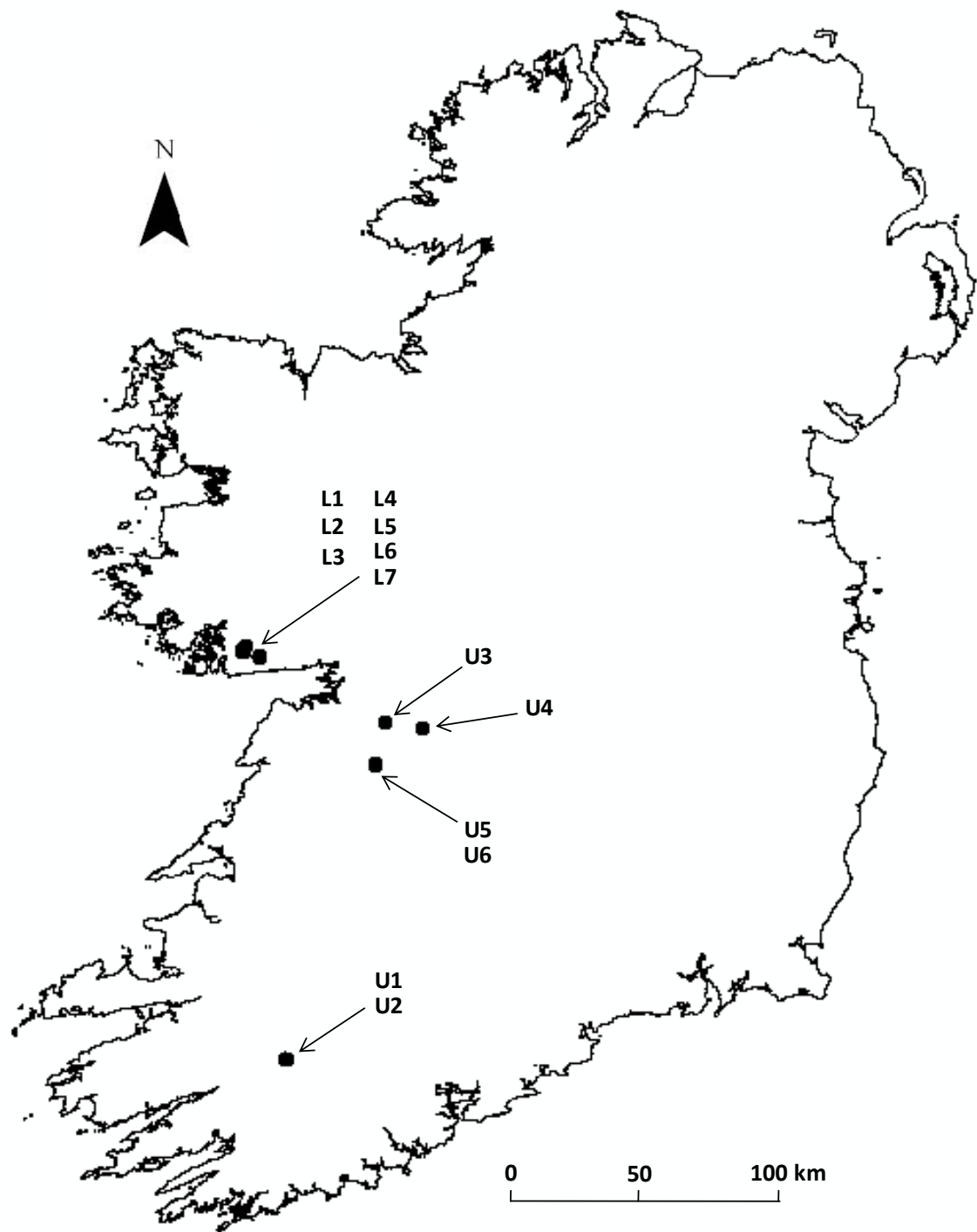


Figure 2.1. Map of Ireland showing the location of the 13 study lakes (U = upland blanket bog and L = lowland blanket bog).

Table 2.1. Geographic location and physical characteristics of the 13 study lakes. Blanket bog classification is based on Fossitt (2000) habitat classification scheme.

Lake code	Latitude/Longitude	Altitude (m)	Lake area (ha)	Mean depth (m)	Catchment area (ha)	Fish present	Underlying geology	Blanket bog classification
U1	N 51°58.953' W 009°11.188'	426	1.6	1.6	2.3	No	Green-grey sandstone & purple siltstone	Upland
U2	N 51°58.960' W 009°10.916'	429	2.2	2.2	17.6	No	Green-grey sandstone & purple siltstone	Upland
U3	N 53°04.899' W 008°40.568'	282	0.9	2.5	10.0	No	Mudstone, siltstone, conglomerate	Upland
U4	N 53°03.747' W 008°28.646'	183	1.2	1.5	10.0	Yes	Mudstone, siltstone, conglomerate	Upland
U5	N 52°56.533' W 008°43.845'	273	0.5	2.1	11.6	Yes	Mudstone, siltstone, conglomerate	Upland
U6	N 52°56.770' W 008°43.710'	262	1.4	1.6	11.5	Yes	Mudstone, siltstone, conglomerate	Upland
L1	N 53°19.239' W 009°25.840'	93	1.2	2.4	12.2	No	Aphyric fine grained granite	Lowland
L2	N 53°18.354' W 009°26.926'	108	1.0	1.4	5.3	Yes	Aphyric fine grained granite	Lowland
L3	N 53°18.210' W 009°26.981'	100	1.2	2.3	15.7	Yes	Aphyric fine grained granite	Lowland
L4	N 53°18.511' W 009°27.485'	80	1.2	3.1	52.7	Yes	Monzogranite, small megacrysts	Lowland
L5	N 50°18.508' W 009°27.379'	86	0.5	2.3	5.2	No	Monzogranite, small megacrysts	Lowland
L6	N 50°17.207' W 009°21.697'	73	4.0	2.5	72.6	Yes	Monzogranite, mafic, megacrystic	Lowland
L7	N 50°17.232' W 009°21.436'	77	1.4	1.8	6.8	No	Monzogranite, mafic, megacrystic	Lowland

2.3.2. Water chemistry sampling and analysis

Water samples were collected in acid-washed polypropylene bottles from the littoral zone of each lake at a similar depth (0.6 m) and distance (7 m) from shore, bimonthly for 12 months, beginning in March 2009. A custom-made floatation device, with a pre-marked length of cord attached, was used to standardise the distance from shore and depth from which the samples were collected. Water samples were stored at 4°C in a cooler box and transported to the laboratory for analysis within 24 hours after collection. Conductivity, dissolved oxygen and temperature were measured on site using WTW portable meters. pH was determined using a WTW pH meter (pH330i) following 2-point calibration with WTW technical buffer solutions (4.01 and 7.00). Alkalinity was measured by Gran titration (Mackereth et al., 1989). Colour was determined by the manual colorimetric method, using diluted HACH colour standards for calibration (APHA, 2005). Total dissolved organic carbon (TDOC) was determined using Shimadzu Total Organic Carbon Analyzer. Ammonia was determined by automated Lachat Quik-Chem 8000 FIA on 0.45 µm-filtered samples (salicylate method QuikChem Method 10-107-06-3-D). Soluble reactive phosphorus (SRP) was determined using the automated Lachat Quik-Chem 8000 FIA on 0.45 µm-filtered samples (QuikChem Method 10-115-01-1-B), based on Murphy and Riley (1962). Total oxidised nitrogen (TON) was determined by automated Lachat Quik-Chem 8000 FIA with copper-amalgamated cadmium column for reduction to nitrite followed by colorimetric detection (QuikChem Method 10-107-04-1-C). Total phosphorus (TP) was determined using the molybdate-ascorbic acid method (Murphy and Riley, 1962), following digestion of the unfiltered sample with persulphate and sulphuric acid. Total nitrogen (TN)

was determined using the automated Lachat Quik-Chem 8000 FIA method (QuikChem Method 10-107-04-1-C) following persulphate oxidation of unfiltered sample with potassium persulphate and boric acid (Grasshoff et al., 1983). Sodium (Na), magnesium (Mg), chloride (Cl) and sulphate (SO_4) were determined by Ion Chromatography (QuikChem Method 10-501-00-1-A/C). Potassium (K), calcium (Ca) and iron (Fe) were determined by the AA flame method. Manganese (Mn) and total monomeric aluminium (tot. Al) (i.e. filtered at 45 μm) were determined by the AA furnace method. Chlorophyll *a* was determined by the manual colorimetric method after extraction with methanol (HMSO, 1983). All samples were analysed by the Aquatic Services Unit (ASU), University College Cork, Ireland. The ASU regularly participates in an international laboratory proficiency scheme (Aquacheck) to ensure the quality of the data generated. Samples were routinely QC checked by an external laboratory.

Marine-derived ions were estimated to determine the relative influence of sea-salt spray on lake hydrochemistry. Marine ions were estimated based on their ratios to Cl in seawater (Henriksen and Posch, 2001). The non-marine fraction is subsequently calculated as the difference between total and marine concentrations (in $\mu\text{eq l}^{-1}$). Negative concentrations of ions can result from variations in deposition, such as high sea-salt inputs or variation in deposition ratios with increasing distance from the sea (Möller, 1990). The concentrations of organic acids were estimated using the methodology based on pH and DOC developed by Oliver et al. (1983).

2.3.3. Chydoridae sampling

Chydoridae were sampled by a semi-quantitative method which involved slowly sweeping a hand-held sweep net (100 μ m mesh, 0.15 m diameter frame) horizontally both inside and outside a stand of vegetation for 30 seconds in the littoral zone of each lake. Mineral benthic substrates were avoided during sampling as this habitat type was not represented in all lakes. Samples were transferred to sealed plastic storage containers and were preserved using 70% ethanol. Littoral chydorids were sampled bimonthly for 12 months, beginning in March 2009.

All zooplankton were counted and identified from randomly-selected 5 ml subsamples using a 40x binocular stereo microscope, until a minimum of 50 individuals of the most common species of chydorid had been identified. All chydorids were identified to species level using standard identification keys (Scourfield and Harding, 1966; Amoros, 1984).

2.3.4. Littoral macroinvertebrate sampling

Littoral macroinvertebrates were sampled in April, June and September 2009 using two separate methods: activity traps and multihabitat sweeps. Ten baited activity traps were used to sample the mobile predatory species in each lake, similar to Downie et al. (1998). The traps were of a submerged funnel and bottle design, with the funnel inserted into the bottle. The aperture diameter of the circular entrance was 22 mm, and the wider funnel opening was 100 mm. The total length of the trap was 230 mm. Traps were submerged and placed in all available mesohabitats per lake. Traps remained *in situ* for three consecutive days during each sampling period.

Mesohabitats included submerged, floating and emergent aquatic vegetation, mineral benthic substrate and peat bank. Not all mesohabitats were available at each lake. Multihabitat sweeps, recommended by the UK Pond Survey (Biggs et al., 1998), were also used for less mobile species. A standard 1 mm mesh size pond net (frame size 0.20 x 0.25 m) was used for sampling. The four-minute sampling time was divided equally among the proportions of different mesohabitats present in each lake. Samples were transferred into plastic bags and preserved using 70% ethanol. All macroinvertebrate individuals were identified to the furthest practical taxonomic level. Macroinvertebrates were identified using standard identification keys (Hynes, 1967; Elliott and Mann, 1979; Hammond, 1983; Elliott et al., 1988; Friday, 1988; Savage, 1989; Smith, 1989; Edington and Hildrew, 1995; Nilsson and Holmen, 1995; Elliott, 1996; Nilsson, 1996; Nilsson, 1997; Wallace et al., 2003).

2.3.5. Macrophyte surveys

Macrophytes were surveyed by walking and wading the perimeter of each study lake. Only species listed in the standard wetland plant list of the UK Pond Survey (PS) method (Biggs et al., 1998) were recorded. The relative abundance of submerged, floating and emergent plant species, as defined in the PS method, was also recorded. The macrophytes were recorded in April and June 2009, to include both early and late flowering species. All macrophytes were identified using standard identification keys (Haslam et al., 1982; Preston and Croft, 1997).

2.3.6. Statistical analyses

Principal component analysis (PCA) was performed, using PRIMER 6 (PRIMER-E, UK), to determine patterns in the lake physico-chemical data. The ordination was based on a Euclidean distance matrix derived from normalised physico-chemical data, with transformations (square-root and fourth-root) of variables where necessary.

Analysis of variance (ANOVA) was performed using PASW Statistic 17, to test for significant among-lake differences in PC axis scores and water chemistry variables with respect to blanket bog type (upland and lowland). Prior to performing ANOVAs, normality and homogeneity of variances were tested using Kolmogorov-Smirnov and Levene's tests, respectively. The ANOVA models were calculated on the basis of Type III sums of squares to take the unbalanced design into account. Dependent variables were transformed where necessary to fulfil the requirements of the parametric tests.

Non-metric multi-dimensional scaling (NMDS) analysis was performed, using PRIMER 6, to determine among-lake patterns in the chydorid and littoral macroinvertebrate communities as it can be used with non-normal and zero rich data (McCune and Grace, 2002). The multihabitat sweep and activity trap data were pooled for the NMDS analysis of the littoral macroinvertebrate communities. The goodness-of-fit associated with each NMDS is given by a stress value, which is obtained as the regression of the interpoint distances from the plot on the corresponding dissimilarities (Clarke and Warwick, 1994). NMDS ranks points in low-dimensional space such that the relative distances apart of all points are in the same rank order as the relative dissimilarities of the samples (Clarke and Gorley,

2006). The ordination was based on a Bray-Curtis dissimilarity matrix. Species abundances were averaged over the sampling period and $\log(x + 1)$ transformed to reduce the impact of dominant species on the analysis. Species comprising of less than 3% abundance of any individual community were excluded from the analysis. The final solutions for each physico-chemical and community analysis were based on 999 permutations.

Analysis of Similarity (ANOSIM; 999 permutations) was performed, using PRIMER 6, to test for significant among-lake differences in communities with respect to blanket bog type (upland and lowland). This analysis is an approximate non-parametric analogue of the standard univariate ANOVA, and it uses the R statistic to test for differences between groups ($R = 0$, no differences; $R = 1$, all dissimilarities between groups are larger than dissimilarity within groups). The BIO-ENV procedure was performed, using PRIMER 6, to determine the physico-chemical variables that best explained the patterns observed in the NMDS ordinations for both the chydorid and littoral macroinvertebrate communities. BIO-ENV maximises rank correlations between the similarity matrices calculated from the community data and from combinations of the environmental variables (Clarke and Ainsworth, 1993).

Community metrics including mean taxon richness and Shannon diversity (H), as well as total abundance per sample were also calculated for the chydorid and littoral macroinvertebrate communities. Mann-Whitney U tests were carried out in PASW Statistic 17 to test for differences in the biotic attributes of the lakes.

2.4. Results

2.4.1. Physico-chemical characteristics

PCA of the 26 physico-chemical variables from the 13 lakes showed that there was a clear separation between the upland and lowland lakes (Fig. 2.2). PC axes 1, 2 and 3 accounted for 33.2%, 17.9% and 14.9% of the total variance, respectively. The mean PC axis 1 scores differed significantly between lake types [$F(1, 11) = 44.012$, $p < 0.001$]; however, there was no significant difference between the mean PC axis 2 scores [$F(1, 11) = 0.372$, $p = 0.554$]. A complete list of water chemistry values for all study lakes can be seen in Table 2.2.

The higher altitude upland lakes scored positively on PC axis 1, and were associated with higher concentrations of TP, chlorophyll *a*, total monomeric Al, SRP, TN, TDOC and TON, and greater colour (Fig. 2.2). Conversely, lowland lakes scored negatively on PC axis 1 and were associated with higher temperature, conductivity, pH and alkalinity values, as well as greater Na, Cl, Mg, Ca, SO₄, K, Fe, Mn and dissolved oxygen concentrations (Fig. 2.2). The lowland lakes were also associated with larger catchment and lake areas, as well as greater depths (Fig. 2.2). PC axis 2 did not differentiate between the upland and lowland lakes (Fig. 2.2).

Univariate analysis of water chemical parameters revealed significant differences between the upland and lowland lakes for a number of variables (Table 2.3). The lowland lakes had significantly higher concentrations of SO₄, Na, Cl, Mg and K, as well as greater conductivity and temperature values (Table 2.3). The upland lakes had significantly higher concentrations of TP, pH, alkalinity, dissolved oxygen, chlorophyll *a*, colour, TDOC, SRP, TN, TON, ammonia, Ca, total

monomeric Al, Mn and Fe values did not significantly differ between the upland and lowland lakes (Table 2.3).

Estimation of the marine fractions for major ions revealed that sea-salt spray had a major influence on the hydrochemistry of the blanket bog lakes, particularly for the lowland lakes (Table 2.4). Sea-salt spray was the overriding source of Na, Mg and K for all lakes. The dominant source of SO₄ for the upland lakes was non-marine, while it was predominantly marine-derived in the lowland lakes (Table 2.4). The dominant source of Ca for all lakes was non-marine (Table 2.4). Concentrations of organic acids were somewhat higher in the upland lakes (Table 2.5).

Traditionally, lake trophic status in Ireland has been assessed using a modified version of the Organisation for Economic Cooperation and Development (OECD) scheme which was based on annual maximum chlorophyll *a* concentration (McGarrigle et al., 2010). Under this scheme, four of the study lakes were classified as mesotrophic and nine as oligotrophic (Table 2.6).

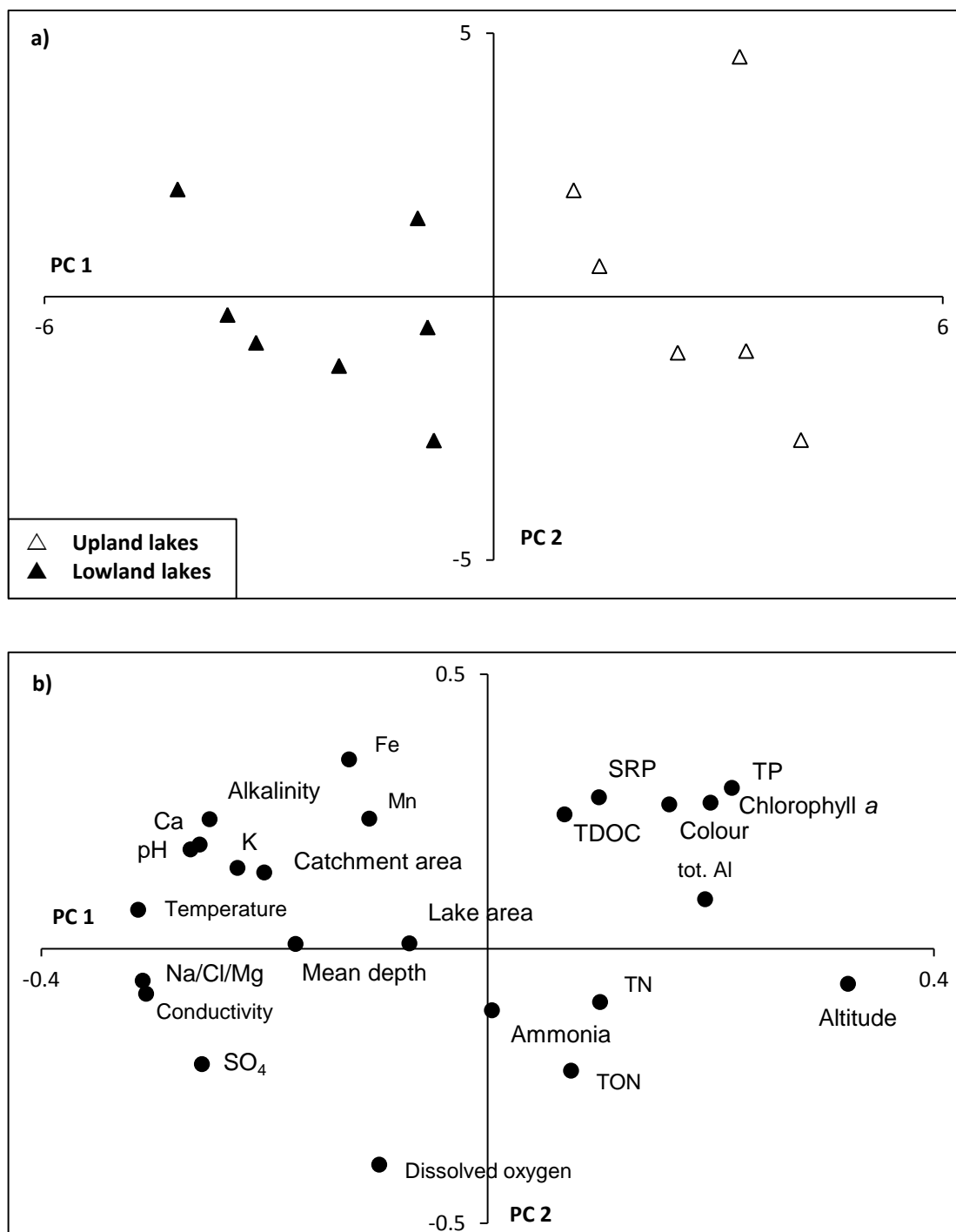


Figure 2.2. Principal component analysis (PCA) ordinations indicating a) the variation in the physico-chemical state among the 13 study lakes and b) the variable loadings on PC axis 1 and PC axis 2.

Table 2.2. Water chemistry of the 13 study lakes showing the mean values and range (min–max) over the 12-month sampling period (n: upland = 6 and lowland = 7).

Chemical variable	Upland		Lowland	
	Mean	Range	Mean	Range
pH (median \pm 95% C.I.)	5.16	4.69 – 5.61	5.62	4.81 – 6.18
Alkalinity (mg l ⁻¹ CaCO ₃)	0.17	-0.93 – 1.43	0.93	-0.38 – 2.62
Conductivity (μ S cm ⁻¹)	36.49	32.57 – 42.75	72.13	63.42 – 76.38
Temperature (°C)	9.91	9.38 – 10.32	10.84	10.40 – 11.57
Dissolved oxygen (mg l ⁻¹)	10.89	10.41 – 11.19	11.14	10.80 – 11.34
Chlorophyll <i>a</i> (μ g l ⁻¹)	5.77	2.82 – 12.49	3.67	2.43 – 5.70
Colour (mg Pt. Co. l ⁻¹)	115.50	89.93 – 138.00	88.90	50.50 – 141.00
TDOC (mg l ⁻¹)	8.21	4.44 – 10.80	7.18	5.56 – 9.53
TP (mg l ⁻¹)	0.011	0.008 – 0.016	0.007	0.005 – 0.013
SRP (mg l ⁻¹)	0.001	0.001 – 0.003	0.001	0.001 – 0.002
TN (mg l ⁻¹)	0.50	0.44 – 0.62	0.48	0.33 – 0.65
TON (mg l ⁻¹)	0.03	0.01 – 0.07	0.02	0.01 – 0.06
Ammonia (mg l ⁻¹)	0.02	0.02 – 0.03	0.03	0.02 – 0.04
SO ₄ (mg l ⁻¹)	1.96	1.55 – 2.12	2.94	2.57 – 3.34
Ca (mg l ⁻¹)	0.92	0.29 – 1.45	1.19	0.86 – 1.59
Na (mg l ⁻¹)	4.13	3.68 – 4.60	9.40	8.31 – 10.08
Cl (mg l ⁻¹)	6.72	5.89 – 7.58	17.27	15.47 – 18.51
Mg (mg l ⁻¹)	0.58	0.51 – 0.63	1.21	1.08 – 1.26
K (mg l ⁻¹)	0.25	0.19 – 0.32	0.33	0.25 – 0.39
Total monomeric Al (μ g l ⁻¹)	44.25	27.63 – 83.68	27.79	9.50 – 41.08
Mn (μ g l ⁻¹)	20.36	2.63 – 47.75	26.78	9.85 – 38.93
Fe (μ g l ⁻¹)	159.44	73.83 – 414.33	321.71	55.17 – 763.00

Table 2.3. Summary of 1 – way ANOVAs of water chemical parameters (mean annual values calculated over the 12-month sampling period), with blanket bog type (upland and lowland) as the main factor.

Chemical variable	d.f.	<i>F</i>	<i>p</i>	Upland v Lowland
pH	1, 11	3.103	0.106	
Alkalinity	1, 11	1.702	0.219	
Conductivity	1, 11	263.313	<0.001	Lowland > Upland
Temperature	1, 11	17.373	0.002	Lowland > Upland
Dissolved oxygen	1, 11	2.814	0.122	
Chlorophyll <i>a</i>	1, 11	2.304	0.157	
Colour	1, 11	2.517	0.141	
TDOC	1, 11	0.947	0.351	
TP	1, 11	5.874	0.034	Upland > Lowland
SRP	1, 11	0.308	0.590	
TN	1, 11	0.161	0.696	
TON	1, 11	0.122	0.734	
Ammonia	1, 11	0.399	0.540	
SO ₄	1, 11	52.754	<0.001	Lowland > Upland
Ca	1, 11	1.906	0.195	
Na	1, 11	385.299	<0.001	Lowland > Upland
Cl	1, 11	496.362	<0.001	Lowland > Upland
Mg	1, 11	357.784	<0.001	Lowland > Upland
K	1, 11	7.837	0.017	Lowland > Upland
Total monomeric Al	1, 11	3.305	0.096	
Mn	1, 11	0.642	0.440	
Fe	1, 11	1.596	0.233	

Significant terms are emboldened.

Table 2.4. Non-marine and marine concentrations ($\mu\text{eq l}^{-1}$) of SO_4 , Ca, Na, Mg and K in the 13 study lakes calculated as mean values over the 12-month sampling period.

Lake	SO_4 ($\mu\text{eq l}^{-1}$)		Ca ($\mu\text{eq l}^{-1}$)		Na ($\mu\text{eq l}^{-1}$)		Mg ($\mu\text{eq l}^{-1}$)		K ($\mu\text{eq l}^{-1}$)	
	Nonmarine	Marine	Nonmarine	Marine	Nonmarine	Marine	Nonmarine	Marine	Nonmarine	Marine
U1	24.6	17.9	8.0	6.4	13.6	149.0	7.5	34.4	1.6	3.1
U2	27.0	17.1	34.5	6.1	17.5	142.6	9.9	32.9	2.3	3.0
U3	21.7	22.0	37.5	7.9	16.4	183.5	9.2	42.3	4.2	3.8
U4	10.7	21.7	34.4	7.8	15.0	180.5	9.5	41.7	4.2	3.8
U5	21.0	18.6	65.5	6.7	21.8	154.6	12.6	35.7	2.8	3.2
U6	23.1	19.8	53.0	7.1	17.1	165.2	10.2	38.1	2.9	3.5
Upland mean	21.3	19.5	38.8	7.0	16.9	162.6	9.8	37.5	3.0	3.4
L1	12.7	44.9	35.0	16.1	-12.9	374.4	2.2	86.4	-0.1	7.9
L2	14.8	52.0	24.1	18.7	-16.0	433.5	1.5	100.0	-1.0	9.1
L3	18.3	51.3	26.9	18.4	-3.0	427.3	1.9	98.6	-1.1	9.0
L4	10.4	50.6	61.2	18.2	-9.8	421.6	6.1	97.3	0.8	8.8
L5	8.2	53.8	32.2	19.3	-9.4	448.0	-0.4	103.4	0.5	9.4
L6	4.4	49.1	57.8	17.7	-6.4	409.3	8.7	94.5	0.9	8.6
L7	9.2	49.4	51.1	17.7	-5.7	411.4	0.0	94.9	-2.4	8.6
Lowland mean	11.1	50.2	41.2	18.0	-9.0	417.9	2.9	96.4	-0.3	8.8

Table 2.5. H^+ ($\mu eq\ l^{-1}$), TDOC ($mg\ l^{-1}$) and organic acid ($\mu eq\ l^{-1}$) concentrations in the 13 study lakes calculated as mean values over the 12-month sampling period.

Lake	H^+ ($\mu eq\ l^{-1}$)	TDOC ($mg\ l^{-1}$)	Organic acids (A^-) ($\mu eq\ l^{-1}$)
U1	20.4	4.4	44.4
U2	8.4	6.9	69.2
U3	20.4	10.8	107.8
U4	5.8	9.4	93.3
U5	3.5	10.0	99.0
U6	2.5	7.8	76.9
Upland mean	10.2	8.2	81.8
L1	2.4	5.6	55.1
L2	11.0	6.2	62.2
L3	15.5	9.5	95.1
L4	1.0	7.8	76.2
L5	3.3	8.5	84.1
L6	0.7	6.4	61.8
L7	0.8	6.4	60.8
Lowland mean	4.9	7.2	70.8

Table 2.6. Trophic classification of the 13 study lakes. Maximum chlorophyll *a* concentrations were calculated from samples taken during May to September.

Lake	Max chlorophyll <i>a</i> ($\mu g\ l^{-1}$)	Trophic classification
U1	9.6	Mesotrophic
U2	12.6	Mesotrophic
U3	3.9	Oligotrophic
U4	16.7	Mesotrophic
U5	3.6	Oligotrophic
U6	7.7	Oligotrophic
L1	4.3	Oligotrophic
L2	2.8	Oligotrophic
L3	9.6	Mesotrophic
L4	3.1	Oligotrophic
L5	7.2	Oligotrophic
L6	3.7	Oligotrophic
L7	2.7	Oligotrophic

2.4.2. Chydoridae communities

Chydorid species richness ranged from 6 – 18 (median = 12) across all lakes and was significantly higher ($U = 1$, $p = 0.002$) in the lowland lakes (Fig. 2.3; Table 2.7). Four species of chydorid were present in all lakes: *Alonopsis elongata* (Sars), *Chydorus sphaericus* (Müller), *Alonella excisa* (Fischer) and *Alonella nana* (Baird). The rarest species were *Alona quadrangularis* (Müller), *Anchistropus emarginatus* Sars and *Pleuroxus laevis* Sars, all only occurring in a single lowland lake. Chydorid abundance was highest in all lakes from July to November (Fig. 2.3). Chydorid diversity was greatest in the lowland lakes in July and in the upland lakes in January and May. Mean taxon richness and H show comparable trends across all sampling months, with greater species richness in the lowland lakes (Fig. 2.3).

The NMDS ordination showed that the chydorid communities of the upland and lowland lakes were reasonably distinct (Fig. 2.4). The lowland lakes were characterised by the greater presence and abundance of *Alona affinis* (Leydig), *Pleuroxus truncatus* (Müller), *Eurycercus lamellatus* (Baird), *Camptocercus rectirostris* Schoedler and *Alona costata* Sars. Conversely, the upland lakes were less species rich and contained higher abundances of *Alona rustica* Scott. However, the difference in community structure between the upland and lowland lakes was not significant according to ANOSIM analysis ($R = 0.208$, $p = 0.066$).

The BIO-ENV analysis of the physico-chemical data of all lakes found that a combination of seven environmental variables – altitude, mean depth, pH, conductivity, dissolved oxygen, alkalinity and Fe – best explained the NMDS ordination of the chydorid communities ($\rho_w = 0.49$; weighted Spearman Rank).

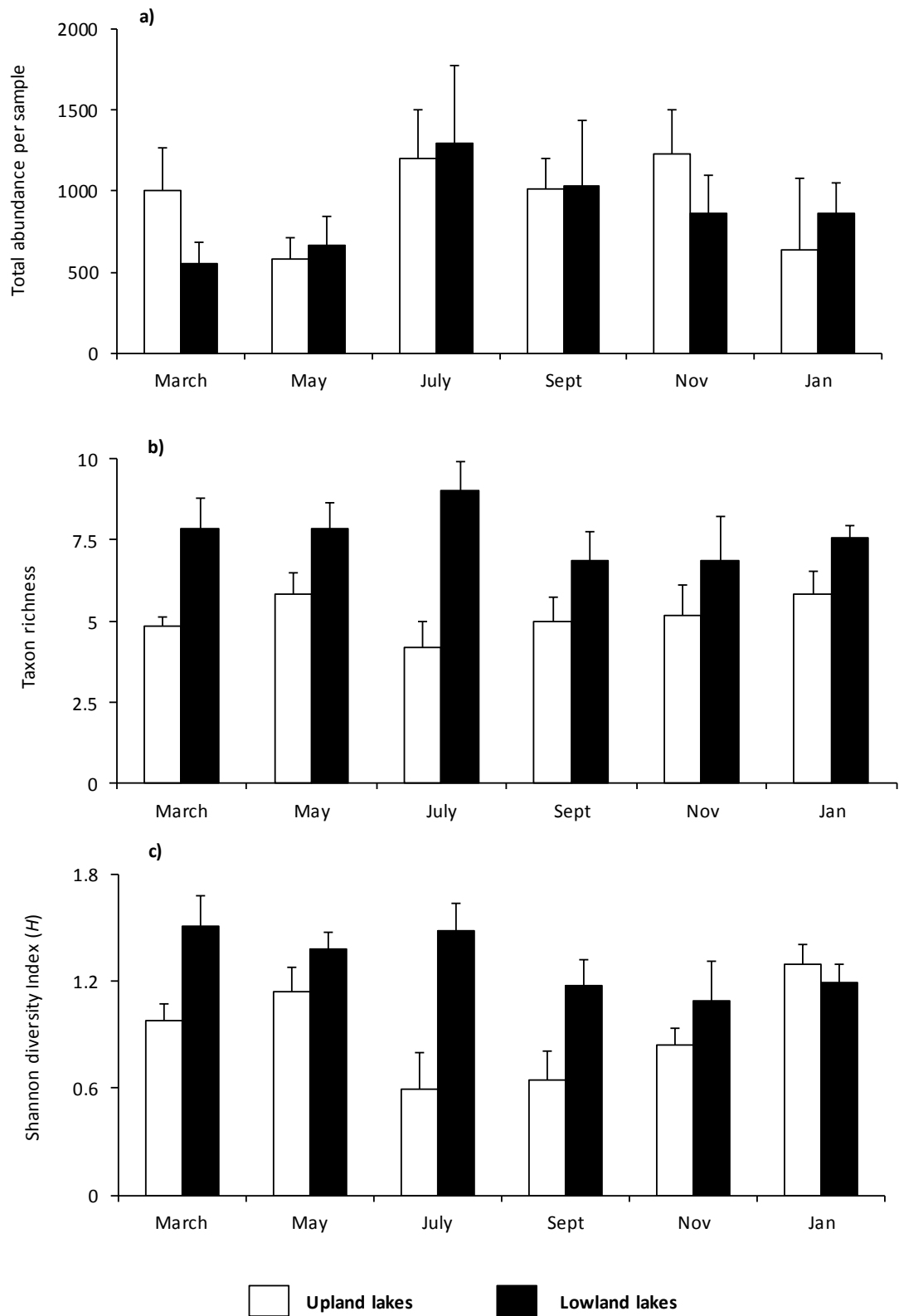


Figure 2.3. Monthly mean: a) total abundance per sample, b) taxon richness and c) Shannon diversity (H) of the littoral chydorid communities from the upland and lowland lakes. Columns on each graph are mean values (± 1 S.E.) calculated over the duration of the sampling period (n: upland = 6 and lowland = 7).

Table 2.7. List of invertebrate taxa recorded during the study. The total abundance for each individual taxon recorded is also shown.

Order	Family (Sub-family)	Species	U1	U2	U3	U4	U5	U6	L1	L2	L3	L4	L5	L6	L7	Total abundance
Cladocera	Bosminidae	<i>Bosmina coregoni</i> Baird	+							+		+		+	+	533
	Chydoridae	<i>Acroperus harpae</i> (Baird)							+	+	+	+	+	+	+	382
		<i>Alona affinis</i> (Leydig)				+	+	+	+	+	+	+	+	+	+	160
		<i>Alona costata</i> Sars							+			+		+	+	27
		<i>Alona guttata</i> Sars				+	+		+	+	+	+	+	+		40
		<i>Alona intermedia</i> Sars							+			+	+		+	18
		<i>Alona quadrangularis</i> (Müller)													+	2
		<i>Alona rustica</i> Scott	+	+	+				+	+	+		+		+	88
		<i>Alonella excisa</i> (Fischer)	+	+	+	+	+	+	+	+	+	+	+	+	+	308
		<i>Alonella exigua</i> (Lilljeborg)				+				+	+		+		+	26
		<i>Alonella nana</i> (Baird)	+	+	+	+	+	+	+	+	+	+	+	+	+	629
		<i>Alonopsis elongata</i> (Sars)	+	+	+	+	+	+	+	+	+	+	+	+	+	2833
		<i>Anchistropus emarginatus</i> Sars													+	1
		<i>Camptocercus rectirostris</i> Schoedler										+		+		43
		<i>Chydorus ovalis</i> Kurz	+	+		+	+			+	+		+	+	+	36
		<i>Chydorus piger</i> Sars	+	+	+		+		+		+	+	+	+	+	93
		<i>Chydorus sphaericus</i> (Müller)	+	+	+	+	+	+	+	+	+	+	+	+	+	1446
		<i>Eurycercus lamellatus</i> (Baird)				+	+	+		+		+		+	+	276
		<i>Graptoleberis testudinaria</i> (Fischer)			+	+	+		+	+	+	+	+	+	+	126
		<i>Monospilus dispar</i> Sars	+						+			+		+		46
		<i>Pleuroxus laevis</i> Sars												+		1
		<i>Pleuroxus truncatus</i> (Müller)				+	+					+	+	+	+	280
		<i>Pseudochydorus globosus</i> (Baird)					+								+	4
		<i>Rhynchotalona rostrata</i> (Koch)										+			+	7
	Daphnidae	<i>Ceriodaphnia setosa</i> Matile			+	+	+	+	+	+	+	+	+	+	+	2372
		<i>Daphnia longispina</i> / <i>hyalina</i> (Müller)/Leydig						+								2
		<i>Scapholeberis mucronata</i> (Müller)				+										34
	Holopedidae	<i>Holopedium gibberum</i> Zaddach				+						+				11
	Macrothricidae	<i>Acantholberis curvirostris</i> (Müller)			+	+	+	+	+	+	+	+	+		+	163
		<i>Ilyocryptus sordidus</i> Sars				+			+						+	10
		<i>Streblocercus serricaudatus</i> (Kock)				+			+		+		+		+	118
	Polyphemidae	<i>Polyphemus pediculus</i> (Linnaeus)				+	+	+	+	+	+	+	+		+	2160
	Sidae	<i>Diaphanosoma brachyurum</i> Lieven	+	+	+	+	+	+	+	+	+	+	+	+	+	1587
		<i>Sida crystallina</i> (Müller)				+			+		+	+	+	+	+	1002

Table 2.7. (cont.) List of invertebrate taxa recorded during the study. The total abundance for each individual taxon recorded is also shown.

Order	Family (Sub-family)	Species	U1	U2	U3	U4	U5	U6	L1	L2	L3	L4	L5	L6	L7	Total abundance
Ephemeroptera	Baetidae	<i>Centroptilum luteolum</i> (Müller)										+		+	+	5
	Caenidae	<i>Caenis luctuosa</i> (Burmeister)										+		+	+	97
	Leptophlebiidae	<i>Leptophlebia vespertina</i> (Linnaeus)	+	+	+	+	+	+	+	+	+	+	+	+	+	8255
	Siphonuridae	<i>Siphonurus alternatus</i> (Say)												+	+	11
Plecoptera	Nemouridae	<i>Nemoura cinerea</i> (Retzius)					+					+		+	+	7
Trichoptera	Ecnomidae	<i>Ecnomus tenellus</i> (Rambur)							+	+			+	+		11
	Polycentropodidae	<i>Cymus flavidus</i> McLachlan					+			+		+	+			16
		<i>Holocentropus dubius</i> (Rambur)			+	+		+	+	+	+	+	+		+	589
		<i>Holocentropus picicornis</i> (Stephens)					+	+	+	+		+	+	+	+	75
		<i>Plectrocnemia conspersa</i> (Curtis)		+			+	+		+			+	+		26
		<i>Polycentropus flavomaculatus</i> (Pictet)	+	+	+				+	+	+		+	+	+	118
		<i>Polycentropus irroratus</i> (Curtis)						+	+	+	+	+	+	+	+	296
		<i>Polycentropus kingi</i> McLachlan	+	+	+		+	+	+	+		+		+		44
		<i>Tinodes waeneri</i> (Linnaeus)						+				+				27
		<i>Oxyethira</i> sp.					+	+				+		+	+	13
		<i>Athripsodes cinereus</i> (Curtis)												+		1
		<i>Ceraclea fulva</i> (Rambur)					+						+			2
		<i>Lepidostoma hirtum</i> (Fabricius)										+			+	21
		<i>Mystacides azurea</i> (Linnaeus)								+		+		+	+	78
		<i>Oecetis furva</i> (Rambur)								+		+	+	+	+	37
		<i>Oecetis lacustris</i> (Pictet)				+					+	+		+		4
		<i>Triaenodes bicolor</i> (Curtis)				+	+		+			+	+	+	+	163
	Limnephilidae	<i>Halesus radiatus</i> (Curtis)	+	+					+	+		+		+	+	40
		<i>Limnephilus lunatus</i> Curtis					+							+		16
		<i>Limnephilus marmoratus</i> Curtis					+	+	+	+	+	+	+	+	+	56
		<i>Limnephilus nigriceps</i> (Zetterstedt)				+	+	+			+					29
		<i>Limnephilus stigma</i> Curtis	+	+	+	+	+	+								214
		<i>Molanna albicans</i> (Zetterstedt)				+										17
		<i>Agrypnia obsoleta</i> (Hagen)	+	+	+	+	+	+								547
	Phryganeidae	<i>Agrypnia varia</i> (Fabricius)				+	+	+		+	+	+	+	+		48
		<i>Sericostoma personatum</i> (Spence in Kirby & Spence)				+		+			+	+	+	+	+	33

Table 2.7. (cont.) List of invertebrate taxa recorded during the study. The total abundance for each individual taxon recorded is also shown.

Order	Family (Sub-family)	Species	U1	U2	U3	U4	U5	U6	L1	L2	L3	L4	L5	L6	L7	Total abundance
Odonata	Coenagrionidae	<i>Coenagrion puella/pulchellum</i> (Linnaeus/Vander Linden)					+						+	+	+	24
		<i>Enallagma cyathigerum</i> (Charpentier)	+	+	+		+		+	+	+	+	+	+	+	489
		<i>Ischnura elegans</i> (Vander Linden)				+						+	+	+	+	31
		<i>Pyrrhosoma nymphula</i> (Sulzer)	+	+	+	+	+	+	+	+	+	+	+	+	+	100
	Lestidae	<i>Lestes sponsa</i> (Hansemann)				+					+	+	+			30
	Aeshnidae	<i>Aeshna juncea</i> (Linnaeus)	+	+	+	+	+	+	+	+	+	+	+	+	+	158
		<i>Aeshna grandis</i> (Linnaeus)										+		+		3
		<i>Brachytron pratense</i> (Müller)										+				1
	Corduliidae	<i>Cordulia aenea</i> (Linnaeus)							+	+	+	+	+			11
	Libellulidae	<i>Libellula quadrimaculata</i> Linnaeus			+	+	+		+	+	+	+	+	+	+	77
		<i>Sympetrum danae</i> (Sulzer)					+	+		+						4
		<i>Sympetrum sanguineum</i> (Müller)				+								+	+	3
Diptera	Chaoboridae	<i>Chaoborus crystallinus</i> (De Geer)		+	+		+		+	+			+			1183
	Ceratopogonidae (Ceratopogoninae)	Undetermined	+	+					+			+	+	+		22
	Chironomidae (Chironominae)	Undetermined	+	+	+	+	+	+	+	+	+	+	+	+	+	2517
	(Orthocladiinae)	Undetermined	+	+	+	+	+	+	+	+	+	+	+	+	+	1394
	(Tanypodinae)	Undetermined	+	+	+	+	+	+	+	+	+	+	+	+	+	1502
	Tabanidae (Chrysopsinae)	Undetermined						+		+	+	+		+	+	10
	(Tabaninae)	Undetermined								+	+					6
	Empididae (Hemerodrominae)	Undetermined		+					+							2
	Limoniidae (Limoniinae)	Undetermined	+				+			+	+				+	7
	Cylindrotomidae	<i>Phalacrocer replicata</i> (Linnaeus)				+										1
	Tipulidae (Tipulinae)	Undetermined	+				+			+			+			6
	Oligochaeta	Undetermined	+	+	+	+	+	+	+	+	+	+	+	+	+	243
Rhynchobdellae	Glossiphoniidae	<i>Helobdella stagnalis</i> (Linnaeus)				+			+						+	12
		<i>Batrachobdella paludosa</i> (Carena)													+	1
		<i>Haemopsis sanguisuga</i> (Linnaeus)				+	+	+					+			8
Pharyngobdellae	Erpobdellidae	<i>Dina lineata</i> (O. F. Müller)						+								1
Acarina	Hydracarina	Undetermined				+	+	+	+	+	+	+	+	+	+	39
Araneae	Cybaeidae	<i>Argyroneta aquatica</i> (Clerck)			+	+	+	+	+	+	+	+	+	+	+	70
Megaloptera	Silaidae	<i>Sialis lutaria</i> (Linnaeus)					+	+			+		+	+		15
Isopoda	Asellidae	<i>Asellus meridianus</i> Racovitza				+	+		+			+	+	+	+	133
Gastropoda	Lymnaeidae	<i>Lymnaea peregra</i> (Müller)												+	+	169

Table 2.7. (cont.) List of invertebrate taxa recorded during the study. The total abundance for each individual taxon recorded is also shown.

Order	Family (Sub-family)	Species	U1	U2	U3	U4	U5	U6	L1	L2	L3	L4	L5	L6	L7	Total abundance
Hemiptera- Heteroptera	Corixidae	<i>Arctocorisa germari</i> (Fieber)			+								+			2
		<i>Callicorixa praeusta</i> (Fieber)		+	+	+	+	+								16
		<i>Callicorixa wollastoni</i> (Douglas & Scott)	+	+		+				+						67
		<i>Corixa affinis</i> Leach		+												4
		<i>Corixa dentipes</i> (Thomson)									+		+			19
		<i>Corixa panzeri</i> (Fieber)		+												1
		<i>Corixa punctata</i> (Illiger)			+											1
		<i>Cymatia bondsdorffii</i> (Sahlberg)			+				+	+	+		+		+	116
		<i>Glaenocorisa propinqua</i> (Fieber)	+	+	+				+	+	+					71
		<i>Hesperocorixa castanea</i> (Thomson)				+	+	+	+	+	+	+	+	+		41
		<i>Hesperocorixa linnaei</i> (Fieber)			+											2
		<i>Hesperocorixa sahlbergi</i> (Fieber)				+	+									2
		<i>Sigara concinna</i> (Fieber)				+										1
		<i>Sigara distincta</i> (Fieber)		+			+	+					+			77
		<i>Sigara nigrolineata</i> (Fieber)			+											1
		<i>Sigara scotti</i> (Douglas & Scott)	+	+	+	+	+	+	+	+	+	+	+	+	+	1260
	Gerridae	<i>Gerris lacustris</i> (Linnaeus)				+		+						+		5
	Hydrometridae	<i>Hydrometra stagnorum</i> (Linnaeus)								+						1
	Nepidae	<i>Nepa cinerea</i> Linnaeus							+	+	+	+	+	+	+	15
	Notonectidae	<i>Notonecta glauca</i> Linnaeus	+		+	+	+	+								13
		<i>Notonecta obliqua</i> Gallen	+		+						+		+			17
Coleoptera	Veliidae	<i>Velia caprai</i> Tamanini	+	+	+			+	+	+	+		+	+	+	20
	Gyrinidae	<i>Gyrinus aeratus</i> Stephens			+				+				+			60
		<i>Gyrinus marinus</i> Gyllenhal				+										1
		<i>Gyrinus minutus</i> Fabricius			+	+		+	+	+	+		+	+		88
		<i>Gyrinus substriatus</i> Stephens	+	+	+	+	+	+	+	+	+		+	+	+	157
	Haliplidae	<i>Haliplus confinis</i> Stephens	+													1
		<i>Haliplus fulvus</i> (Fabricius)					+	+	+		+		+	+	+	72
		<i>Haliplus lineatocollis</i> Mannerheim	+													1
		<i>Haliplus ruficollis</i> (De Geer)	+				+									2
		<i>Noterus clavicornis</i> (De Geer)				+			+							14
	Psephenidae	<i>Hygrobia hermanni</i> (Fabricius)		+				+								3
	Dytiscidae (Agabinae)	<i>Agabus affinis</i> (Paykull)										+				1

Table 2.7. (cont.) List of invertebrate taxa recorded during the study. The total abundance for each individual taxon recorded is also shown.

Order	Family (Sub-family)	Species	U1	U2	U3	U4	U5	U6	L1	L2	L3	L4	L5	L6	L7	Total abundance
Coleoptera	Dytiscidae (Agabinae)	<i>Agabus arcticus</i> (Paykull)	+	+	+											60
		<i>Agabus bipustulatus</i> (Olivier)	+	+	+	+	+	+		+	+		+	+		83
		<i>Agabus nebulosus</i> (Forster)			+	+	+									4
		<i>Agabus sturmii</i> Gyllenhal	+	+	+			+								26
		<i>Ilybius aenescens</i> Thomson			+	+	+	+	+	+	+					46
		<i>Ilybius fuliginosus</i> (Fabricius)						+	+							9
		<i>Ilybius guttiger</i> (Gyllenhal)			+	+	+									4
		<i>Ilybius quadriguttatus</i> (Lacordaire)			+											3
	(Colymbetinae)	<i>Colymbetes fuscus</i> (Linnaeus)	+		+	+	+	+								206
		<i>Rhantus exsoletus</i> (Forster)				+	+	+			+	+	+			43
		<i>Rhantus frontalis</i> (Marsham)			+		+									2
	(Dytiscinae)	<i>Acilius canaliculatus</i> (Nicolai)			+											2
		<i>Acilius sulcatus</i> (Linnaeus)	+	+	+				+		+		+	+		368
		<i>Dytiscus lapponicus</i> Gyllenhal	+	+												547
	(Hydroporinae)	<i>Dytiscus marginalis</i> Linnaeus					+	+								6
		<i>Dytiscus semisulcatus</i> Müller	+	+	+	+	+	+								36
		<i>Hydaticus seminiger</i> (De Geer)			+	+										2
		<i>Hydroporus erythrocephalus</i> (Linnaeus)	+		+			+	+						+	286
		<i>Hydroporus gyllenhalii</i> (Schiödte)		+	+	+				+			+	+		8
		<i>Hydroporus incognitus</i> Sharp			+	+									+	6
		<i>Hydroporus obscurus</i> Sturm	+		+	+		+		+	+	+	+	+	+	75
		<i>Hydroporus palustris</i> (Linnaeus)	+		+		+								+	6
		<i>Hydroporus planus</i> (Fabricius)						+								1
		<i>Hydroporus pubescens</i> (Gyllenhal)	+	+	+	+	+	+	+	+	+		+	+	+	74
		<i>Hydroporus melanarius</i> Sturm		+												1
		<i>Hydroporus tristis</i> (Paykull)	+	+		+		+					+		+	15
		<i>Hygrotus inaequalis</i> (Fabricius)		+	+		+	+		+						7
		<i>Hyphydrus ovatus</i> (Linnaeus)					+		+	+			+			13
		<i>Nebrioporus assimilis</i> (Paykull)						+	+	+	+	+	+	+	+	220
		<i>Porhydrus lineatus</i> (Fabricius)			+											1
		<i>Stictotarsus duodecimpustulatus</i> (Fabricius)								+		+			+	21
		<i>Stictonectes lepidus</i> (Olivier)		+				+								35
	(Laccophilinae)	<i>Laccophilus minutus</i> (Linnaeus)	+		+			+	+	+						14

Table 2.7. (cont.) List of invertebrate taxa recorded during the study. The total abundance for each individual taxon recorded is also shown.

Order	Family (Sub-family)	Species	U1	U2	U3	U4	U5	U6	L1	L2	L3	L4	L5	L6	L7	Total abundance
Coleoptera	Helophoridae	<i>Helophorus aequalis</i> Thomson				+	+							+		4
		<i>Helophorus brevipalpis</i> Bedel				+	+	+						+		6
		<i>Helophorus flavipes</i> Fabricius		+	+	+	+	+					+			22
		<i>Helophorus minutus</i> Fabricius				+	+									3
	Hydrophilidae (Hydrophilinae)	<i>Anacaena globulus</i> (Paykull)	+	+	+		+	+	+	+			+			39
		<i>Anacaena lutescens</i> (Stephens)												+	+	2
		<i>Enochrus affinis</i> (Thunberg)				+					+			+		5
		<i>Enochrus coarctatus</i> (Gredler)				+										2
		<i>Enochrus fuscipennis</i> (Thomson)				+						+		+		3
		<i>Helochaeres punctatus</i> Sharp												+		1
		<i>Hydrobius fuscipes</i> (Linnaeus)				+										2
	Elmidae (Elminae)	<i>Oulimnius tuberculatus</i> (Müller)								+					+	3
	Dryopidae	<i>Dryops luridus</i> (Erichson)								+					+	3
	Chrysomelidae (Donaciinae)	<i>Donacia crassipes</i> Fabricius									+					1
		<i>Donacia obscura</i> Gyllenhal						+								2
		<i>Donacia thalassina</i> Germar													+	6

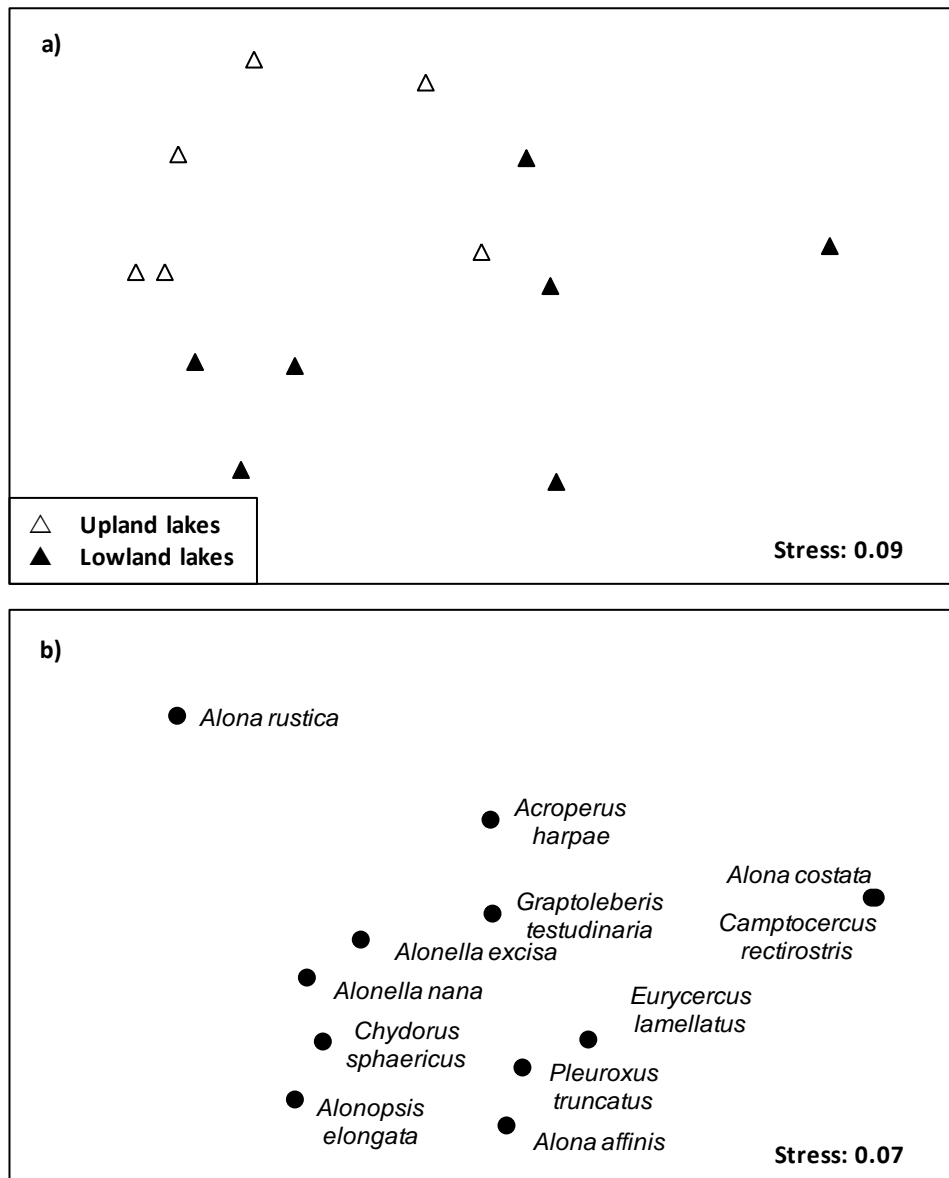


Figure 2.4. Non-metric multi-dimensional scaling (NMDS) analysis of the Chydoridae communities showing a) site scores of the 13 study lakes and b) species scores.

2.4.3. Littoral macroinvertebrate communities

A total of 147 macroinvertebrate taxa were recorded across all the 13 study lakes (Table 2.7). Taxon richness per lake varied from 40 – 61 (median 54) across all lakes. The taxon richness of the lowland lakes (median = 54) was not significantly different than that from the upland blanket bog lakes (median = 56.5) ($U = 20$, $p = 0.868$). The most common species, occurring in all lakes, were *Leptophlebia vespertina* (Linnaeus), *Pyrrhosoma nymphula* (Sulzer), *Aeshna juncea* (Linnaeus) and *Sigara scotti* (Douglas and Scott). Macroinvertebrate abundance was highest in April, with the mean taxon richness and H highest in all lakes in June and lower in both April and September (Fig. 2.5).

The mean number of macroinvertebrate taxa recorded in the four-minute multihabitat sweep samples was 32. The greatest number of taxa recorded during a four-minute multihabitat sweep was in June (39 taxa), with 27 taxa being recorded in April and 29 taxa in September. Activity traps proved successful in capturing mobile predatory taxa with 69.8% of all coleopteran individuals captured using this method. However, in terms of species richness, 54 aquatic coleopteran species were recorded using sweeps as opposed to 43 using activity traps. Similarly, sweeps were also more successful at capturing aquatic heteropteran species, with 22 species being recorded using sweeps as opposed to 15 using activity traps. In terms of species richness, aquatic Coleoptera on average constituted 32% of macroinvertebrate taxa recorded in any one lake followed by Trichoptera (21%), aquatic Heteroptera (13%), Diptera (11%) and Odonata (11%), and Ephemeroptera (3%). Species from other orders, including Plecoptera, Gastropoda, Megaloptera and Isopoda, were recorded infrequently (Fig. 2.6).

Similar to the chydorids, the NMDS ordination showed a clear separation between the upland and lowland macroinvertebrate communities (Fig. 2.7). ANOSIM analysis revealed significant differences in the littoral macroinvertebrate community structure between lake types ($R = 0.835$, $p = 0.001$). Lowland lakes were characterised by the greater presence and abundance of the gastropod *Lymnaea peregra* (Müller), the ephemeropteran *Caenis luctuosa* (Burmeister), the trichoperans *Mystacides azurea* (Linnaeus), *Polycentropus irroratus* (Curtis), *Holocentropus dubius* (Rambur) and smaller dytiscids such as *Hydroporus erythrocephalus* (Linnaeus) and *Nebrioporus assimilis* (Paykull). Conversely, the upland blanket bog lakes were characterised by the greater presence and abundance of larger dytiscids such as *Dytiscus lapponicus* Gyllenhal, *Colymbetes fuscus* (Linnaeus), *Acilius sulcatus* (Linnaeus) and Dytiscinae larvae, as well as the trichopteran *Agrypnia obsoleta* (Hagen).

The BIO-ENV analysis of the physico-chemical data of all lakes found that a combination of seven environmental variables – altitude, pH, conductivity, temperature, dissolved oxygen, Ca and Na – best explained the NMDS ordination of littoral macroinvertebrate communities ($\rho_w = 0.75$; weighted Spearman Rank).

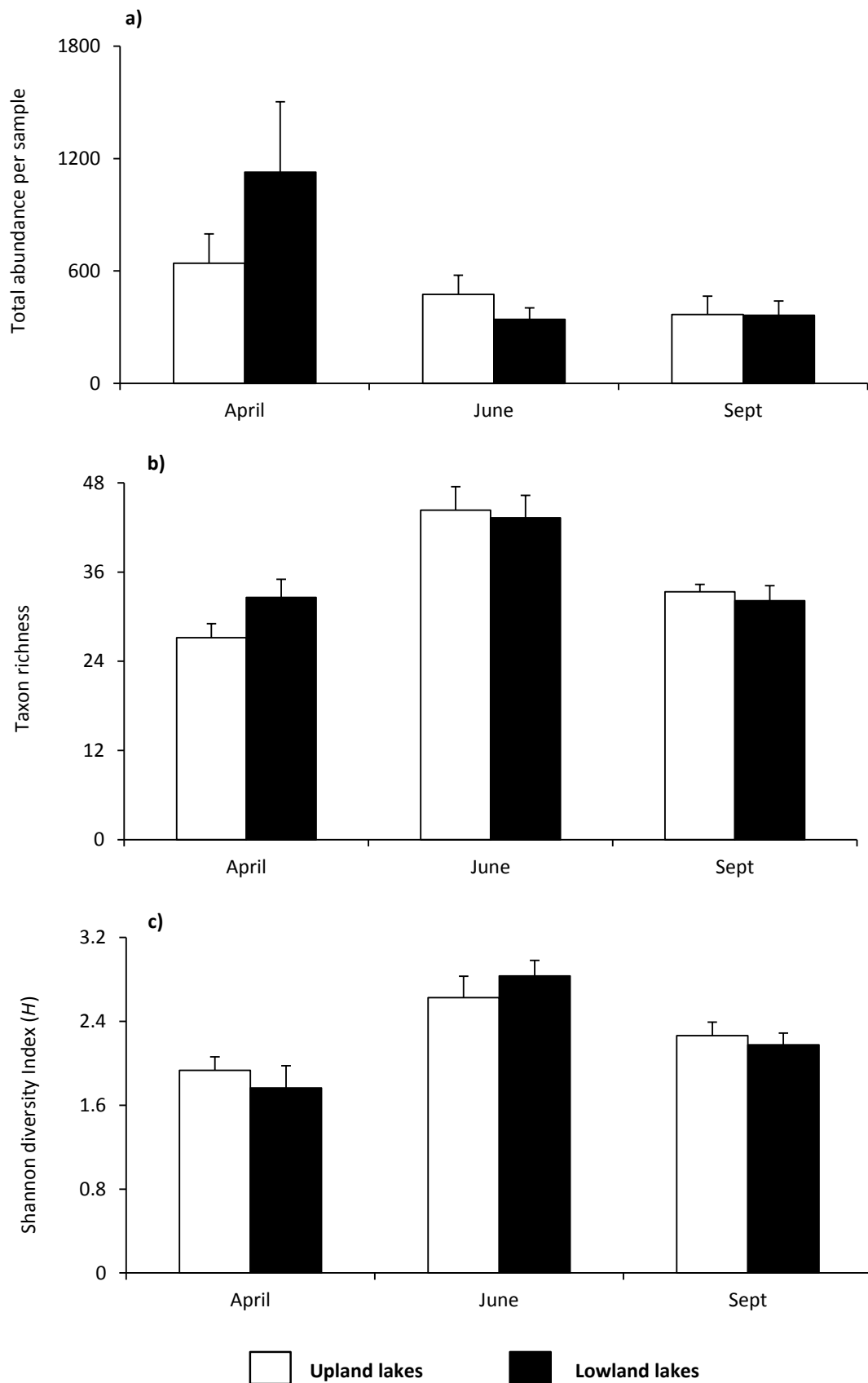


Figure 2.5. Monthly mean: a) total abundance per sample, b) taxon richness and c) Shannon diversity (H) of the littoral macroinvertebrate communities from the upland and lowland lakes. Columns on each graph are mean values (± 1 S.E.) calculated over the duration of the sampling period (n: upland = 6 and lowland = 7).

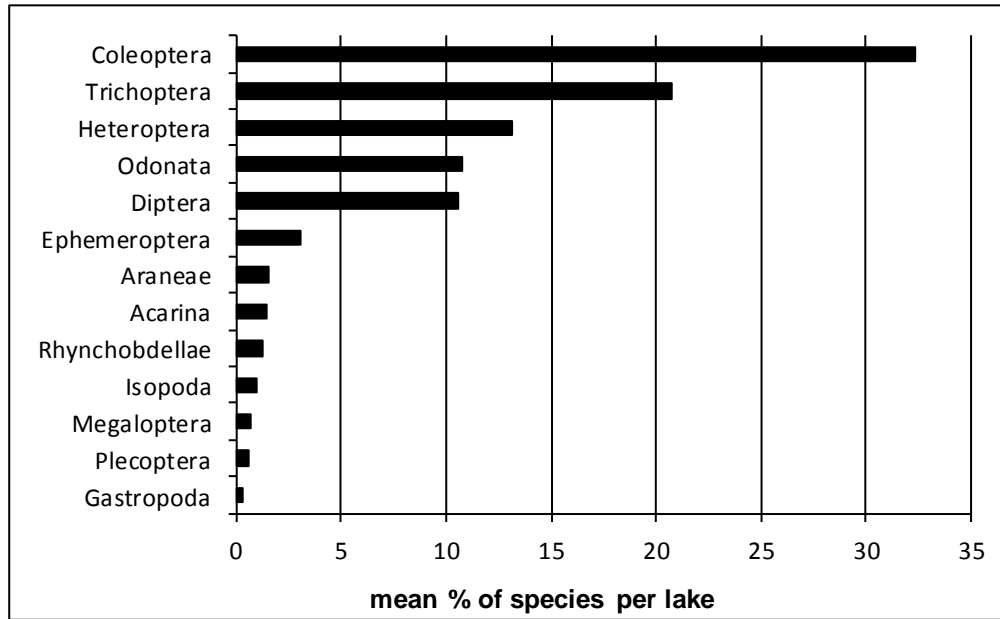


Figure 2.6. Mean percentage of species per lake in the main macroinvertebrate groups.

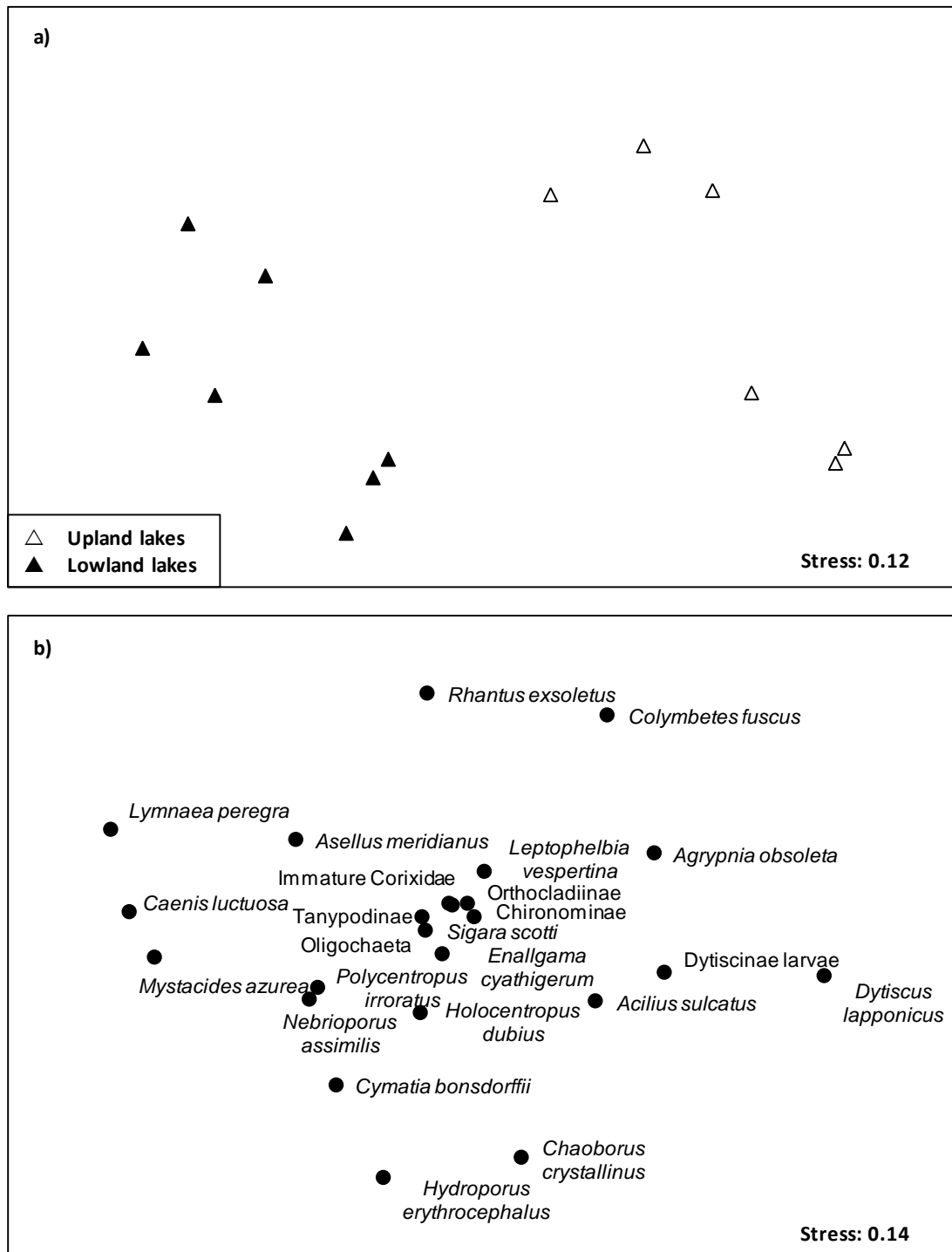


Figure 2.7. Non-metric multi-dimensional scaling (NMDS) analysis of the littoral macroinvertebrate communities showing a) site scores of the 13 study lakes and b) species scores.

2.4.4. Macrophyte communities

A total of 24 macrophyte species were recorded across all the 13 lakes (Table 2.8). Species richness per lake varied from 1 – 14 (median = 9) across all lakes. The species richness of the lowland lakes (median = 11) was significantly greater than that from the upland blanket bog lakes (median = 5) ($U = 6.5$, $p = 0.035$). The species-poor communities of the upland lakes were characterised by *Juncus bulbosus* Linnaeus, *Carex rostrata* Stokes and *Menyanthes trifoliata* Linnaeus. The greater diversity of the lowland lakes was attributable to a number of species, such as *Cladium mariscus* (Linnaeus) Pohl, *Eleogiton fluitans* (Linnaeus) Link, *Eriocaulon aquaticum* (Hill) Druce, *Utricularia intermedia* Hayne sensu lato and *Hypericum elodes* Linnaeus, which were only recorded from this lake type. Other species which were common to both upland and lowland lakes but were more abundant in the latter include *Potamogeton polygonifolius* Pourret and *Lobelia dortmanna* Linnaeus, both occurring only once in the upland lakes (Table 2.8).

Table 2.8. List of macrophyte species recorded in the 13 study lakes. The abundance of each species was scored on the DAFOR scale (Dominant, Abundant, Frequent, Occasional and Rare).

Species	U1	U2	U3	U4	U5	U6	L1	L2	L3	L4	L5	L6	L7
<i>Carex rostrata</i> Stokes			O	F	F	F							
<i>Carex vesicaria</i> Linnaeus										O	O	F	
<i>Cladium mariscus</i> (Linnaeus) Pohl									F	O			
<i>Eleocharis palustris</i> (Linnaeus) Roemer & Schultes				O									
<i>Eleogiton fluitans</i> (Linnaeus) Link							O		O	F	O	F	
<i>Equisetum fluviale</i> Linnaeus				D	F								
<i>Eriocaulon aquaticum</i> (Hill) Druce							O	A	O	R		O	F
<i>Hydrocotyle vulgaris</i> Linnaeus											R		
<i>Hypericum elodes</i> Linnaeus											R	R	
<i>Juncus bulbosus</i> Linnaeus	F	O	A	F		F	O	F	O	A	F	F	F
<i>Lobelia dortmanna</i> Linnaeus						F	F	F	O	F		O	F
<i>Menyanthes trifoliata</i> Linnaeus			O	O	O	R			O	F	F	O	O
<i>Nuphar lutea</i> (Linnaeus)				A			A		A	A	A	R	F
<i>Nymphaea alba</i> Linnaeus							R						
<i>Phragmites australis</i> (Cavanilles) Trinius ex Steudel				A	F	F	O	R	O	F	O	F	A
<i>Potamogeton natans</i> Linnaeus					A	O				R			
<i>Potamogeton polygonifolius</i> Pourret				O			O	F	O	F	O	O	A
<i>Potentilla palustris</i> (Linnaeus) Scopoli				O	O	R							
<i>Ranunculus flammula</i> L. subsp. <i>flammula</i>										O			
<i>Schoenoplectus lacustris</i> (Linnaeus) Palla					D								A
<i>Sparganium angustifolium</i> Michaux				O	O		F	R	O		A		
<i>Subularia aquatica</i> Linnaeus										R			
<i>Utricularia intermedia</i> Hayne sensu lato									R	O	O	O	R
<i>Utricularia minor</i> Linnaeus				O									

2.4.5. Species rarity and uncommon species

The first discovery of larvae of *Cordulia aenea* (Linnaeus) (the Downy Emerald dragonfly), one of the rarest and least recorded of the resident Irish dragonflies (Drinan et al., 2011), was recorded from five of the lowland lakes. Of the 60 aquatic coleopteran species recorded during this study, two species – *Agabus arcticus* (Paykull) and *D. lapponicus* – were listed as near threatened in the Irish Red List for water beetles (Foster et al., 2009).

The rarest plant species recorded during this study was *E. aquaticum*. This species has a very limited distribution in northern Europe, being confined to peatland lakes of Scotland and western Ireland. Preston and Croft (1997) also noted that two aquatic plant species recorded during this study, *J. bulbosus* and *P. polygonifolius*, have a restricted global distribution. These species are endemic to Europe, or have primarily European distributions with populations in neighbouring regions or a few outlying areas elsewhere (Preston and Croft, 1997). No Irish Red List vascular plant species was recorded (Curtis and McGough, 1988).

Ireland's only species of newt *Lissotriton vulgaris* (Linnaeus) was also recorded from two of the upland lakes in the mid-west.

2.5. Discussion

Small undisturbed lakes in blanket bog catchments represent one of a very few number of freshwater habitats remaining in northern Europe that are minimally impacted by humans. Although similar habitats exist in Britain, especially in Scotland (Lindsay et al., 1988; Standen, 1999), they have received little attention from biologists and little baseline data exists on their physical, chemical or biological state in Ireland (Curtis et al., 2009), despite their reported high biological conservation value (Maitland, 1999).

The overall base-poor and low plant nutrient concentrations of the lakes studied was similar to that found in blanket bog pools located in the east of Ireland (Hannigan et al., 2011). The higher conductivity of lowland lakes, reflecting higher concentrations of marine-derived ions, notably Na, Cl, Mg, SO₄ and K, indicates that the main determinant of hydrochemistry in western Irish lakes situated on ombrotrophic blanket bogs is atmospheric deposition rather than underlying geology. Hydrochemical variation in relation to distance from sea has been shown by others for both British and Irish bogs (Gorham, 1958; Holden, 1961), with the deposition of marine-derived ions decreasing with increasing distance inland from the coast (Aherne and Farrell, 2002). The importance of atmospheric deposition as a source of solutes in bog pools is well recognised (Proctor, 2003). Although Na, Cl and Mg are known to originate from sea spray, Ca, K and S are generally held to originate from terrestrial sources (Gorham, 1958; Proctor, 1994). Marine deposition of S can, however, also be considerable (Aherne and Farrell, 2002). The greater concentrations of marine-derived Ca, K and SO₄ in the lowland lakes is not a surprising finding given that others have previously demonstrated high

concentrations of these ions in bog pools along Atlantic coastlines due to marine influences (Gorham, 1957; Sparling, 1967; Proctor, 1992).

The lower pH of upland lakes can likely be ascribed to both the reduced buffering capacity, due to the lower alkalinity and base cation concentrations, and also the higher organic acid and non-marine SO_4 concentrations. In naturally humic waters the overall acidity is produced by organic rather than mineral acids (Oliver et al., 1983). Increasing DOC concentrations can lead to increased concentrations of organic acids which are known to significantly reduce the pH of low alkalinity waters (Harriman and Taylor, 1999). Non-marine SO_4 is also known to be a significant source of acidity in Irish lakes (Aherne et al., 2002). The findings of this study are in agreement with those of Aherne et al. (2002), who showed that the concentration of non-marine SO_4 increases with increasing acidity in organic anion dominated lakes. An increase in DOC export from uplands has been observed for upland catchments in the UK (Freeman et al., 2001). Changes in soil pH, temperature and moisture content are likely regulators (Kalbitz et al., 2000); however, the exact mechanism responsible remains unclear. Further work is required to determine the environmental driver responsible for the higher TDOC concentrations recorded from the upland lakes.

The higher Al concentrations in the upland lakes, albeit not significant, is also likely explained by the somewhat higher TDOC concentrations, as it is recognised that Al-organic complexes exert a major influence on Al concentrations in soils (Vance et al., 1996). Humic substances bind Al and other cations because of their high content of oxygen-containing functional groups such as carboxyl, phenolic and alcoholic groups (Gensemer and Playle, 1999). Al complexation is known to increase with increasing organic matter content (Helmer et al., 1990); therefore,

lakes containing higher concentrations of TDOC would be expected to contain greater concentrations of Al, albeit in a complexed rather than a free mineral form.

In contrast to the higher concentrations of Al in the upland lakes, the lowland lakes contained higher concentrations of Fe, albeit not significantly higher. Although also known to be dependent on organic matter for mobility (Driscoll et al., 1988), it is unlikely that the higher Fe concentration in these lakes is due to chelation with organic matter as the TDOC concentrations were lower. Similarly, the yellow-brown colour of bog lakes is attributable primarily to the Fe-organic complexes and this was not reflected in the colour differences between both lake types. It is more likely that the sea-derived cations, entrained from sea surfaces during periods of high wind, are temporarily changing the equilibria among cations in soil solution and cations on soil exchange sites, the result of which is the displacement of metal ions (such as Al and Fe) from exchange sites by marine base cations and their subsequent release to receiving waters. Although not as frequently reported for Fe, such changes in runoff chemistry by sea-salt inputs have been shown to occur for Ca, Al and H^+ in the UK (Evans et al., 2001). Other potential sources of the higher Fe in the lowland lakes may be due to groundwater, as water draining from igneous basic and ultrabasic geologies can occasionally supply high concentrations of heavy metals (Proctor, 2008). Sea-salt driven variations in the redox conditions of the peat soil may also be responsible for Fe leaching in the lowland catchments.

The greater chlorophyll *a* concentrations of the upland lakes, with three of the six classified as mesotrophic, is also likely due to the higher concentration of P. The potential source of this P may include the deposition of airborne particulate P derived from the more productive mineral soils surrounding the upland catchments, or the release of P from Fe/Al-organic complexes associated with the higher in-lake

TDOC concentrations, both of which are known to be a source of P for receiving lakes (Francko and Heath, 1982; Carpenter et al., 1998). Disentangling both of their relative influences, however, requires further work.

The littoral chydorid species recorded in this study are typical of blanket bog water bodies (Griffiths, 1973; Hannigan et al., 2011), and are generally tolerant of low alkalinities and pH (Duigan and Kovach, 1991; Duigan, 1992; de Eyto et al., 2002). The marked difference in chydorid diversity and community structure between the upland and lowland lakes suggests that hydrochemistry was the main determinant of biological differences. Chydorid communities are known to respond to changes in trophic state (Hofmann, 1996; Bos and Cumming, 2003), acidity and alkalinity (Fryer, 1980; Duigan and Kovach, 1991), water temperature (Bos and Cumming, 2003), catchment area (Duigan and Kovach, 1994) and complexity of the littoral habitat (Tremel et al., 2000). The change in chydorid communities in this study suggests that pH, alkalinity and base cation concentrations have a greater influence on the chydorid communities of blanket bog lakes than productivity. This view is supported by the greater occurrence and abundance of species such as *E. lamellatus*, *C. rectirostris* and *A. costata* in the lowland lakes, known to be less tolerant of lower pH (Duigan and Kovach, 1994; Walseng et al., 2008), and conversely, the higher abundance of *A. excisa*, *Chydorus piger* Sars, *A. rustica* in the upland lakes, known to be acid-tolerant (Fryer, 1968; Duigan and Kovach, 1991, 1994). Chydorid species richness is also known to decrease with increasing acidity (Fryer, 1980), thereby explaining the reduced species richness of the upland lakes. Interestingly, the greater primary production of the upland lakes had no discernible influence on *C. sphaericus*, a species known to respond well to eutrophication (Hofmann, 1996).

The littoral macroinvertebrate communities of the study lakes, as for chydorids, were characteristic of blanket bog water bodies (Laurie, 1942; Crisp and Heal, 1958; Griffiths, 1973; Downie et al., 1998; Standen, 1999; Towers, 2004; Hannigan et al., 2011; Hannigan and Kelly-Quinn, 2012). The dominance of aquatic Coleoptera and Heteroptera in bog standing water habitats has previously been reported in Scotland (Downie et al., 1998; Towers, 2004), with predatory dytiscids being the most species-rich group of coleopterans and Corixidae being the most species-rich group of heteropterans. Aquatic Coleoptera assemblages associated with standing water bodies on bog have been shown to be quite distinct from other assemblages found in other freshwater habitats found throughout Ireland (Foster et al., 1992).

Similar to the chydorid communities, there was a marked difference in the littoral macroinvertebrate communities between the upland and lowland lakes. The greater diversity of ephemeropteran and trichopteran species in the lowland lakes, such as *C. luctuosa*, *Centroptilum luteolum* (Müller), *Siphonurus alternatus* (Say) and Leptoceridae trichopterans, is likely explained by the less acidic conditions and higher base cation concentrations as many ephemeropteran and trichopteran species are known to be intolerant of low pH (Ormerod et al., 1987; Punzo and Thompson, 1990; Bendell and McNicol, 1995; Lyche Solheim, 2005). The greater presence and abundance of the caseless trichopterans, Polycentropodidae, in the lowland lakes may also be due to their preference for mineral substrates (Heino, 2000; Tolonen et al., 2001), which were more common in the lowland lakes. A notable change in coleopteran communities was also observed with the lowland lakes dominated numerically by smaller dytiscids (Hydroporinae) and the upland lakes dominated by larger bodies dytiscids (Dytiscinae). It is quite likely that the higher abundances of

larger coleopterans in the upland lakes was due to the lack of fish predation in three of the most elevated lakes, however, these differences may be also due to changes in hydrochemistry, altitude and habitat, all of which are known to influence coleopteran communities (Nilsson and Holmen, 1995; Fairchild et al., 2000; Eyre et al., 2005, 2006).

The aquatic macrophytes, similar to the invertebrates, were characteristic of blanket bog water bodies (Crisp and Heal, 1958; Griffiths, 1973; van Groenendaal et al., 1983; Murphy, 2002). The greater macrophyte species richness of the lowland lakes, as for the invertebrates, is likely explained by their higher pH and base cation concentrations as increasing acidity is known to reduce macrophyte species richness (Vestergaard and Sand-Jensen, 2000). Differences in benthic substrate between the lakes, the lowland lakes characterised by a mineral benthos as opposed to a more peat-dominated benthos in the upland lakes, is also likely to have been a determinant of the higher species richness of the lowland lakes. In a study of macrophyte assemblages of standing waters in Britain, Palmer et al. (1992) found that softwater lakes with mineral substrates contained a greater diversity of species in comparison with more upland lakes without a mineral benthos.

A number of rare species were recorded during this study. The first discovery of the larvae of *C. aenea* from Ireland (Drinan et al., 2011) was the most notable finding. Adults of *C. aenea* had previously been recorded from just four hectads in Ireland and are essentially confined to a few standing waters in the south-west (Nelson and Thompson, 2004). Two coleopteran species listed as near threatened in the Irish Red Data list for water beetles (Foster et al., 2009) were also recorded. *A. arcticus* and *D. lapponicus* are usually restricted to upland habitats in Ireland and are considered glacial relict species (McCormack, 2005), with upland lakes on peat

being their preferred habitat (Foster et al., 2009). Similarly, the rare European plant species *E. aquaticum* was also recorded. This plant has a very limited distribution in northern Europe, confined to lakes on bog in Scotland and western Ireland (Murphy 2002).

2.6. Conclusions

The findings of this study reveal that blanket bog lakes are important habitats for both aquatic macrophyte and invertebrate biodiversity. The majority of the species recorded are characteristic of water bodies on blanket bog found elsewhere, e.g. Britain (Downie et al., 1998; Standen, 1999; Murphy, 2002). Although regional differences in biotic communities among lakes existed, extensive species overlap among regions provides strong evidence for a definite link between the biotic assemblages and the blanket bog lake habitat. A regional difference in some species distribution within this habitat, e.g. *D. lapponicus*, does, however, pose a serious conservation issue. The spatial configuration of blanket bog within Ireland is not contiguous and very often patches of this habitat are configured within a mosaic of other interconnected habitats within the overall landscape. This greatly limits the ability of a species to expand its range, especially in upland blanket bog areas where the distance required to colonise a similar habitat exceeds the dispersion capabilities of a given species.

The disproportionate extent of European blanket bog in Ireland, especially lowland blanket bog, should yield a greater research effort to ensure blanket bog lake habitat degradation is prevented, however, this is not reflected in the sampling effort being afforded by statutory bodies (Irvine et al., 2007). Considering the insufficiencies of baseline data and the threats facing blanket bog lakes (Holden et al., 2004), it is quite possible that future habitat degradation of these lakes in Ireland may go unnoticed, thereby leading to significant loss of biodiversity and possibly irreparable damage to this habitat.

2.7. References

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Chapter 3

The impact of catchment conifer plantation forestry on the hydrochemistry of peatland lakes



An example of an upland blanket bog lake surrounded by conifer plantations.

3.1. Summary

The hydrochemistry of 26 small blanket bog lakes was examined to assess the impact of conifer plantation forestry on lake water chemistry. Lakes were selected from three distinct catchment land use categories: i) unplanted blanket bog only present in the catchment, ii) mature (closed-canopy) conifer plantation forests only present in the catchment and iii) catchments containing mature conifer plantation forests with recently clearfelled areas. All three catchment land uses were replicated across two geologies: sedimentary (sandstone) and igneous (granite). Lakes with afforested catchments across both geologies had elevated concentrations of phosphorus (P), nitrogen (N), total dissolved organic carbon (TDOC), aluminium (Al) and iron (Fe), with the highest concentrations of each parameter recorded from lakes with catchment clearfelling. Dissolved oxygen concentrations were also significantly reduced in the afforested lakes, particularly the clearfell lakes. Analysis of runoff from a nearby recently clearfelled site revealed high biological and chemical oxygen demands, consistent with at least part of the elevated concentrations of TDOC emanating from clearfelled sites having higher biochemical lability. Inorganic fertilisers applied at the start of the forest cycle, the decay of the underlying peat soil and accumulated surface tree litter, and leachate from felled trees are the likely sources of the elevated concentrations of plant nutrients, TDOC, heavy metals and major ions, with excessive peat soil disturbance during clearfelling likely exacerbating the runoff into lakes. This study has demonstrated a clear, deleterious impact of conifer plantations on the water quality draining from blanket bog catchments, with major implications for the management of afforested peatlands.

3.2. Introduction

Plantation forests currently cover approximately 10% of the Irish landscape, 80% of which is comprised of exotic conifers (NFI, 2007). Forest activities including afforestation, draining, thinning, clearfelling, reforestation and forest road construction, can result in severe alterations to major nutrient sinks and sources, increases in soil temperature and humidity, changes to soil structure caused by harvesting machinery, and increased fluxes of soluble and particulate matter from forested soils to receiving waters (Laiho et al., 1999; Bhatti et al., 2000; Saari et al., 2009; Zummo and Friedland, 2011). Waters draining catchments planted with conifer plantations have been found to have elevated concentrations of plant nutrients, heavy metals, both dissolved and particulate organic matter, major ions, as well as increased acidity (Kortelainen and Saukkonen, 1998; Binkley et al., 1999; Pühr et al., 2000; Neal et al., 2001; Vuorenmaa et al., 2002; Cummins and Farrell, 2003a, 2003b; Harriman et al., 2003; Neal et al., 2004a, 2004b; Feller, 2005; Ågren et al., 2010; Ågren and Löfgren, 2012).

Although the effect of forestry on lentic systems is less frequently studied than for lotic systems (Laird and Cumming, 2001; Northcote and Hartman, 2004), forestry practices can affect the chemical and ecological state of lakes by increasing catchment loadings of plant nutrients, major ions, humic substances and sediment (Rask et al., 1998; Carignan and Steedman, 2000; Carignan et al., 2000; Steedman, 2000; Watmough et al., 2003; Feller, 2005; Kreutzweiser et al., 2008). Elevated concentrations of these substances can persist for a long time in lakes and may lead to widespread and pervasive changes to lake ecosystems, in comparison with their impact in streams which may be reduced by overriding factors such as hydraulic

disturbance and riparian shading. The few short-term studies of forestry impacts on lakes have reported increases in dissolved organic carbon (DOC), leading to modification of the euphotic depth (Rask et al., 1998; Carignan et al., 2000), and an increase in nutrient loads leading to higher primary production (Planas et al., 2000; Prepas et al., 2001).

Surface water acidification associated with conifer plantation forestry has received greater research effort in comparison with other issues concerning forest-surface water interactions (Nisbet, 2001). Canopy interception of airborne pollutants is deemed to be the main process by which forest plantations contribute to the acidification of surface waters; coniferous trees (especially the needles) are known to be more efficient at scavenging atmospheric pollutants, such as sulphur (S) and nitrogen (N) compounds, in comparison with non-forested sites (Reynolds et al., 1994). Increased scavenging of marine-derived ions, such as sodium (Na) and magnesium (Mg), can also result in acid runoff from plantation forests through the displacement of hydrogen (H^+) and aluminium (Al) cations within the soil, this generally termed the 'sea-salt effect' (Harriman et al., 2003; Hindar, 2005; Larssen and Holme, 2006). The acidification of streams draining afforested catchments, via the interception of both marine and non-marine derived acidifying compounds, has been widely documented throughout poorly-buffered catchments in Britain and Europe (Ormerod et al., 1989; Pühr et al., 2000; Ågren et al., 2010; Neal et al., 2010; Ågren and Löfgren, 2012).

Eutrophication of water bodies in Ireland has become more prevalent in recent years and is attributed mainly to diffuse nutrient runoff from agriculture (Toner et al., 2005). The ability of catchment soils to retain phosphorus (P), applied as fertiliser, is a major determinant of P loadings to receiving waters (Cummins and

Farrell, 2003a). Many plantation forests in Ireland, predominantly monoculture stands of exotic conifers, have been planted on peat soil blanket bogs since the 1950s – peat soils being the dominant (42.1%) soil type upon which these forests have been established (NFI, 2007). Peat soils contain very low concentrations of iron (Fe) and aluminium (Al) oxides, and thereby have a very low capacity to sorb and retain P (Cuttle, 1983). Any P fertiliser applied to forests on peat bogs may, therefore, pose a high risk to receiving waters, particularly given their inherently nutrient poor status. Although occupying a much smaller surface area than agricultural lands in Ireland, plantation forestry may, nevertheless, pose a considerable risk to naturally oligotrophic aquatic systems (Cummins and Farrell, 2003a; McElarney et al., 2010; Rodgers et al., 2010).

The chemical effects of plantation forests on stream systems may be difficult to discern, due to the pulsed nature of forestry-derived inputs, these being concentrated at times of major disturbance such as planting, thinning and harvesting (Giller and O'Halloran, 2004). Stream-flow concentrations of plant nutrients and other materials are highly dependent on rainfall, which both flushes chemicals into streams and dilutes them, further adding to the difficulty of determining the scale of plantation forestry inputs. Dissolved and particulate substances tend to accumulate in downstream lakes, which act as nutrient sinks, due to their enhanced nutrient cycling and internal loading in comparison with streams (Søndergaard et al., 2003). Therefore, lakes may provide a more integrated assessment of catchment chemical influxes associated with forestry operations.

Although the rate of peatland afforestation has decreased considerably during the past two decades (Black et al., 2009), many of the previously planted blanket bog forests are now reaching harvestable age and concerns have been raised about the

potential for plant nutrient and sediment loss to receiving surface waters (Kortelainen and Saukkonen, 1998; Ahtiainen and Huttunen, 1999). This study has two main objectives: i) to determine whether catchment forestry operation yields a similar hydrochemical response in lakes as has been described for running waters and ii) to determine whether or not this hydrochemical change is predominantly acidification or eutrophication driven. Small (typically < 2.5 ha) replicate lakes were selected in homogenous blanket bog catchments, with catchment land use restricted to either unplanted blanket bog or conifer plantation forestry, to ensure that any change in water chemistry could be unambiguously attributed to plantation forestry, rather than from other concurrent catchment inputs, particularly those from agricultural activity. The potential mitigating impact of underlying geology was examined by selecting lakes in sedimentary (sandstone) and igneous (granite) catchments. To further investigate potential differences in the biochemical lability of TDOC emanating from afforested catchments, water samples were collected from three separate streams from a nearby recently clearfelled site: i) a stream draining from the clearfelled site, ii) a stream draining from the mature plantation and iii) a stream draining from nearby undisturbed blanket bog.

3.3. Materials and methods

3.3.1. Site description

3.3.1.1. Study lakes

Potential study lakes in areas of upland and lowland blanket bog throughout the west of Ireland were identified using ArcGIS (ESRI ArcMap v.9.3). Lakes were selected on the basis of size (all lakes but one were ≤ 4 ha), geology, soil type and catchment land use. The three distinct catchment land uses selected included i) blanket bog (B): unplanted blanket bog only present in the catchment, ii) mature plantation (M): catchment dominated by closed-canopy conifer plantation forest only and iii) clearfell (C): catchment containing closed-canopy conifer plantation forest and recently clearfelled areas (within previous 2 – 5 years). A forestry database was provided by Coillte Teoranta, the Irish semi-state forestry body. Conifer plantation forests surrounding the lakes were dominated by sitka spruce (*Picea sitchensis* Bongard) with some lodgepole pine (*Pinus contorta* Douglas ex Loudon) also present. Forestry operations were carried out to current Irish best management practices (Forest Service, 2000). The plant species surrounding the undisturbed blanket bog lakes were typical blanket bog species (Fossitt, 2000). These included purple moor-grass (*Molinia caerulea* (Linnaeus)), cross-leaved heath (*Erica tetralix* Linnaeus), deergrass (*Scirpus cespitosus* Linnaeus), common cottongrass (*Eriophorum angustifolium* Roth), bog asphodel (*Narthecium ossifragum* (Linnaeus) Hudson) and white beak-sedge (*Rhynchospora alba* (Linnaeus) Vahl).

A total of 26 lakes were selected following site visits: 13 lakes had catchments of unplanted blanket bog, seven lakes had catchments dominated by mature conifer plantation forests and no clearfelling and six lakes had catchments containing mature (closed-canopy) conifer plantation forests with recently clearfelled areas (Table 3.1). Lakes were situated in three different regions in the west of Ireland (Fig. 3.1). The 12 lakes in the south-west and mid-west were underlain by sandstone (S) geology, whereas the 14 lakes in the west were underlain by granite geology (G). Lake area ranged from 0.5 – 5.5 ha (mean = 1.8 ha), mean depth ranged from 1.4 – 3.5 m (mean = 2.2 m) and catchment area ranged from 2.3 – 72.6 ha (mean = 21.8 ha). The 13 blanket bog lakes selected in this study were the same as those studied in chapter 2 (Section 2.3.1.).

3.3.1.2. Clearfell site – Glennamong

The Glennamong catchment (total area 685 ha) is situated some 50 km north of the western lakes (Fig. 3.1). The catchment is dominated by blanket bog which is underlain by quartzite and schist of low buffering capacity. Lodgepole pine comprised 86% of the tree crop and sitka spruce 13%. Clearfelling of an 8 ha coupe commenced at the site on the 8th February 2011, following current Irish forestry best practice. Water samples were collected from three separate streams on site: i) a stream draining from the clearfelled site, ii) a stream draining from the mature plantation and iii) a stream draining from nearby undisturbed blanket bog.

Table 3.1. Geographic location, physical characteristics and catchment land use of the non-forested lakes. Blanket bog classification is based on Fossitt (2000) habitat classification scheme (S = sandstone, G = granite, B = blanket bog, M = mature plantation and C = clearfell).

Lake code	Latitude/Longitude	Altitude (m)	Lake area (ha)	Mean depth (m)	Catchment area (ha)	% Blanket bog	% Mature plantation	% Clearfell	Underlying geology	Blanket bog classification
SB1	N 51°58.953' W 009°11.188'	426	1.6	1.6	2.3	100.0	0.0	0.0	Green-grey sandstone & purple siltstone	Upland
SB2	N 51°58.960' W 009°10.916'	429	2.2	2.2	17.6	100.0	0.0	0.0	Green-grey sandstone & purple siltstone	Upland
SB3	N 53°04.899' W 008°40.568'	282	0.9	2.5	10.0	100.0	0.0	0.0	Mudstone, siltstone, conglomerate	Upland
SB4	N 53°03.747' W 008°28.646'	183	1.2	1.5	10.0	100.0	0.0	0.0	Mudstone, siltstone, conglomerate	Upland
SB5	N 52°56.533' W 008°43.845'	273	0.5	2.1	11.6	100.0	0.0	0.0	Mudstone, siltstone, conglomerate	Upland
SB6	N 52°56.770' W 008°43.710'	262	1.4	1.6	11.5	100.0	0.0	0.0	Mudstone, siltstone, conglomerate	Upland
GB1	N 53°19.239' W 009°25.840'	93	1.2	2.4	12.2	100.0	0.0	0.0	Aphyric fine grained granite	Lowland
GB2	N 53°18.354' W 009°26.926'	108	1.0	1.4	5.3	100.0	0.0	0.0	Aphyric fine grained granite	Lowland
GB3	N 53°18.210' W 009°26.981'	100	1.2	2.3	15.7	100.0	0.0	0.0	Aphyric fine grained granite	Lowland
GB4	N 53°18.511' W 009°27.485'	80	1.2	3.1	52.7	100.0	0.0	0.0	Monzogranite, small megacrysts	Lowland
GB5	N 50°18.508' W 009°27.379'	86	0.5	2.3	5.2	100.0	0.0	0.0	Monzogranite, small megacrysts	Lowland
GB6	N 50°17.207' W 009°21.697'	73	4.0	2.5	72.6	100.0	0.0	0.0	Monzogranite, mafic, megacrystic	Lowland
GB7	N 50°17.232' W 009°21.436'	77	1.4	1.8	6.8	100.0	0.0	0.0	Monzogranite, mafic, megacrystic	Lowland

Table 3.1. (cont.) Geographic location, physical characteristics and catchment land use of the afforested lakes. Blanket bog classification is based on Fossitt (2000) habitat classification scheme (S = sandstone, G = granite, B = blanket bog, M = mature plantation and C = clearfell).

Lake code	Latitude/Longitude	Altitude (m)	Lake area (ha)	Mean depth (m)	Catchment area (ha)	% Blanket bog	% Mature plantation	% Clearfell	Underlying geology	Blanket bog classification
SM1	N 51°59.242' W 009°14.428'	366	1.2	2.2	13.8	6.9	93.1	0.0	Green sandstone & purple siltstone	Upland
SM2	N 51°58.982' W 009°14.125'	373	0.9	1.6	20.2	0.8	99.2	0.0	Green sandstone & purple siltstone	Upland
SM3	N 51°58.591' W 009°12.555'	383	2.1	1.9	29.1	12.3	87.7	0.0	Green sandstone & purple siltstone	Upland
GM1	N 53°19.340' W 009°24.141'	114	3.5	2.8	33.2	3.0	97.0	0.0	Aphyric fine grained granite	Lowland
GM2	N 53°22.108' W 009°23.130'	150	4.0	2.8	32.2	1.6	98.4	0.0	Monzogranite, mafic, megacrystic	Upland
GM3	N 53°22.740' W 009°23.529'	233	1.0	2.3	9.3	2.2	97.8	0.0	Monzogranite, mafic, megacrystic	Upland
GM4	N 53°23.398' W 009°23.165'	239	1.1	2.1	35.3	2.4	97.6	0.0	Monzogranite, mafic, megacrystic	Upland
SC1	N 53°02.562' W 008°34.388'	185	2.5	1.6	25.0	0.0	67.1	32.9	Mudstone, siltstone, conglomerate	Upland
SC2	N 53°01.446' W 008°37.110'	122	1.4	1.9	16.7	16.7	51.9	31.4	Mudstone, siltstone, conglomerate	Lowland
SC3	N 52°57.372' W 008°44.332'	291	5.5	2.9	43.1	0.0	87.3	12.7	Mudstone, siltstone, conglomerate	Upland
GC1	N 53°20.912' W 009°19.059'	75	2.7	1.7	42.5	0.0	85.0	15.0	Monzogranite, mafic, megacrystic	Lowland
GC2	N 53°20.064' W 009°20.572'	85	2.2	1.8	30.0	2.2	65.0	32.9	Monzogranite, mafic, megacrystic	Lowland
GC3	N 53°20.020' W 009°20.507'	86	1.1	3.5	3.7	9.4	12.1	78.6	Monzogranite, mafic, megacrystic	Lowland

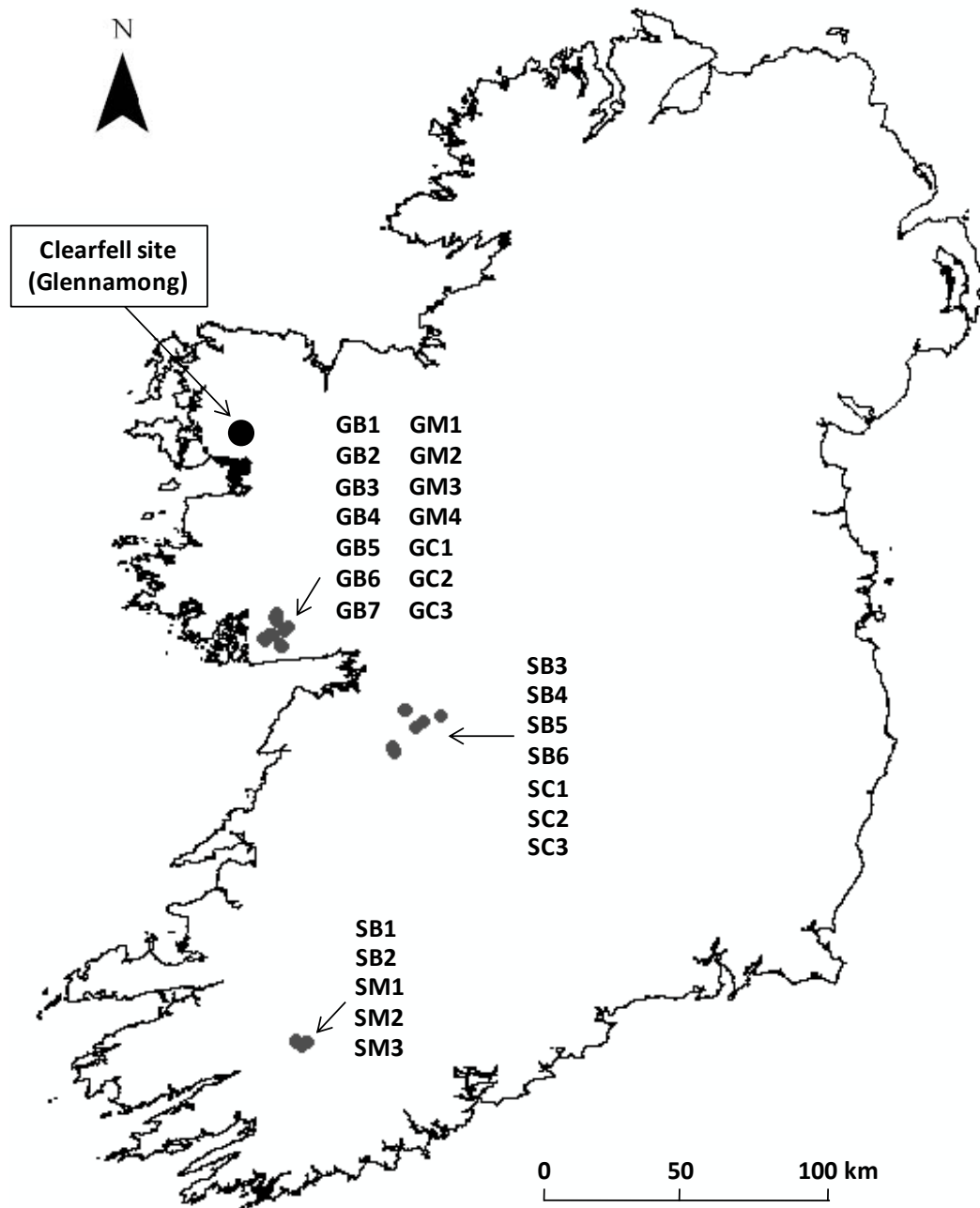


Figure 3.1. Map of Ireland showing the location of the 26 study lakes and the clearfell study site – Glennamong (S = sandstone, G = granite, B = blanket bog, M = mature plantation and C = clearfell).

3.3.2. Water chemistry sampling

3.3.2.1. Lake samples

Water samples were taken from the littoral zone of each lake at a similar depth (0.6 m) and distance (7 m) from shore, bimonthly for 12 months, beginning in March 2009. Water samples were collected in acid-washed polypropylene bottles, stored at 4°C in a cooler box and transported to the laboratory for analysis within 24 hours after collection. Conductivity, dissolved oxygen and temperature were measured on site using WTW portable meters.

A total of 19 water chemistry parameters were analysed: pH, alkalinity, colour, total dissolved organic carbon (TDOC), total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), total oxidised nitrogen (TON), ammonia, sodium (Na), chloride (Cl), magnesium (Mg), sulphate (SO₄), potassium (K), calcium (Ca), iron (Fe), manganese (Mn), total monomeric aluminium (tot.Al) and chlorophyll *a*. Methods for water chemistry analyses are described in chapter 2 (Section 2.3.2.).

3.3.2.2. Clearfell site samples – Glennamong

Dip samples were collected from the three streams from the Glennamong site on a single occasion on the 5th May 2011. Samples were taken and stored in the same manner as lake samples. Three parameters were analysed for streams from the Glennamong site. Biological oxygen demand (BOD) was measured using a standard five-day test method. Dissolved oxygen of thoroughly mixed samples was measured

using a calibrated WTW dissolved oxygen metre before and after five days of incubation at 20°C in the dark. BOD was calculated as the difference between the initial and final dissolved oxygen concentrations. Chemical oxygen demand (COD) was measured using closed reflux colourimetric method. Hach COD vials (0-150 mg O₂/l) and Reagcon COD vials (0-1500 mg O₂ l⁻¹) were used. Calibration was carried out using potassium hydrogen phthalate standards. TDOC was analysed as per the lake samples.

3.3.3. Statistical analyses

Principal component analysis (PCA) analysis was performed, using PRIMER 6 (PRIMER-E, UK), to determine patterns in lake water chemistry. The ordinations were based on a Euclidean distance matrix derived from a normalised and log (x + y) transformed data set, y = smallest non-zero value in the data set.

Analysis of variance (ANOVA) was performed, using PASW Statistic 17, to test for significant among-lake differences in chemical variables with respect to catchment land use (blanket bog, mature plantation and clearfell) and geology (sandstone and granite). Using a Bonferroni correction for multiple tests (Sokal and Rohlf, 1995), significance criteria were set at a conservative $p < (0.05 / 22)$. Prior to performing ANOVAs, normality and homogeneity of variances were tested using Kolmogorov-Smirnov and Levene's tests, respectively. The ANOVA models, with Bonferroni correction applied, were calculated on the basis of Type III sums of squares to take the unbalanced design into account. Significant results were tested for pair-wise comparisons using Bonferroni *post-hoc* tests. Dependent variables were log (x + y) transformed where necessary to fulfil the requirements of the parametric

tests. Pearson correlation analyses were carried out, using PASW Statistic 17, to explore relationships within the water chemistry data from the lakes.

3.4. Results

3.4.1. Lake water chemistry

3.4.1.1. Principal Component Analysis – Sandstone lakes

PCA revealed a strong effect of plantation forestry on sandstone lake water chemistry, with clearfell lakes, and to a lesser extent mature plantation lakes, being chemically distinct from the non-forested blanket bog lakes (Fig. 3.2). PC axis 1 accounted for 42.4% of the total variance in the water chemistry variables. PC axis 2 and PC axis 3 accounted for 16.2% and 11.2% of the total variance, respectively.

Clearfell lakes scored negatively on PC axis 1, and were associated with elevated concentrations of TP, SRP, TN, ammonia, chlorophyll *a*, TDOC, total monomeric Al, Fe, Mn and major ions, higher colour and conductivity, and lower dissolved oxygen concentrations (Fig. 3.2). PC axis 2 represented pH, alkalinity, temperature, SO₄ and K; however, this axis did not differentiate among lakes of contrasting catchment land use (Fig. 3.2).

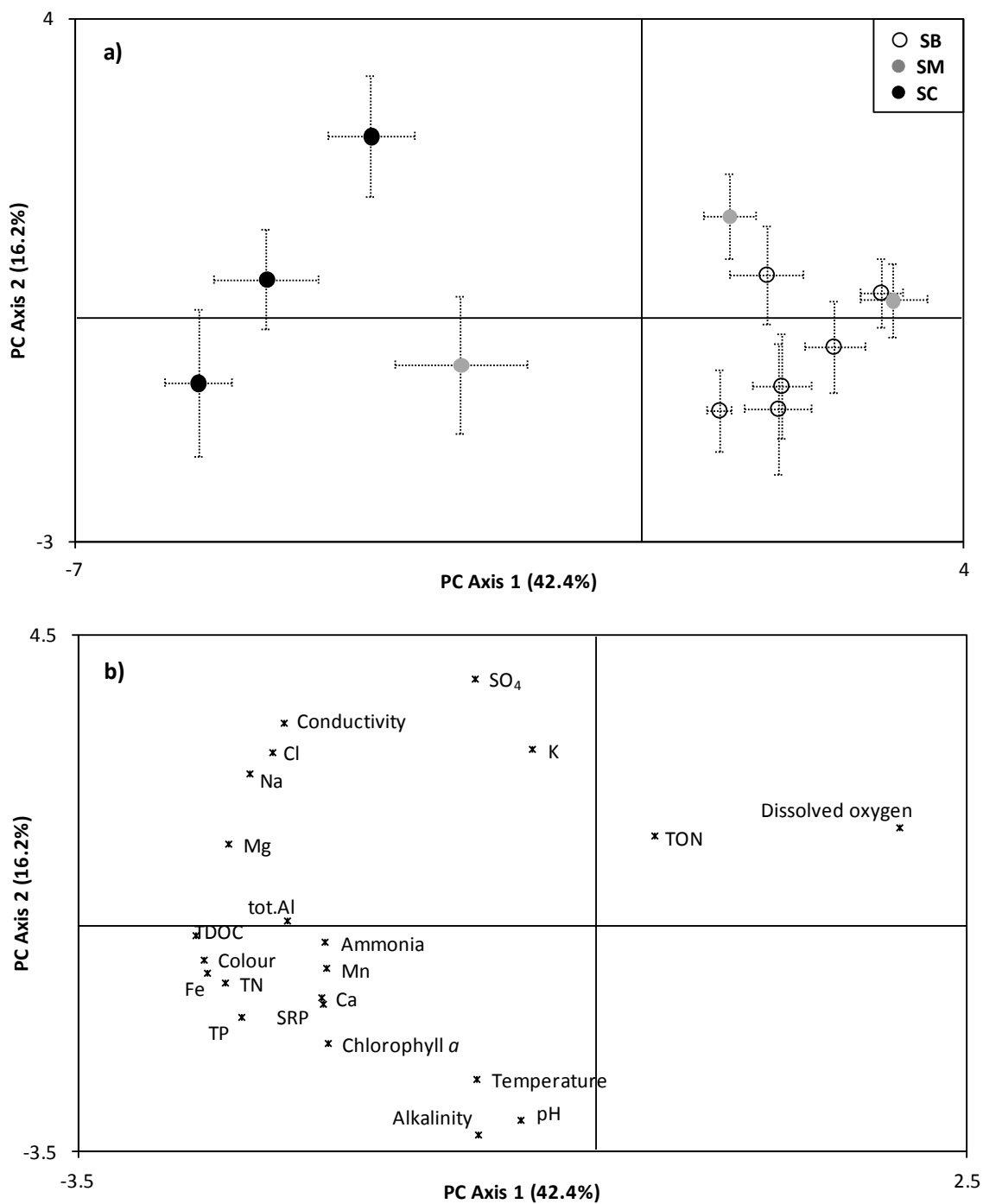


Figure 3.2. Principal component analysis (PCA) ordinations indicating **a)** the variation in chemical status of the sandstone lakes and **b)** the variable loadings of the chemical variables on PC axis 1 and PC axis 2. Group centroids represent the mean lake scores (± 1 S.E.) over the 12-month sampling period (S = sandstone, B = blanket bog, M = mature plantation and C = clearfell).

3.4.1.2. Principal Component Analysis – Granite lakes

As for the sandstone lakes, PCA of the granite lakes revealed a strong effect of plantation forestry on lake water chemistry (Fig. 3.3). PC axis 1 accounted for 30.3% of the total variance in the water chemistry variables. PC axis 2 and PC axis 3 accounted for 24.1% and 12.8% of the total variance, respectively.

Clearfell and mature plantation lakes tended to score negatively on PC axis 1, and were associated with elevated concentrations of TP, SRP, TN, ammonia, TDOC, total monomeric Al, Fe, Mn, higher colour and lower dissolved oxygen concentrations (Fig. 3.3). PC axis 2 largely represented major ions and conductivity. Unlike the hydrochemistry pattern for sandstone lakes, forestry operations in the granite catchments were much less associated with elevated major ions (Na, Cl, Mg and SO₄) and conductivity, which were more associated with non-forested blanket bog lakes (Fig. 3.3). As with the sandstone lakes, pH, alkalinity and TON did not separate the non-forested from the forestry-affected lakes.

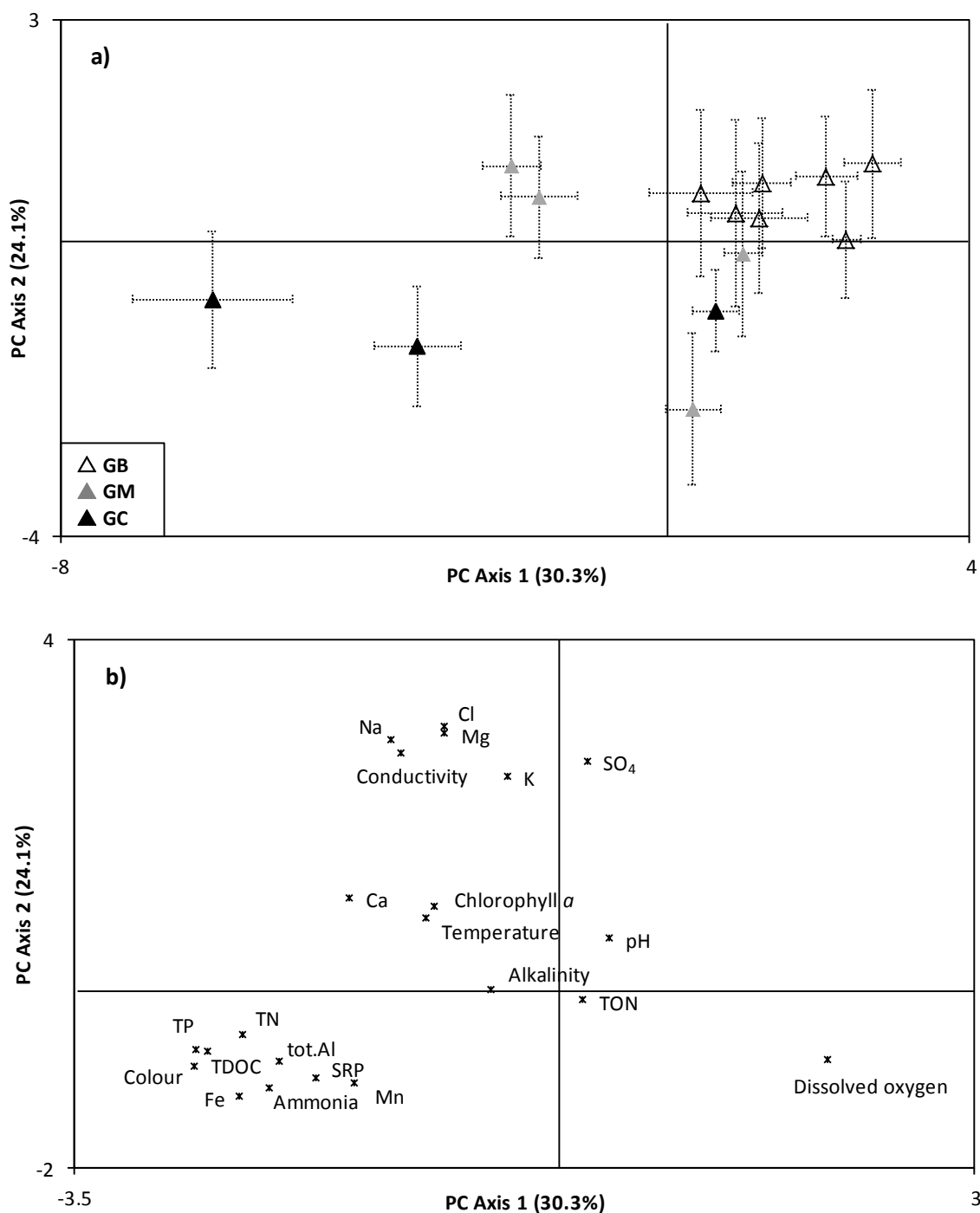


Figure 3.3. Principal component analysis (PCA) ordinations indicating **a)** the variation in chemical status of the granite lakes and **b)** the variable loadings of the chemical variables on PC axis 1 and PC axis 2. Group centroids represent the mean lake scores (± 1 S.E.) over the 12-month sampling period (S = sandstone, G = granite, B = blanket bog, M = mature plantation and C = clearfell).

3.4.2. Univariate analysis of lake water chemistry

Univariate analysis of water chemical parameters revealed significant differences among lakes with respect to catchment land use and geology (Fig. 3.4; Table 3.2). The forestry-affected lakes had significantly higher TDOC, TP, K, total monomeric Al and Fe concentrations, increased colour and lower dissolved oxygen concentrations in comparison with the unplanted blanket bog lakes (Fig. 3.4; Table 3.2). Clearfell lakes also had significantly higher concentrations of TDOC and Fe, increased colour and lower concentrations of dissolved oxygen than mature plantation lakes (Fig. 3.4; Table 3.2). K concentrations were significantly lower only in the mature plantation lakes (Fig. 3.4; Table 3.2). With respect to geology, the lakes underlain by granite geology had significantly higher marine ion concentrations, as well as higher conductivity and temperature values (Fig. 3.4; Table 3.2). A significant interaction between catchment land use and geology occurred for SO_4 , Cl and Mg, with higher concentrations in sandstone clearfelled lakes but lower concentrations in granite clearfelled lakes (Fig. 3.4; Table 3.2). The differences in lake pH, alkalinity, chlorophyll *a*, SRP, TN, TON, ammonia, Ca and Mn concentrations across catchment land use and geology were not significant (Fig. 3.4; Table 3.2).

Correlation analysis revealed strong linkages between individual hydrochemical parameters within lakes (Table 3.3). TDOC and colour were both strongly positively correlated with TP, SRP, TN, ammonia, total monomeric Al, Mn and Fe. TP was also strongly correlated with Fe and TDOC (Fig. 3.5; Table 3.3). The strong positive correlation of Cl with Na, Mg and SO_4 , indicates that these ions were mainly of marine origin, assuming Cl is entirely marine-derived and unreactive

within the catchment (Evans et al., 2001). Although strongly correlated with alkalinity, pH did not show any other significant correlation with SO₄, marine-derived ions, TDOC or TON (Table 3.3).

Traditionally, lake trophic status in Ireland has been assessed using a modified version of the Organisation for Economic Cooperation and Development (OECD) scheme which was based on annual maximum chlorophyll *a* concentration (McGarrigle et al., 2010). Under this scheme, nine of the thirteen blanket bog lakes, four of the mature plantation and only one of the clearfell lakes were classified as oligotrophic. The two most trophically enriched lakes were both afforested: SC2 was hypereutrophic and SM2 was strongly eutrophic (Table 3.4).

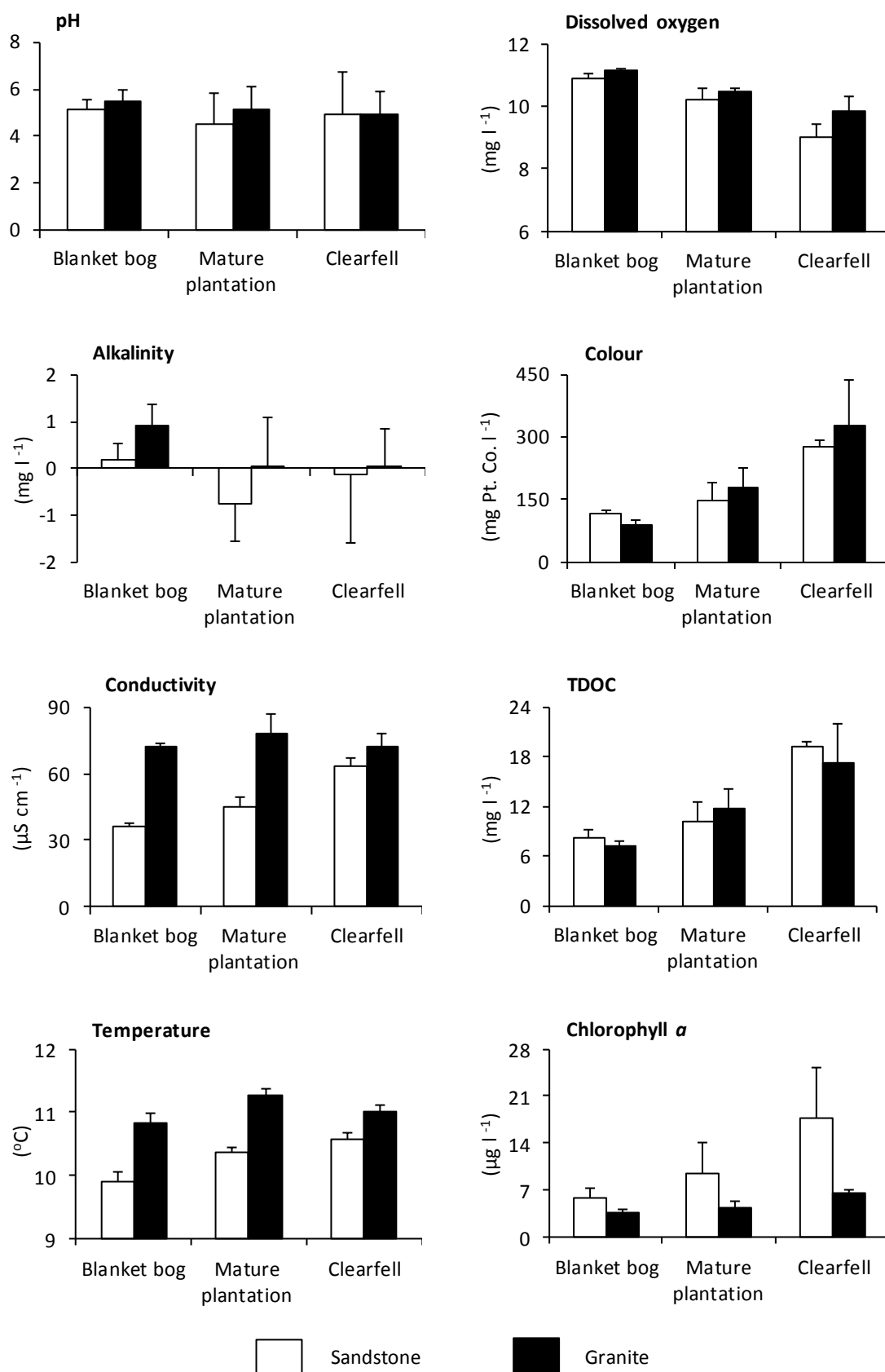


Figure 3.4. Mean \pm 1 S.E. (pH = median \pm 95% C.I.) values/concentrations of hydrochemical parameters for lakes in each catchment land use across both geologies (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 3).

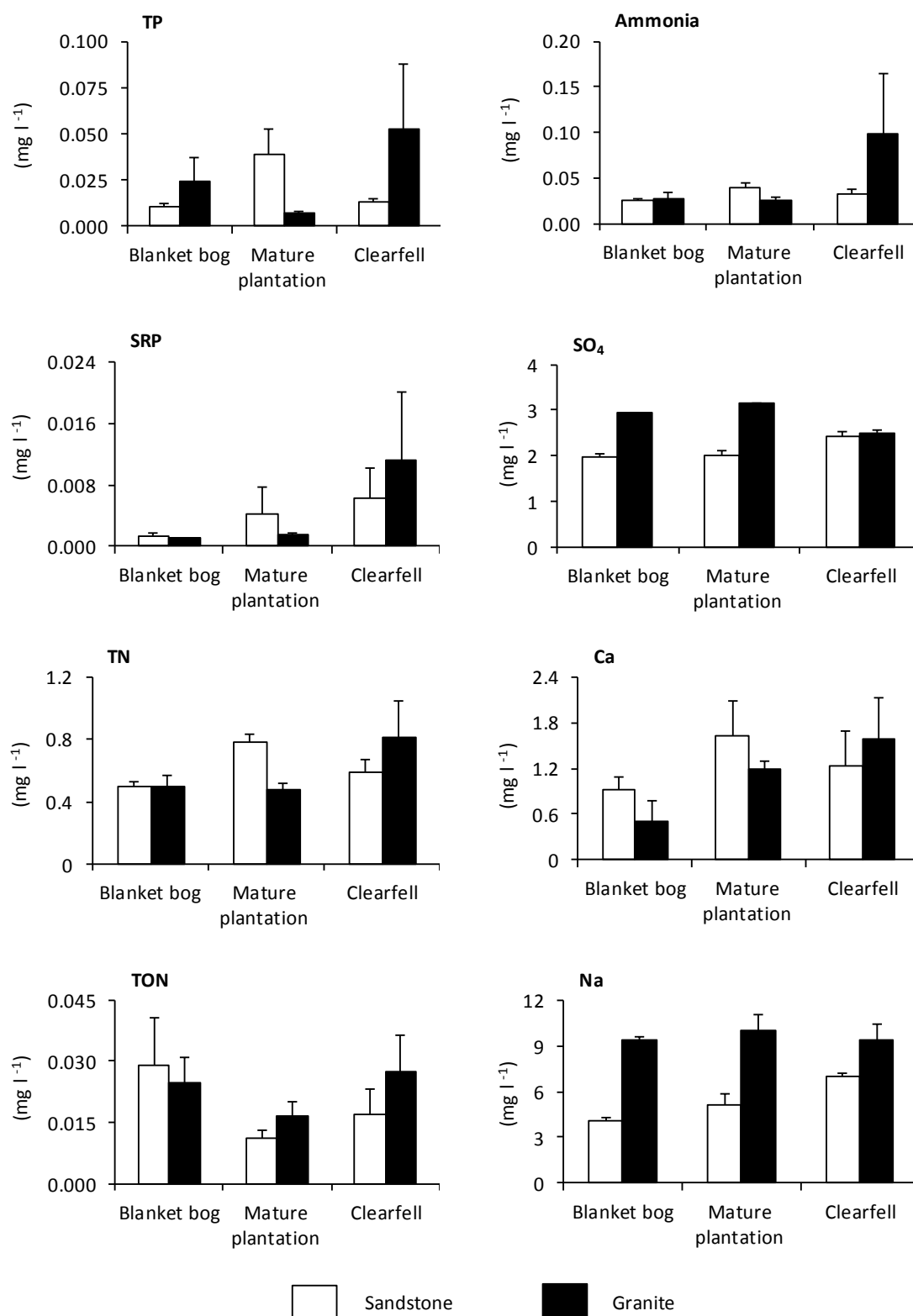


Figure 3.4. (cont.) Mean \pm 1 S.E. concentrations of hydrochemical parameters for lakes in each catchment land use across both geologies (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 3).

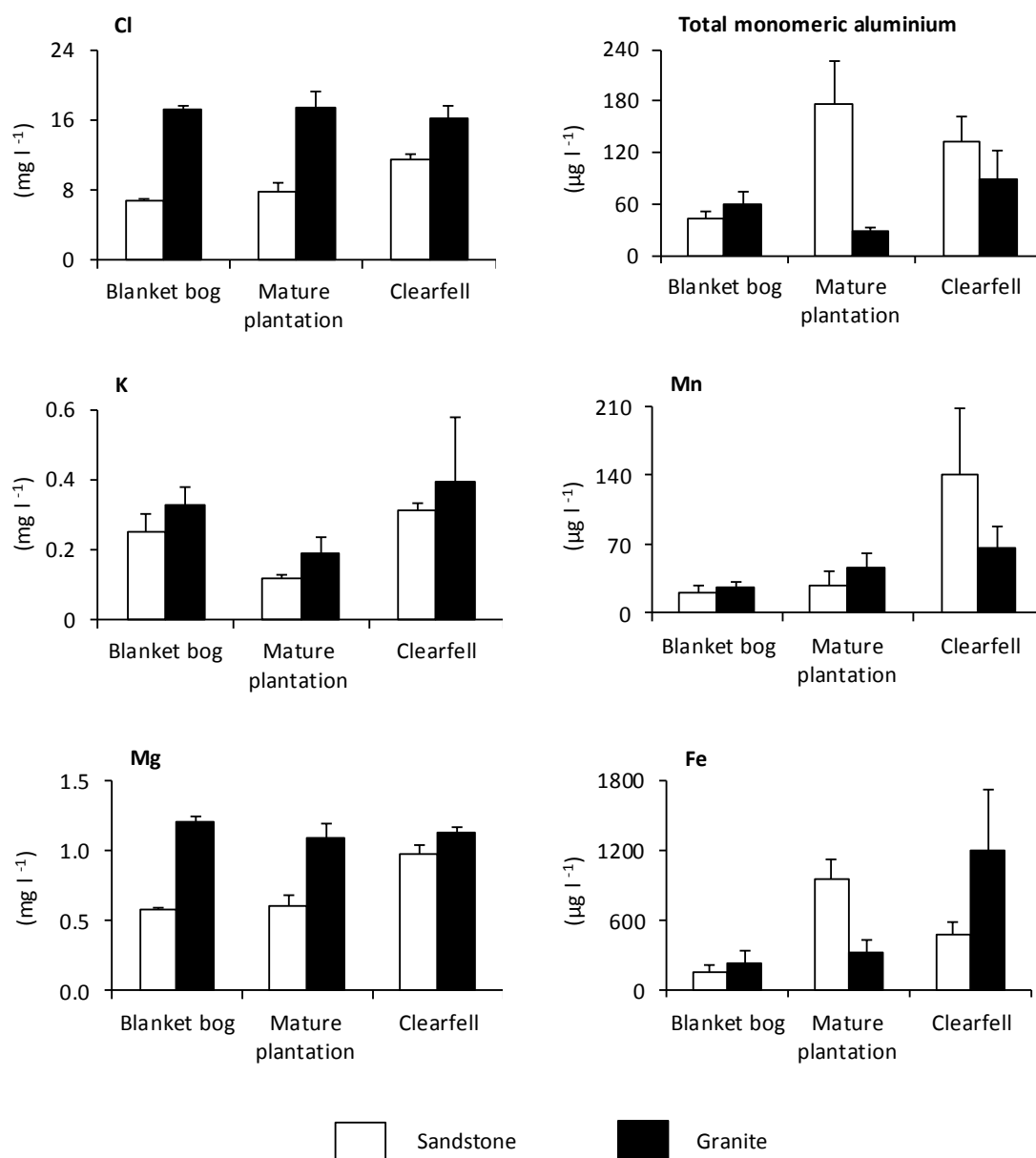


Figure 3.4. (cont.) Mean ± 1 S.E. concentrations of hydrochemical parameters for lakes in each catchment land use across both geologies (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 3).

Table 3.2. Summary of 2 – way Bonferroni corrected ANOVAs of water chemical parameters (mean annual values calculated over the 12-month sampling period), with catchment land use (blanket bog, mature plantation and clearfell) and geology (sandstone and granite) as main factors. Any two catchment land uses sharing a common letter are not significantly different.

	2 - way ANOVA				<i>post-hoc</i> Bonferroni tests		
		d.f.	<i>F</i>	<i>p</i>	Blanket bog	Mature plantation	Clearfell
pH	Land use	2, 20	2.045	0.156	-	-	-
	Geology	1, 20	2.034	0.169	-	-	-
	Interaction	2, 20	0.166	0.848	-	-	-
Alkalinity	Land use	2, 20	0.795	0.465	-	-	-
	Geology	1, 20	1.322	0.264	-	-	-
	Interaction	2, 20	0.009	0.991	-	-	-
Conductivity	Land use	2, 20	6.832	0.005	-	-	-
	Geology	1, 20	58.299	<0.001	Granite > Sandstone		
	Interaction	2, 20	6.854	0.005	-	-	-
Temperature	Land use	2, 20	5.941	0.009	-	-	-
	Geology	1, 20	30.008	<0.001	Granite > Sandstone		
	Interaction	2, 20	1.059	0.365	-	-	-
Dissolved oxygen	Land use	2, 20	23.575	<0.001	a	b	c
	Geology	1, 20	6.182	0.022	-	-	-
	Interaction	2, 20	1.004	0.384	-	-	-
Colour	Land use	2, 20	12.598	<0.001	a	a	b
	Geology	1, 20	0.046	0.832	-	-	-
	Interaction	2, 20	0.842	0.446	-	-	-
TDOC	Land use	2, 20	12.518	<0.001	a	a	b
	Geology	1, 20	0.155	0.698	-	-	-
	Interaction	2, 20	0.547	0.587	-	-	-
Chlorophyll <i>a</i>	Land use	2, 20	6.276	0.008	-	-	-
	Geology	1, 20	9.973	0.005	-	-	-
	Interaction	2, 20	0.681	0.517	-	-	-
TP	Land use	2, 20	8.983	0.002	a	ab	b
	Geology	1, 20	0.889	0.357	-	-	-
	Interaction	2, 20	0.237	0.792	-	-	-
SRP	Land use	2, 20	4.790	0.020	-	-	-
	Geology	1, 20	0.063	0.804	-	-	-
	Interaction	2, 20	0.155	0.858	-	-	-
TN	Land use	2, 20	7.030	0.005	-	-	-
	Geology	1, 20	0.131	0.722	-	-	-
	Interaction	2, 20	0.352	0.708	-	-	-

Significant terms are emboldened.

Table 3.2. (cont.) Summary of 2 – way Bonferroni corrected ANOVAs of water chemical parameters (mean annual values calculated over the 12-month sampling period), with catchment land use (blanket bog, mature plantation and clearfell) and geology (sandstone and granite) as main factors. Any two catchment land uses sharing a common letter are not significantly different.

		2 - way ANOVA			<i>post-hoc</i> Bonferroni tests		
		d.f.	<i>F</i>	<i>p</i>	Blanket bog	Mature plantation	Clearfell
TON	Land use	2, 20	1.069	0.362	-	-	-
	Geology	1, 20	1.052	0.317	-	-	-
	Interaction	2, 20	0.206	0.815	-	-	-
Ammonia	Land use	2, 20	4.665	0.022	-	-	-
	Geology	1, 20	1.517	0.232	-	-	-
	Interaction	2, 20	0.705	0.506	-	-	-
SO₄	Land use	2, 20	0.461	0.637	-	-	-
	Geology	1, 20	47.783	<0.001	Granite > Sandstone		
	Interaction	2, 20	8.286	0.002	-	-	-
Ca	Land use	2, 20	2.722	0.090	-	-	-
	Geology	1, 20	2.100	0.163	-	-	-
	Interaction	2, 20	0.892	0.426	-	-	-
Na	Land use	2, 20	6.193	0.008	-	-	-
	Geology	1, 20	106.076	<0.001	Granite > Sandstone		
	Interaction	2, 20	6.947	0.005	-	-	-
Cl	Land use	2, 20	4.651	0.022	-	-	-
	Geology	1, 20	144.179	<0.001	Granite > Sandstone		
	Interaction	2, 20	8.873	0.002	-	-	-
K	Land use	2, 20	15.074	<0.001	a	b	a
	Geology	1, 20	6.688	0.018	-	-	-
	Interaction	2, 20	0.035	0.965	-	-	-
Mg	Land use	2, 20	7.877	0.003	-	-	-
	Geology	1, 20	89.622	<0.001	Granite > Sandstone		
	Interaction	2, 20	10.904	0.001	-	-	-
Total monomeric Al	Land use	2, 20	13.807	<0.001	a	b	b
	Geology	1, 20	0.429	0.520	-	-	-
	Interaction	2, 20	4.165	0.031	-	-	-
Mn	Land use	2, 20	4.046	0.033	-	-	-
	Geology	1, 20	0.810	0.379	-	-	-
	Interaction	2, 20	0.541	0.590	-	-	-
Fe	Land use	2, 20	9.539	0.001	a	a	b
	Geology	1, 20	1.882	0.185	-	-	-
	Interaction	2, 20	0.376	0.691	-	-	-

Significant terms are emboldened.

Table 3.3. Summary statistics from the correlation analysis of all chemical variables from the 26 study lakes.

Variable	pH	Cond.	Temp.	DO	Colour	Alkalinty	Chl. <i>a</i>	TDOC	TP	SRP	TN	Ammonia	SO ₄	tot.Al	Ca	Na	Cl	K	Mg	Mn
Conductivity																				
Temperature		0.710**																		
Dissolved oxygen																				
Colour				-0.758**																
Alkalinity	0.927**																			
Chlorophyll <i>a</i>				-0.754**																
TDOC		0.389*		-0.864**	0.949**		0.482*													
TP				-0.589**	0.814**		0.414*	0.683**												
SRP				-0.446*	0.780**			0.616**	0.972**											
TN		0.418*		-0.657**	0.905**		0.395*	0.876**	0.810**	0.763**										
TON																				
Ammonia					0.773**			0.604**	0.883**	0.904**	0.803**									
SO ₄		0.865**	0.639**																	
tot.Al		0.416*		-0.686**	0.639**		0.410*	0.740**			0.643**									
Ca	0.621**			-0.509**	0.528**	0.780**		0.567**	0.498**	0.446*	0.543**	0.447*								
Na		0.978**	0.752**										0.869**		0.408*					
Cl		0.970**	0.733**										0.885**			0.992**				
K		0.398*							0.464*	0.514**	0.494*	0.611**			0.457*	0.430*	0.448*			
Mg		0.922**	0.720**										0.843**		0.505**	0.942**	0.953**	0.511**		
Mn				-0.664**	0.512**		0.606**	0.554**	0.523**	0.430*	0.443*				0.485*					
Fe		0.429*		-0.673**	0.889**			0.797**	0.849**	0.798**	0.815**	0.800**		0.478*	0.619**	0.436*		0.556**	0.408*	0.597**

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

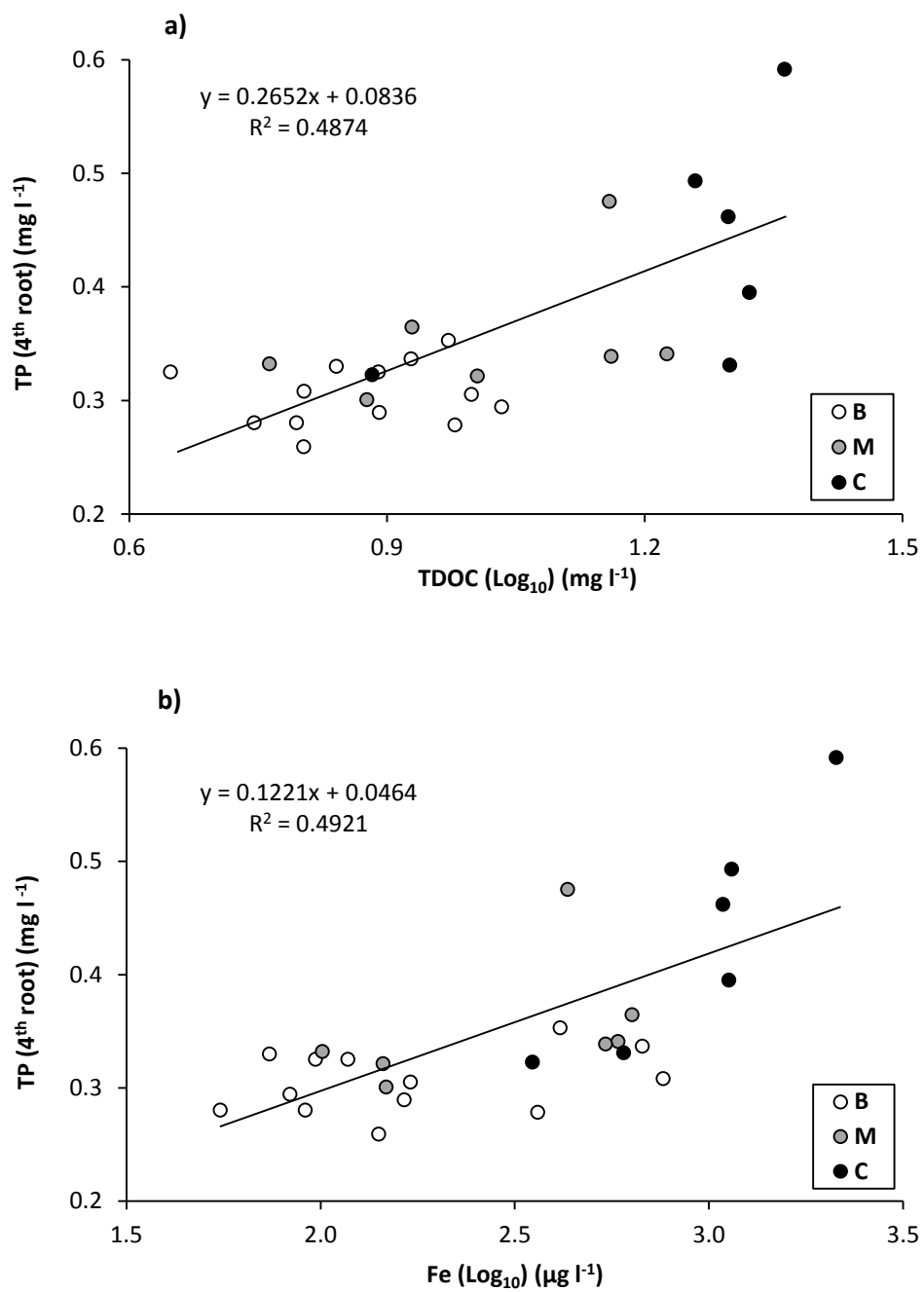


Figure 3.5. Correlation between **a)** TP and TDOC and **b)** TP and Fe for all study lakes (B = blanket bog, M = mature plantation and C = clearfell).

Table 3.4. Trophic classification of all 26 study lakes with respect to catchment land use. Maximum chlorophyll *a* concentrations were calculated from samples taken during May to September.

Catchment land use	Lake	Max chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	Trophic classification
Blanket bog	SB1	9.6	Mesotrophic
	SB2	12.6	Mesotrophic
	SB3	3.9	Oligotrophic
	SB4	16.7	Mesotrophic
	SB5	3.6	Oligotrophic
	SB6	7.7	Oligotrophic
	GB1	4.3	Oligotrophic
	GB2	2.8	Oligotrophic
	GB3	9.6	Mesotrophic
	GB4	3.1	Oligotrophic
	GB5	7.2	Oligotrophic
	GB6	3.7	Oligotrophic
	GB7	2.7	Oligotrophic
Mature plantation	SM1	5.1	Oligotrophic
	SM2	52.7	Strong Eutrophic
	SM3	5.8	Oligotrophic
	GM1	9.5	Mesotrophic
	GM2	3.1	Oligotrophic
	GM3	16.8	Mesotrophic
	GM4	2.5	Oligotrophic
Clearfell	SC1	21.8	Mesotrophic
	SC2	88.0	Hypereutrophic
	SC3	15.2	Mesotrophic
	GC1	5.8	Oligotrophic
	GC2	9.8	Mesotrophic
	GC3	11.8	Mesotrophic

3.4.3. Glennamong clearfell site water chemistry

TDOC concentrations were highest in runoff from the clearfelled site and lowest in runoff from the blanket bog (Fig. 3.6). The BOD and COD of runoff water from the clearfell catchment were also strongly elevated, with the BOD exceeding guideline concentrations for good status under the European Communities Environmental Objectives (Surface Waters) Regulations 2009 (Fig. 3.6).

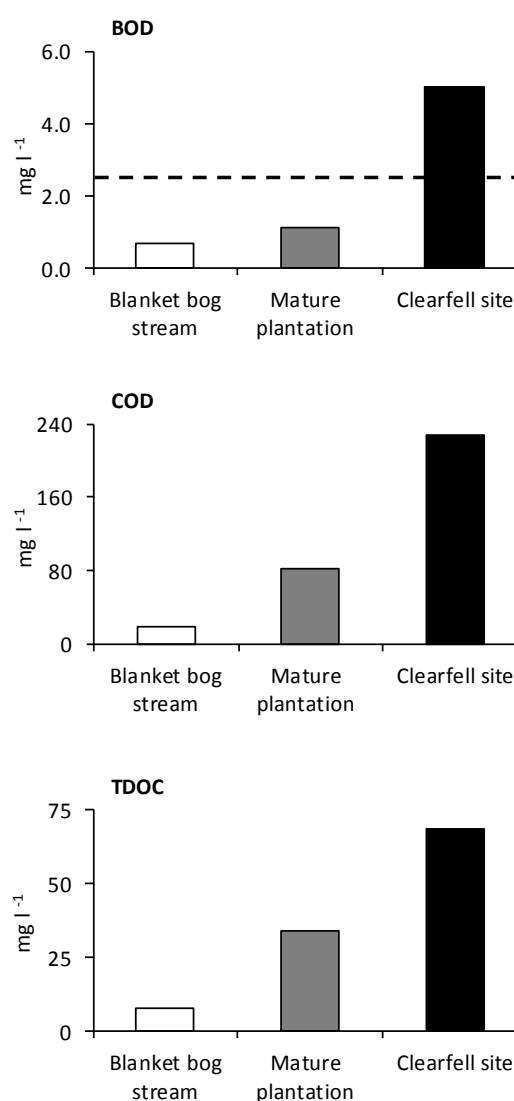


Figure 3.6. The concentrations of chemical parameters sampled from the Glennamong clearfell site. The dashed line indicates the guideline for annual mean concentrations for 'good water status' listed in the European Communities Environmental Objectives (Surface Waters) Regulations 2009.

3.5. Discussion

Forestry impacts on receiving waters are complex and depend strongly on local and regional catchment and atmospheric factors (Tetzlaff et al., 2007). Much attention over the past decades has focused on the potential impact of forestry on the acidification of running waters (Ormerod et al., 1989; Puhr et al., 2000; Harriman et al., 2003; Ågren et al., 2010; Neal et al., 2010; Ågren and Löfgren, 2012). Recent reductions in acid episodes in streams draining forested catchments have been linked to reductions in atmospheric S emissions (Malcolm et al., in press). Others studies, however, have shown that forestry-associated acidification is still occurring despite these reductions (Kowalik and Ormerod, 2006; Ormerod and Durance, 2009). Nutrient loadings to receiving waters as a result of forestry operations have received less attention in comparison, although forestry practices, particularly clearfelling, have been shown to lead to enhanced levels of P, N and C leaching to receiving waters (Kortelainen and Saukkonen, 1998; Cummins and Farrell, 2003a, 2003b; Feller, 2005; Kortelainen et al., 2006; Kreutzweiser et al., 2008; Rodgers et al., 2010). The net chemical impact of forestry on receiving waters will be greatly influenced by catchment characteristics (slope, soil type, location, altitude and latitude), regional rainfall patterns and the nature of forestry operations themselves. The impacts of forestry on hydrochemistry will also tend to differ between streams and lakes: streams will be affected more by rainfall-driven effluxes of substances from forests, whereas lakes will tend to demonstrate a more temporally integrated pattern of water chemistry. The results of this study reveal several clear patterns of lake hydrochemistry with respect to forestry. Firstly, catchment forestry operations were associated with elevated concentrations of plant nutrients, heavy metals (Al, Fe

and Mn) and TDOC. This effect was seen most strongly for clearfelling, but was also apparent for mature forest plantations. Secondly, despite the strong hydrochemical effect of forestry, particularly Al concentrations, there was little discernible effect on the pH of lakes. Thirdly, concentrations of marine-derived ions – Na, Cl and Mg – were elevated in forestry-impacted lakes in sandstone catchments but reduced in forestry-impacted lakes in coastal granite catchments. Finally, concentrations of dissolved oxygen were markedly reduced in forestry-impacted lakes, particularly those associated with clearfelling.

3.5.1. Plant nutrients

The potential source of the plantation-derived plant nutrients include i) fertilisers applied to the forest crop during the forest cycle (Foy and Bailey-Watts, 1998), ii) decomposition/mineralization of the underlying peat soil and clearfell residues (Sundström et al., 2000; Piirainen et al., 2004) and iii) increased atmospheric deposition via enhanced scavenging (Miller et al., 1996). Different nutrients can come from distinct sources. For example, P in water draining afforested peat catchments is mainly derived from the application of fertilisers to the tree crop (Cummins and Farrell, 2003a), while the source of leached N is predominantly from the peat soil itself, through mineralization of soil organic matter (Nieminen, 1998, 2003).

In Ireland, P is the main nutrient fertiliser applied (as rock phosphate), with N (urea) and K (muriate of potash) occasionally applied as remedial fertilisers (Forest Service, 2000). Although current fertilisation rates are being reduced in Ireland, fertilisation rates of $> 50 \text{ kg P ha}^{-1}$ have previously been applied (Dickson and Savill,

1974). Although this anthropogenic input is generally considered low in comparison with most agricultural systems, the potential impact to receiving waters on peatland are exacerbated due to blanket peats having a very low capacity to sorb P (Malcolm et al., 1977). Fertiliser-induced leaching of P from peatlands drained for plantation forestry has been the focus of a range of studies in Ireland and Scandinavia, in recognition of the potential environmental damage of excess plant nutrients on the ecological status of aquatic ecosystems (Nieminen and Ahti, 1993; Nieminen and Jarva, 1996; Cummins and Farrell, 2003a). Although the majority of applied P is assumed to be quickly sequestered by the trees, elevated P concentrations in runoff, associated with fertilisation, are evident for up to 10 years post-fertilisation (Kenttämies, 1981).

Application of P fertilisers has also been demonstrated to stimulate the release of N and K through enhanced decomposition of the peat soil (Malcolm et al., 1977). After N (urea) fertilisation, hydrolysis is rapid and this can lead to rapid runoff of ammonia to receiving waters. Oxidation of ammonia may also lead to the leaching of nitrate from the forest floor when conditions amenable to nitrification are present. For the study lakes, however, given the saturated and acidic character of the peat soil, it seems likely that sub-optimal conditions for nitrification on the peat surface may have given rise to elevated concentrations of ammonia rather than TON being leached.

The loss of soil N from conifer plantations on peat soils to surface waters is strongly regulated by rates of soil N mineralization and immobilisation. Although peat soils are recognised as being nutrient-deficient, the top metre of deep organic soils can contain relatively large quantities of elements such as N, S, P and C (Miller et al., 1996). Mineralization-immobilisation responses of soil N are dependent upon

environmental factors (temperature, redox potential and pH) and substrate factors (stage of decomposition, organic matter quality, nutrient content, chemistry of the soil solution and the presence of chemical and biological inhibitors to microbial activity), many of which are altered following forestry drainage and clearfell operations (Holden et al., 2004). The lowering of the water table during forest drainage of peat soils leads to an increase in the air-filled porosity of the peat which stimulates aerobic decomposition rates (Clymo, 1983). Subsequently, this enhances the mineralization of nutrients (Holden et al., 2004), resulting in the increased leaching of nutrients that were previously immobilised within partly decomposed plants (Laiho and Laine, 1994). This has been previously demonstrated in both Finland (Laiho et al., 1999) and Sweden (Sundström et al., 2000), where elevated P and N concentrations were recorded from the upper soil layers following forest drainage.

The decomposition of clearfell residues is another major source of leached plant nutrients, TDOC and major ions being received by the clearfell lakes (Laskowski et al., 1995; Qualls et al., 2000; Finér et al., 2003; Palviainen et al., 2004a, 2004b; Piirainen et al., 2004). Fine clearfell residues, such as foliage, fine roots and small branches, are the probable source of leached nutrients soon after clearfelling because they are the most nutrient-rich parts of the trees and they decompose faster than coarse residues: stumps, coarse roots and branches (Hyvönen et al., 2000; Palviainen et al., 2004b). Consequently, it can take several years or even decades for nutrients to be released from coarse clearfell residues (Laiho and Prescott, 1999). Although the data is limited to lake water chemistry, it is likely that changes in soil temperature and moisture conditions, coupled with the increased

mechanical disturbance from the harvesting machinery, led to an enhanced decomposition of these residues post-clearfell in the clearfell lake catchments.

K concentrations were significantly lower in the mature plantation lakes and were only slightly higher than undisturbed levels in the clearfell lakes. This suggests that a significant proportion of the potential K pool of a site may be bound in tree matter during the growing phase and subsequently released during the decomposition of clearfell residues and tree stumps post-clearfell. K release from clearfell residues can be considerable (Palviainen et al., 2004a; Piirainen et al., 2004).

Given the location of all the study lakes in the west of Ireland, coupled with the fact that Ireland receives less atmospheric pollution than most other European countries (Aherne and Farrell, 2002), the potential input of plant nutrients from atmospheric deposition seems negligible.

3.5.2. TDOC

Concentrations of TDOC in the mature plantation and clearfell lakes were strongly associated with plant nutrients and heavy metals suggesting that the source and release mechanisms responsible are similar. Kortelainen et al. (2006) have demonstrated that TOC export accounted for as much as 95% of the variance in TON export, and 61 – 73% of the variance in ammonia, Fe and TP export from peatland catchments. Similarly, Kreutzweiser et al. (2008) suggested that the hydrological and biogeochemical processes that increase DOC fluxes from clearfelled catchments can increase the export of P. Previous studies have demonstrated similar results of increased DOC fluxes as a result of forestry operations, especially clearfelling, on

peatlands (Nieminen, 2004; O'Driscoll et al., 2006; Piirainen et al., 2007; Saari et al., 2009).

There are three potential sources of the leached TDOC being received by the mature plantation and clearfell lakes: the decomposition of clearfell residues (Qualls et al., 2000), canopy leachate from living trees and litterfall during the mature forest stage (Qualls et al., 1991; Fröberg et al., 2007), and the decomposition of the organic matter within the Oe (moderately decomposed [hemic]) and Oa (highly decomposed [sapric]) horizons of the forest peat soil (Michalzik et al., 2001; Park and Matzner, 2003).

DOC in freshwaters is often categorised with respect to bacterial degradability into labile (L-DOC) and refractory (R-DOC) fractions. It has been suggested that DOC leached from plant tissues is more labile in nature than that leached from forest soils (Qualls and Haines, 1992). Kalbitz et al. (2003), investigating the biodegradation of DOM of different origins, showed that 56.9% of the DOC present within a spruce forest litter layer was labile in nature, and that this L-DOC is rapidly mineralized, having a half-life of only about 3 days. In a similar study by Qualls and Haines (1992), the most biodegradable DOC was recorded from throughfall and from the Oi (litter layer) horizon, and that 33% of the litter DOC was degraded after 134 days. Although the TDOC within the study lakes was not categorised, the high BOD and COD of water draining from the clearfell site in Glennamong suggests that a considerable quantity of labile TDOC draining off the site is derived from clearfell residues.

3.5.3. Heavy metals

The source(s) of the elevated heavy metal concentrations within the mature plantation and clearfell lakes are likely to be somewhat similar to those of the elevated TDOC concentrations. Palviainen et al. (2004a) demonstrated that fine roots of logged trees can release large amounts of Fe and Al soon after clearfelling. Cummins and Farrell (2003b) similarly showed an increase in Al concentrations, in conjunction with elevated DOC, from a clearfelled area of a blanket peatland forest in Ireland. Forestry drainage of peatland can also release substantial quantities of Fe and Al (Joensuu et al., 2002).

The co-leaching of TDOC and heavy metals has been previously shown for peatland forestry operations in Finland (Kortelainen and Saukkonen, 1998; Joensuu et al., 2001), Canada (Dillon and Molot, 1997) and Scotland (Grieve and Marsden, 2001). It is widely recognised that the complexation between heavy metals and DOC controls the speciation, toxicity, bioavailability and ultimate fate of metals (Bidoglio and Stumm, 1994). The close association of TDOC, TP and Fe in this study highlights the importance of humic complexes for P and Fe mobilisation to surface waters (Kortelainen and Saukkonen, 1998; Kortelainen et al., 2006).

Interestingly, lake Al and Fe concentrations, as well as P and N, revealed dissimilar responses to catchment forestry between the two geologies. Concentrations of P, N, Al and Fe from the mature plantation lakes were higher than those recorded from the clearfell lakes underlain by sandstone geology, whereas the opposite trend was recorded for the forestry-affected granite lakes. Site-specific responses of receiving water hydrochemistry to catchment forestry have been previously noted (Tetzlaff et al., 2007; Kreutzweiser et al., 2008). This variation in

response may be due to differences in catchment characteristics, lake morphology or forestry operations. For example, the drainage of peatland for forestry can release substantial quantities of Fe and Al, with the concentrations of Al in runoff displaying high spatial variation among sites (Joensuu et al., 2002). Similarly, slope of peatland catchments has a major influence on catchment export of N, DOC and Fe (Kortelainen et al., 2006). Further research is needed to elucidate the exact process(es) responsible for the observed differences between catchment geologies and individual lakes.

3.5.4. Dissolved oxygen

The lower dissolved oxygen concentration recorded in the mature and clearfell lakes is consistent with other studies on the impact of forestry on lake oxygen levels (Rask et al., 1993; Evans et al., 1996). In general, lake oxygen concentrations are dependent upon seasonal temperature variation, depth, wind and trophic status (Wetzel, 2001). Increased loadings of TDOC, leading to dark, peat-stained water, can increase the absorption of incoming solar radiation which is subsequently transferred into heat in a thinner layer of water, thereby reducing the solubility of dissolved oxygen within the water column. Increasing TDOC concentrations can also reduce dissolved oxygen concentrations via enhanced aerobic bacterial decomposition, predominantly at the sediment-water interface where bacterial decomposition is higher (Wetzel, 2001). Although necessarily limited in scope, the small-scale investigation into the biological and chemical reactivity of the TDOC in runoff from a single clearfell site indicated that clearfelling can input considerable

quantities of L-DOC into receiving waters, potentially accounting for the reduced concentrations of dissolved oxygen in clearfell lakes.

3.5.5. Conductivity, marine ions, temperature and acidity

Conductivity, temperature and concentrations of Na, Cl, Mg and SO₄ ions were all significantly higher in the lakes underlain by granite geology. These lakes are nearer to the coast than the sandstone lakes, and are at a somewhat lower altitude, such that marine deposition (via sea spray, occult deposition) is likely to be greater in the former lakes, potentially accounting for the higher conductivity. Aherne et al. (2002) have previously shown that the deposition of marine-derived ions in Irish lakes decreases with increasing distance inland from the coast. The significantly lower temperature of the upland lakes is most likely explained by their location at higher altitude.

Interestingly, the findings of this study revealed that conifer plantations had no significant effect on the pH of naturally acidic blanket bog lakes. This has previously been shown for streams draining clearfelled areas (Neal et al., 2004b). The atmospheric deposition of acidifying S and N compounds has dramatically reduced in both Britain and Ireland during the previous two decades (Aherne and Farrell, 2002; Fowler et al., 2005; Malcolm et al., in press). However, this alone cannot explain the lack of a pH effect in the study lakes, as forestry is still responsible for low pH receiving waters in many poorly-buffered European catchments (Ågren et al., 2010; Ågren and Löfgren, 2012; Malcolm et al., in press). Sea-salt deposition within a catchment has also been shown to lead to lower pH in surface waters (Hindar, 2005; Larssen and Holme, 2006). The lakes in coastal

granite catchments unsurprisingly, had considerably higher marine-derived ion concentrations than the more inland sandstone catchments, yet had a somewhat higher pH than sandstone lakes. The lack of a pH response to catchment afforestation may potentially be due to the increased loadings of TDOC, as TDOC is known to be the principal buffer in highly humic acid (pH 4 – 5) surface waters (Kullberg et al., 1993).

3.5.6. Chlorophyll *a*

The increase in chlorophyll *a* concentrations in the mature and clearfell lakes, especially in the lakes underlain by sandstone, is consistent with other studies demonstrating the potential eutrophication effects of forestry on lakes (Kortelainen and Saukkonen, 1998; Bredesen et al., 2002). The increase in primary production is most likely attributable to the increase in plant nutrient concentrations, primarily P. Arvola and Tulonen (1998) also demonstrated the effects of allochthonous DOM on the growth of bacteria and algae from a highly humic lake by showing that algal production increased with increasing DOM concentrations. The difference in chlorophyll *a* concentrations between the two separate geologies, also not significant, is likely explained by the greater concentration of ambient plant nutrients available in the lakes underlain by sandstone in comparison with the lakes underlain by granite.

3.6. Conclusions

The findings of this study demonstrate that plantation forestry has a major impact on the hydrochemistry of blanket bog lakes in Ireland, with this effect being most apparent post-clearfell. Previous attempts to quantify the catchment export of chemicals associated with conifer plantation forestry were usually confounded by co-occurring (and usually overriding) catchment land uses such as agriculture. Previously, it was suggested that nutrient release from plantation forestry was negligible and would unlikely amount to any change in the chemical or ecological state of receiving surface waters (Nisbet, 2001). However, this study provides empirical evidence that plantation forestry present in lake catchments does lead to significant changes in lake water chemistry. Previous work by the author has also demonstrated that such catchment effluxes associated with peatland conifer forestry have a major impact on the biological communities of receiving waters, with the biological response being consistent with a trophic rather than an acidic effect (Drinan et al., 2013).

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Chapter 4

The impact of conifer plantation forestry on the Chydoridae (Cladocera) communities of peatland lakes



Alona costata Sars, an example of a chydorid recorded during this study. This photograph was kindly supplied by Dr Elvira de Eyto.

4.1. Summary

Conifer plantation forestry is recognised as a potential source of diffuse pollution to surface waters and represents a risk to their ecological status. In this study, the water chemistry and littoral Chydoridae (Cladocera) communities of 26 small blanket bog lakes were investigated to assess the impact of plantation forestry. The study was conducted over a 12-month period in 2009–10 by comparing lakes with three distinct catchment land uses: i) unplanted blanket bog only present in the catchment, ii) mature conifer plantation forests only present in the catchment and iii) catchments containing mature conifer plantation forests with recently clearfelled areas. All three catchment land uses were replicated across two geologies: sandstone and granite. Lakes with afforested catchments had very high concentrations of plant nutrients (phosphorus [P] and nitrogen [N]), total dissolved organic carbon (TDOC) and heavy metals (aluminium [Al] and iron [Fe]), the highest concentrations being recorded from lakes with catchment clearfelling. Similarly, the chydorid communities differed among lakes of contrasting catchment land use. The dominance of *Alonopsis elongata* in the unplanted blanket bog lakes shifted to dominance by the smaller bodied *Chydorus sphaericus*, along with *Alonella nana*, *Alonella excisa* and *Alonella exigua*, in the plantation forestry-affected lakes, consistent with a shift in lake trophy. This study has shown that plantation forestry can have a profound impact on the water quality of small peatland lakes, especially at the clearfell stage. The response of the chydorid communities is consistent with plantation forestry exerting a trophic, rather than an acidic or toxic, effect on lake ecosystems.

4.2. Introduction

Plantation forests cover an estimated 10% of the Irish land surface area, approximately 80 – 85% of which is coniferous (NFI, 2007). Plantation forestry practices, including clearfelling and thinning, are recognised as a potential source of pollution to receiving waters and represents a risk to the ecological status of surface waters (Rask et al., 1998; Steedman, 2000; Watmough et al., 2003; Giller and O'Halloran, 2004). A majority of studies have focused on the acidification impacts of plantation forestry on receiving waters (Harriman and Morrison, 1982; Ormerod et al., 1989; Jenkins et al., 1990; Kelly-Quinn et al., 1996). However, more recent studies have shown the potential for plantation forestry to result in the eutrophication of receiving waters, due primarily to phosphorus (P) fertilisation at the time of planting (Miller et al., 1996; Foy and Bailey-Watts, 1998; Cummins and Farrell, 2003a).

An estimated 42% of state-owned and 77% of privately-owned forests in Ireland are on peat soils (NFI, 2007); this soil type is known to pose the greatest risk to receiving waters (Hutton et al., 2008). Peat soils, such as those present in blanket bogs, are known to leach P, nitrogen (N) and dissolved organic carbon (DOC) as a result of forestry operations (Cummins and Farrell, 2003a, 2003b; Renou-Wilson and Farrell, 2007). Associated with the obvious eutrophication threat, the increased loading of allochthonous DOC from catchment plantation forestry may also lead to fundamental changes in lake trophic and biological processes (Cole et al., 2010; Solomon et al., 2011). Increased in-lake DOC concentrations have been shown to cause oligotrophic lakes to attain a net heterotrophic status through bacterial utilisation of the allochthonous, catchment-derived carbon (Pålsson et al., 2005).

The impact of plantation forestry operations on aquatic biota have been studied to a greater extent in running waters than in lakes. Studies investigating the impact of forestry on lake biota have revealed a wide range of results, with the majority showing slight and short lived changes in species assemblages (Paterson et al., 1998; Rask et al., 1998; Patoine et al., 2000; Planas et al., 2000; Laird and Cumming, 2001, Laird et al., 2001; Bredeisen et al., 2002), whereas others show significant changes in biological communities (Lott et al., 1994; Koster et al., 2005). Distinguishing the impact of forestry on biota, however, has been shown to be difficult due to background environmental variation (Paterson et al., 1998).

In this study, littoral Chydoridae (Branchiopoda, Anomopoda) were used to determine the effects of plantation forestry on the biota of small blanket bog lakes. Chydorids are a speciose group of cladocerans that primarily inhabit the littoral zone of lakes. Chydorids are known to be important contributors to secondary production in small lakes and can also provide prey for many species of fish (Frey, 1995; Parke et al., 2009). Importantly, as chydorid communities respond in a predictable manner to acidification and nutrient enrichment, they can also be used as biological indicators in lakes (Hofmann, 1996; Walseng and Karlsen, 2001; de Eyto et al., 2002; Bos and Cumming, 2003). Chydorids have been previously used to assess the impact of forestry operations on lakes in Canada (Bredeisen et al., 2002).

The objective of this study was to investigate the effect of conifer plantation forestry on the chydorid community composition of small lakes in blanket bog catchments. Water chemistry and chydorid communities were compared between lakes with afforested and non-afforested catchments. Studies investigating anthropogenic impacts on lake water chemistry and biota generally involve evaluating the relative impact of multiple land uses and it can be difficult to

determine the impact of one individual land use (Dodson et al., 2005). The homogenous and undisturbed nature of blanket bog lakes in this study, however, provides a valuable tool to quantify the impacts of conifer plantation forestry on lake biota.

4.3. Materials and methods

4.3.1. Site description

The 26 study lakes studied in this chapter are the same as those studied in the previous chapter (described in Section 3.3.1.1.).

4.3.2. Water chemistry sampling

Water samples were collected in acid-washed polypropylene bottles from the littoral zone of each lake at a similar depth (0.6 m) and distance (7 m) from shore, bimonthly for 12 months, beginning in March 2009. Water samples were stored at 4°C in a cooler box and transported to the laboratory for analysis within 24 hours after collection. Conductivity, dissolved oxygen and temperature were measured on site using WTW portable meters.

A total of 11 water chemistry parameters were analysed: pH, alkalinity, total dissolved organic carbon (TDOC), total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), ammonia, calcium (Ca), iron (Fe), total monomeric aluminium (tot.Al) and chlorophyll *a*. Methods for water chemistry analyses are described in chapter 2 (Section 2.3.2.).

4.3.3. Chydoridae sampling

Chydoridae were sampled bimonthly for 12 months, beginning in March 2009. Chydorids were sampled by a semi-quantitative method which involved slowly sweeping a hand-held sweep net (100 μ m mesh, 0.15 m diameter frame) horizontally both inside and outside a stand of vegetation for 30 seconds in the littoral zone of each lake, similar to Walseng et al. (2006). Mineral benthic substrates were avoided during sampling as this habitat type was not represented in all lakes. Samples were transferred to sealed plastic storage containers and were preserved using 70% ethanol. Although chydorid communities are known to vary among different microhabitats (Tremel et al., 2000), the aim was to collect chydorids from similar habitats in each lake so as to remove microhabitat differences as an among-lake confounding factor, following de Eyto et al. (2002). The results, therefore, are not intended to reflect the entire chydorid communities, rather to compare microhabitat-specific sub-communities among lakes.

All zooplankton in all samples were identified and counted where possible, however, when a large number of individuals (> 500) were present in a sample, successive, randomly-selected 5 ml subsamples were examined from a known volume until a minimum of 50 individuals of the most common species of chydorid had been identified. The remaining fraction was also analysed to ensure that all species were recorded in the sample. Zooplankton were identified and enumerated in a custom-made, rotating, circular counting tray using a binocular dissecting microscope. The total counts for all chydorids in each study lake can be seen in Table 4.1. All cladocerans were identified to species level using standard identification keys (Scourfield and Harding, 1966; Amoros, 1984).

Table 4.1. Total number of chydorids recorded from all sweep samples from each lake over the duration of the sampling period.

Geology	Catchment land use	Lake	Total chydorids
Sandstone	Blanket bog	SB1	5267
		SB2	5507
		SB3	3065
		SB4	8332
		SB5	5233
		SB6	6524
	Mature plantation	SM1	8514
		SM2	7603
		SM3	5372
	Clearfell	SC1	6795
		SC2	5174
		SC3	11580
Granite	Blanket bog	GB1	2367
		GB2	4955
		GB3	4752
		GB4	4487
		GB5	12704
		GB6	5078
		GB7	2523
	Mature plantation	GM1	1983
		GM2	6609
		GM3	8590
		GM4	6575
	Clearfell	GC2	8863
		GC3	3816

4.3.4. Statistical analyses

Non-metric multi-dimensional scaling (NMDS) analysis was performed, using PC-ORD (version 6; MjM Software, Gleneden Beach, Oregon), to determine among-lake patterns in the chydorid communities, as it can be used with non-normal and zero rich data (McCune and Grace, 2002). NMDS ranks points in low-dimensional space such that the relative distances apart of all points are in the same rank order as the relative dissimilarities of the samples (Clarke and Gorley, 2006). The ordination was based on a Bray-Curtis dissimilarity matrix with varimax rotation, based on a presence/absence data matrix. Significance of the axes was determined using Monte

Carlo simulation using 999 permutations. Singletons, species occurring only once, were also removed (McCune and Grace, 2002). One lake (GC1) had to be excluded from the NMDS analysis as only two individuals of a single species of chydorid (*Alona guttata* Sars) were recorded from this lake over the 12-month sampling period. The chydorid communities were ordinated in bi-plots to reveal patterns with the environmental variables. The final solution for the NMDS analysis was based on 999 permutations.

Similarity Percentage routine (SIMPER) was performed, using PRIMER 6 (PRIMER- E, UK), to reveal which species contributed to community structure among lakes of contrasting catchment land use across both geologies. SIMPER calculates the contribution of each species to the average Bray-Curtis dissimilarity between two groups of samples and to the average similarity within a group (Clarke and Warwick, 2001). Community analysis, including species richness and mean chydorid abundance per lake, were also carried out for the chydorid communities. Species richness was calculated as the total number of chydorid species recorded at a specific lake over the 12-month sampling period.

Analysis of variance (ANOVA) was performed, using PASW Statistic 17, to test for significant among-lake differences in selected chydorid species abundances and community parameters with catchment land use and geology as main factors. Prior to performing ANOVAs, normality and homogeneity of variances were tested using Kolmogorov-Smirnov and Levene's tests, respectively. The ANOVA models were calculated on the basis of Type III sums of squares to take the unbalanced design into account. Significant results were tested for pair-wise comparisons by *post-hoc* Bonferroni tests. Dependent variables were transformed where necessary to fulfil the requirements of the parametric tests.

4.4. Results

4.4.1. Physico-chemical characteristics of the study lakes

There was a clear distinction in water chemistry among lakes of contrasting catchment land use (Table 4.2). Clearfell and mature plantation lakes tended to have higher concentrations of chlorophyll *a*, TDOC, TP, SRP, TN, ammonia, total monomeric Al and Fe and lower dissolved oxygen concentrations than blanket bog lakes. pH was slightly reduced in the afforested lakes, while alkalinity and Ca showed no clear differences among lakes of differing catchment land use. The lakes underlain by granite geology, situated at lower altitudes and in closer proximity to the sea, had higher pH, conductivity and temperature values than the lakes underlain by sandstone geology (Table 4.2).

Table 4.2. Mean (± 1 S.E.) water chemistry values for all 26 lakes across the three catchment land uses and both geologies (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 3). Means calculated over the 12-month sampling period (pH = median \pm C.I.).

Chemical variable	Sandstone			Granite		
	Blanket bog	Mature plantation	Clearfell	Blanket bog	Mature plantation	Clearfell
pH	5.16 (± 0.40)	4.54 (± 1.31)	4.92 (± 1.80)	5.49 (± 0.51)	5.16 (± 0.95)	4.93 (± 0.95)
Alkalinity (mg l ⁻¹)	0.17 (± 0.37)	-0.75 (± 0.79)	-0.12 (± 1.47)	0.93 (± 0.43)	0.06 (± 1.03)	0.05 (± 0.79)
Conductivity (μ S cm ⁻¹)	36.49 (± 1.38)	44.65 (± 4.69)	63.10 (± 4.15)	72.13 (± 1.65)	77.72 (± 9.17)	72.28 (± 5.56)
Temperature (°C)	9.91 (± 0.14)	10.38 (± 0.07)	10.56 (± 0.12)	10.84 (± 0.16)	11.26 (± 0.12)	11.02 (± 0.10)
Dissolved oxygen (mg l ⁻¹)	10.89 (± 0.14)	10.23 (± 0.36)	9.00 (± 0.45)	11.14 (± 0.07)	10.48 (± 0.10)	9.87 (± 0.45)
Chlorophyll <i>a</i> (μ g l ⁻¹)	5.77 (± 1.42)	9.55 (± 4.56)	17.77 (± 7.37)	3.67 (± 0.43)	4.23 (± 1.07)	6.63 (± 0.38)
TDOC (mg l ⁻¹)	8.21 (± 0.95)	10.11 (± 2.49)	19.29 (± 0.58)	7.18 (± 0.54)	11.83 (± 2.27)	17.22 (± 4.83)
TP (mg l ⁻¹)	0.011 (± 0.001)	0.025 (± 0.013)	0.039 (± 0.014)	0.007 (± 0.001)	0.013 (± 0.002)	0.053 (± 0.035)
SRP (mg l ⁻¹)	0.001 (± 0.0003)	0.004 (± 0.004)	0.006 (± 0.004)	0.001 (± 0.0001)	0.001 (± 0.0003)	0.011 (± 0.009)
TN (mg l ⁻¹)	0.503 (± 0.026)	0.493 (± 0.078)	0.783 (± 0.045)	0.481 (± 0.041)	0.587 (± 0.084)	0.808 (± 0.238)
Ammonia (mg l ⁻¹)	0.025 (± 0.002)	0.028 (± 0.006)	0.040 (± 0.005)	0.026 (± 0.003)	0.032 (± 0.006)	0.099 (± 0.065)
Ca (mg l ⁻¹)	0.92 (± 0.16)	0.50 (± 0.28)	1.62 (± 0.46)	1.19 (± 0.11)	1.23 (± 0.47)	1.59 (± 0.53)
Total monomeric Al (μ g l ⁻¹)	44.25 (± 8.27)	59.13 (± 14.87)	176.54 (± 51.02)	27.79 (± 4.54)	132.41 (± 29.93)	90.06 (± 33.21)
Fe (μ g l ⁻¹)	159.44 (± 52.86)	226.44 (± 104.21)	945.11 (± 171.45)	321.71 (± 109.36)	477.29 (± 111.53)	1202.17 (± 514.33)

4.4.2. Chydoridae communities

A total of 23 chydorid species were recorded across the 26 lakes (Table 4.3), with species richness per lake ranging from 1 to 18. The median number of species per lake was 10.5, although certain lakes contained very few species. Only two individuals of *A. guttata* were recorded from GC1 over the 12-month sampling period. *Chydorus sphaericus* (O. F. Müller) and *Alonella nana* (Baird) were the most common species and were present in all but one lake. The rarest species was *Anchistropus emarginatus* Sars, which occurred in only one lake (GB7).

NMDS of the chydorid communities required two axes to reduce stress to a minimal level – final stress 0.22 (Monte Carlo test). The NMDS ordination of the chydorid communities from all lakes revealed community differences with respect to catchment land use and geology (Fig. 4.1). The SIMPER analysis showed that the clearfell and mature plantation lakes were characterised by greater abundances of *C. sphaericus*, *A. nana* and *Alonella excisa* (Fischer) (Table 4.4). Conversely, blanket bog lakes were characterised by greater abundances of *Alonopsis elongata* (Sars). The communities of the forestry-affected lakes, especially clearfell lakes, were associated with elevated TDOC, Fe, TP, total monomeric Al, ammonia, SRP, TN and chlorophyll *a* concentrations. Conversely, the blanket bog lakes were associated with higher dissolved oxygen concentrations (Fig. 4.1). The separation between geologies appeared to be driven by the increased pH, alkalinity and Ca concentrations of the granite lakes (Fig. 4.1).

Univariate analysis revealed that *A. elongata* and *C. sphaericus* abundances varied significantly among lakes of differing catchment land use (Fig. 4.2; Table 4.5). *A. elongata* was significantly more abundant in the blanket bog lakes in

comparison with the mature plantation and clearfell lakes. Conversely, *C. sphaericus* was significantly more abundant in the mature plantation and clearfell lakes. *A. excisa* was significantly more abundant in the sandstone lakes, while *A. harpae* was significantly more abundant in the granite lakes (Fig. 4.2; Table 4.5). Univariate analysis of chydorid community parameters revealed that species richness differed significantly between geologies; the granite lakes contained more species. However, no significant difference was found among lakes of contrasting catchment land use. No significant differences were found in mean chydorid abundance among lakes with respect to catchment land use or geology (Fig. 4.2; Table 4.5).

Table 4.3. Percentage occurrence of all chydorid species in lakes of differing catchment land use across both geologies (S = sandstone, G = granite, B = blanket bog, M = mature plantation and C = clearfell) (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 3).

Species	All lakes	SB	GB	SM	GM	SC	GC
<i>Acroperus harpae</i> (Baird)	53.8	-	100	33	75	100	66.7
<i>Alona affinis</i> (Leydig)	53.8	50	100	-	25	100	-
<i>Alona costata</i> Sars	15.4	-	57.1	-	-	-	-
<i>Alona guttata</i> Sars	80.8	33.3	85.7	100	100	100	100
<i>Alona intermedia</i> Sars	23.1	-	57.1	-	25	33.3	-
<i>Alona quadrangularis</i> (O. F. Müller)	19.2	-	14.3	33.3	25	33.3	33.3
<i>Alona rustica</i> Scott,	57.7	50	71.4	66.7	75	33.3	33.3
<i>Alonella excisa</i> (Fischer)	92.3	100	100	100	75	100	66.7
<i>Alonella exigua</i> (Lilljeborg)	42.3	16.7	57.1	-	100	66.7	-
<i>Alonella nana</i> (Baird)	96.2	100	100	100	100	100	66.7
<i>Alonopsis elongata</i> (Sars)	80.8	100	100	66.7	100	33.3	33.3
<i>Anchistropus emarginatus</i> Sars	3.8	-	14.3	-	-	-	-
<i>Camptocercus rectirostris</i> Schoedler	11.5	-	28.6	-	25	-	-
<i>Chydorus ovalis</i> Kurz	57.7	66.7	71.4	33.3	75	66.7	-
<i>Chydorus piger</i> Sars	57.7	66.7	85.7	33.3	50	33.3	33.3
<i>Chydorus sphaericus</i> (O. F. Müller)	96.2	100	100	100	100	100	66.7
<i>Disparalona rostrata</i> (Koch)	7.7	50	57.1	-	75	33.3	33.3
<i>Eurycercus lamellatus</i> (Baird)	46.2	50	100	66.7	100	100	66.7
<i>Graptoleberis testudinaria</i> (Fischer)	80.8	16.7	42.9	-	-	-	-
<i>Monospilus dispar</i> Sars	15.4	-	14.3	-	25	-	33.3
<i>Pleuroxus laevis</i> Sars	11.5	33.3	57.1	33.3	75	33.3	33.3
<i>Pleuroxus truncatus</i> (O. F. Müller)	46.2	16.7	14.3	-	-	-	-
<i>Pseudochydorus globosus</i> (Baird)	7.7	-	28.6	-	-	-	-

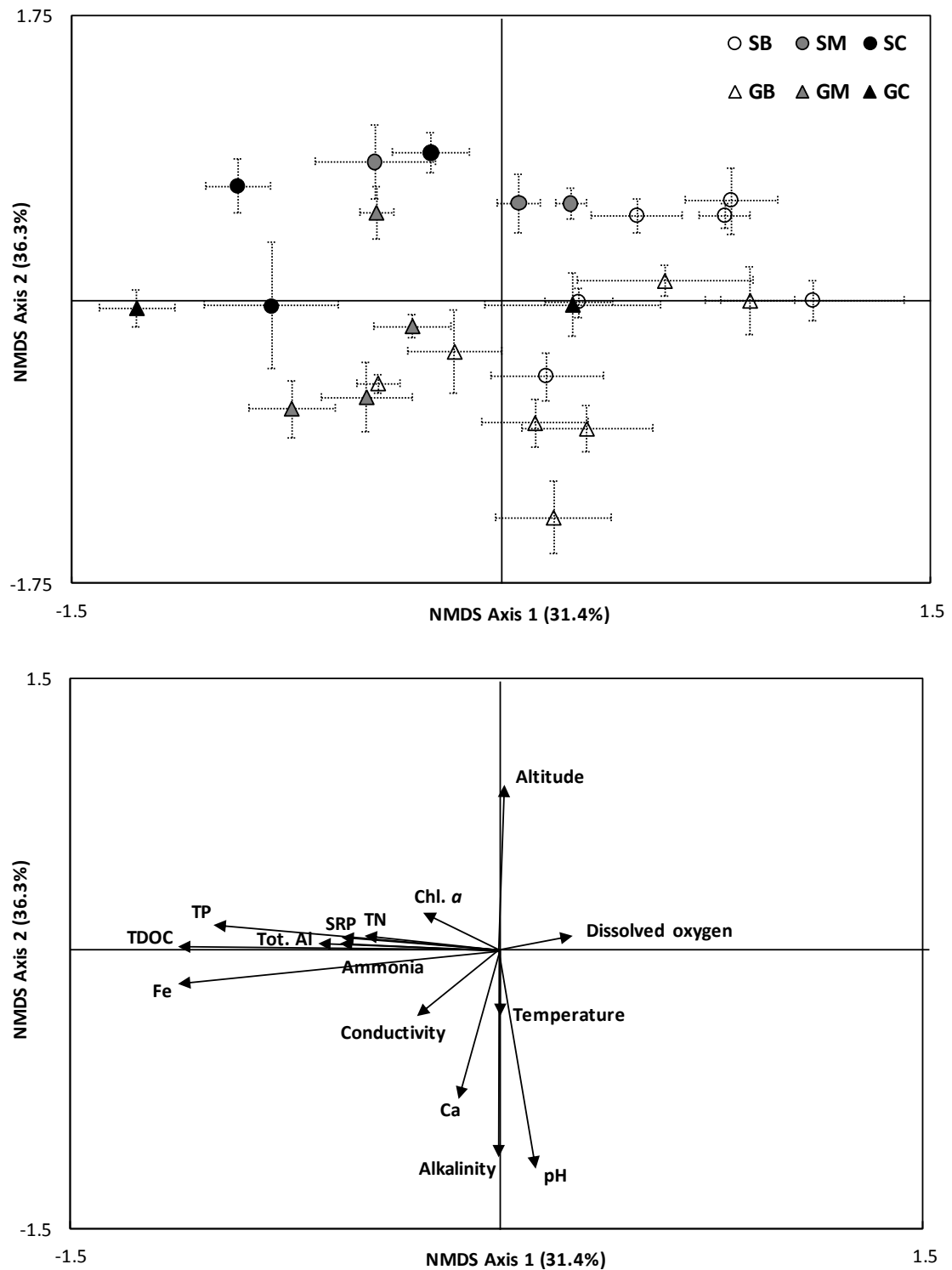


Figure 4.1. Non-metric multi-dimensional scaling (NMDS) analysis of chydorid communities from each of the 25 study lakes, including lake scores (top) and environmental variables (bottom). Group centroids represent the mean lake scores (± 1 S.E.) over the 12-month sampling period. Only environmental variables significantly correlated with either axis 1 or 2 are displayed (S = sandstone, G = granite, B = blanket bog, M = mature plantation and C = clearfell).

Table 4.4. SIMPER (Similarity Percentages) analysis results of log (x + 1) transformed abundance data showing the chydorid species identified as contributing the most to community composition of the different lake types (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 2).

Sandstone				Granite			
Blanket bog				Blanket bog			
Average similarity: 81.0				Average similarity: 67.4			
Species	Av.Abund	Contrib%	Cum.%	Species	Av.Abund	Contrib%	Cum.%
<i>Alonopsis elongata</i>	6.3	35.5	35.5	<i>Alonopsis elongata</i>	5.6	24.5	24.5
<i>Chydorus sphaericus</i>	4.8	25.5	61.0	<i>Chydorus sphaericus</i>	4.7	20.2	44.8
<i>Alonella nana</i>	4.1	19.5	80.5	<i>Alonella nana</i>	3.4	12.6	57.4
<i>Alonella excisa</i>	3.5	16.4	96.9	<i>Acroperus harpae</i>	3.3	11.3	68.7
Mature plantation				Mature plantation			
Average similarity: 72.3				Average similarity: 70.5			
Species	Av.Abund	Contrib%	Cum.%	Species	Av.Abund	Contrib%	Cum.%
<i>Chydorus sphaericus</i>	6.3	34.0	34.0	<i>Chydorus sphaericus</i>	5.8	22.8	22.8
<i>Alonella excisa</i>	4.9	26.2	60.2	<i>Alonella nana</i>	4.6	15.8	38.6
<i>Alonella nana</i>	4.7	24.5	84.7	<i>Alonella exigua</i>	4.2	13.3	51.8
<i>Alonopsis elongata</i>	3.9	11.0	95.7	<i>Alonopsis elongata</i>	4.0	12.7	64.5
Clearfell				Clearfell			
Average similarity: 72.9				Average similarity: 64.0			
Species	Av.Abund	Contrib%	Cum.%	Species	Av.Abund	Contrib%	Cum.%
<i>Chydorus sphaericus</i>	6.5	38.0	38.0	<i>Chydorus sphaericus</i>	6.1	29.7	29.7
<i>Alonella nana</i>	5.5	31.8	69.8	<i>Acroperus harpae</i>	4.3	20.7	50.4
<i>Alonella excisa</i>	4.6	27.3	97.1	<i>Alonella nana</i>	4.3	19.9	70.3
<i>Graptoleberis testudinaria</i>	2.1	2.1	99.2	<i>Graptoleberis testudinaria</i>	3.1	16.2	86.5

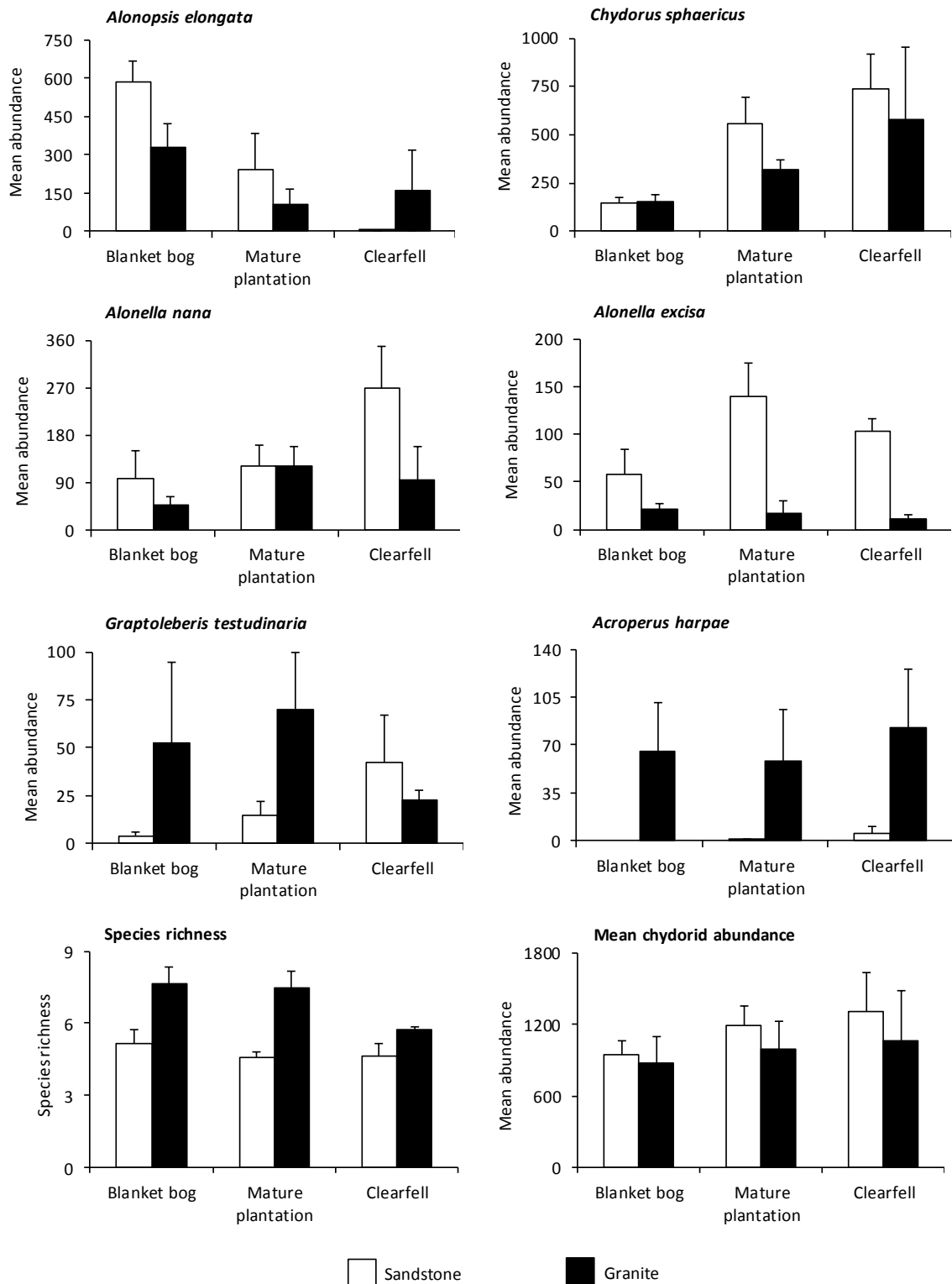


Figure 4.2. Mean abundance of selected chydorid species, species richness and mean chydorid abundance in the blanket bog, mature plantation and clearfell lakes across both geologies (sandstone and granite). Columns on each graph are mean values (± 1 S.E.) for each catchment land use calculated over the 12-month sampling period (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 2).

Table 4.5. Summary of 2 – way ANOVAs of mean abundance of selected chydorid species, species richness and mean chydorid abundance with catchment land use (blanket bog, mature plantation and clearfell) and geology (sandstone and granite) as main factors. Any two catchment land uses sharing a common letter are not significantly different.

		2 - way ANOVA			<i>post-hoc</i> Bonferroni tests		
		d.f.	<i>F</i>	<i>p</i>	Blanket bog	Mature plantation	Clearfell
<i>Alonopsis elongata</i>	Land use	2, 19	14.518	<0.001***	a	b	b
	Geology	1, 19	1.360	0.258	-	-	-
	Interaction	2, 19	2.525	0.107	-	-	-
<i>Chydorus sphaericus</i>	Land use	2, 19	13.246	<0.001***	a	b	b
	Geology	1, 19	1.522	0.232	-	-	-
	Interaction	2, 19	0.383	0.687	-	-	-
<i>Alonella nana</i>	Land use	2, 19	2.959	0.076	-	-	-
	Geology	1, 19	2.038	0.170	-	-	-
	Interaction	2, 19	0.345	0.713	-	-	-
<i>Alonella excisa</i>	Land use	2, 19	0.159	0.854	-	-	-
	Geology	1, 19	19.075	<0.001***	Sandstone > Granite		
	Interaction	2, 19	3.211	0.063	-	-	-
<i>Graptoleberis testudinaria</i>	Land use	2, 19	3.173	0.065	-	-	-
	Geology	1, 19	2.032	0.170	-	-	-
	Interaction	2, 19	0.738	0.491	-	-	-
<i>Acroperus harpae</i>	Land use	2, 19	0.967	0.398	-	-	-
	Geology	1, 19	26.109	<0.001***	Granite > Sandstone		
	Interaction	2, 19	0.100	0.905	-	-	-
Species richness	Land use	2, 19	1.231	0.314	-	-	-
	Geology	1, 19	14.792	0.001**	Granite > Sandstone		
	Interaction	2, 19	0.533	0.595	-	-	-
Mean chydorid abundance	Land use	2, 19	0.776	0.474	-	-	-
	Geology	1, 19	1.100	0.307	-	-	-
	Interaction	2, 19	0.043	0.958	-	-	-

Significant terms are emboldened.

4.5. Discussion

The findings of this study have demonstrated that conifer plantation forestry has a major impact on both the hydrochemical status and chydorid communities of blanket bog lakes in Ireland. The effect of plantation forestry was evident at the mature plantation stage, but greatest at the clearfell stage. The effect was common to lakes across geologies and regions, indicating that the anthropogenic effect of plantation forestry overrides any effect of catchment geology, altitude and proximity to sea. Lakes with plantation forestry present in the catchment were associated with increased concentrations of plant nutrients, heavy metals, dissolved organic matter, as well as other ions. This trend has regularly been demonstrated in receiving waters draining forested areas, although the majority of studies have focused on running waters (Binkley and Brown, 1993; Neal et al., 1998; Binkley et al., 1999; Cummins and Farrell, 2003a, 2003b). This change in lake hydrochemical status has subsequently contributed to profound changes within the chydorid communities, with the dominance of the relatively large-bodied *A. elongata* in unplanted blanket bog lakes shifting to dominance by *C. sphaericus* and other smaller bodied species in mature plantation and clearfell lakes.

Chydorid communities have been shown to respond to changes in trophic state (Hofmann, 1996; Bos and Cumming, 2003), acidity or alkalinity (Fryer, 1980; Duigan and Kovach, 1991; Walseng and Karlsen, 2001), water temperature (Bos and Cumming, 2003), and complexity of the littoral habitat (Tremel et al., 2000), all of which are known to be influenced by plantation forestry. Considering the number of studies documenting the acidification effect of plantation forestry on aquatic biota (Ormerod et al., 1993; Tierney et al., 1998; Ormerod et al., 2004; Feeley et al.,

2011), it seemed likely that acidification would be the main driver of forestry-related community changes in this study. However, chydorids in this study appeared to respond primarily to forestry-mediated changes in trophic status (via plant nutrients and TDOC), suggesting that forestry exerts its biological effect in these blanket bog lakes through eutrophication. Similar community change in forestry-affected lakes in Canada has also been ascribed to eutrophication (Bredesen et al., 2002). Water quality (dissolved oxygen concentrations) and metal toxicity (Al and Fe ions) also had a likely influence on communities in this study, albeit to a lesser degree. The overall increased species richness of the lower altitude, more coastal granite lakes was driven by the increased pH and base cation concentrations, a result of marine-derived atmospheric deposition. Such deposition is known to have a major influence on the hydrochemistry of coastal blanket bog water bodies in western Ireland (Proctor, 1992).

The trophic status of the mature plantation and clearfell lakes, including both autotrophic and heterotrophic components, was altered by the delivery of both plant nutrients and allochthonous TDOC from plantation forestry practices in the catchment. The increased input of plant nutrients has led to a stimulation of primary production, however, the increased availability of TDOC may have also stimulated primary production through osmotrophy – the uptake of organic molecules directly by numerous algae and cyanobacteria (Droop, 1974; Wetzel, 2001) and phagotrophy – bacterial assimilation of the organic molecules with subsequent consumption by photosynthetic mixotrophs (Vaqué and Pace, 1992). Osmotrophy is also known to occur in zooplankton (Speas and Duffy, 1998). Coupled with its increased availability, the TDOC entering lakes from plantation forests is also likely to be more assimilable than that entering the unplanted blanket bog lakes. The majority of

the DOC pool in lakes is generally considered to be refractory and so not available to consumers (Wetzel, 2001). However, low molecular weight carbon (LMWC) can originate from the leaching of C from recently cut stems, bark and roots and recently deposited litter (e.g. brash mats) in conifer forests (van Hees et al., 2005). This LMWC, although reported as only comprising between 1 – 8% of the total DOC pool present, may potentially support between 15 – 100% of the bacterial DOC consumption (Berggren et al., 2010). This increased loading of allochthonous TDOC, coupled with its more labile nature, has most likely increased the dependency of these systems towards heterotrophic processes, already known to be important in such oligotrophic lakes (Pålsson et al., 2005), and occurring when DOC concentrations increase above 5 mg l⁻¹ (Jansson et al., 2000).

Changes in lake trophic are known to influence chydorid communities, with *C. sphaericus* particularly responding positively to eutrophication (Hofmann, 1996; Vijverberg and Boersma, 1997; Brodersen et al., 1998), often better than *A. elongata* (de Eyto and Irvine, 2001). The shift towards smaller-bodied species in forestry-impacted lakes is likely due to the increased availability of smaller food particles, which smaller bodied cladocerans are known to ingest more efficiently than larger species (Geller and Müller, 1981). In eutrophic lakes, detrital particles with attached bacteria can often be more quantitatively important food for zooplankton than algae (Gons et al., 1992). The increased supply of allochthonous TDOC is also likely stimulating pelagic bacterial production in this study, thereby leading to an increase in the standing stock of bacteria (Tranvik, 1988). *C. sphaericus* is a very efficient filter feeder, due to its fine-meshed filtration abilities, and can feed readily on smaller food particles, such as bacteria and other microbes (Geller and Müller, 1981; de Eyto and Irvine, 2001). In contrast, *A. elongata*, although capable of filtering

suspended material, collects the majority of its food from benthic surfaces (Fryer, 1968). In the presence of high concentrations of suspended organic particles, *A. elongata* may be unable to forage effectively due to the increased respiratory demands associated with cleaning its thoracic legs; such a phenomenon is known to occur for zooplankton (Porter et al., 1982). This difference in feeding and filtration abilities may explain why *A. elongata* tends to be associated with small oligotrophic humic lakes, in which suspended material is extremely sparse (Fryer, 1968; Duigan and Kovach, 1991). The reduction in size of the dominant Cladocera with increasing trophicity has also been previously demonstrated in other studies (Pejler, 1975; Ewald, 1991), with the decrease being attributed to the invasion of the pelagic zone by small-bodied species usually restricted to the littoral zone.

Other factors that may have influenced the chydorid communities in this study include microhabitat availability, toxicity associated with heavy metal ions (Al and Fe) and proximity to sea. Chydorid species are known to have distinct microhabitat preferences (Tremel et al., 2000), with presence or absence of some substrata, e.g. mud, mineral or macrophyte, restricting the occurrence of certain chydorids. However, Walseng et al. (2008) revealed that habitat type is of lesser importance to community composition in comparison with pH. *A. elongata* is known to rest on mineral benthic substrates, especially stones, and collect its food using scrapers whilst scrambling along firm surfaces (Fryer, 1968). *C. sphaericus* on the other hand does not retain any habitat preferences, as it has two alternative ways of living: i) on macrophytes or a muddy benthos (Whiteside, 1974) or ii) in open water (Vijverberg et al., 1990). Similarly, Flössner (1964) recorded *A. nana* from so many littoral habitats that he designated it as ubiquitous. Although not quantified during this study, it was noted that plantation forestry-affected lakes contained greater

abundances of *Sphagnum* spp., known to be favoured by *A. excisa* (Fryer, 1968). Similar findings of increased *Sphagnum* spp. growth have been noted in small oligotrophic lakes with afforested catchments in Scotland (Raven, 1988). Changes in lake trophy are known to influence the extent and structure of macrophytes (Thoms et al., 1999). The lack of microhabitat preference of *C. sphaericus* and *A. nana*, coupled with the requirement of mineral substrates of *A. elongata*, suggest that changes in microhabitat availability that may arise as a result of catchment plantation forestry will be more detrimental to the latter.

Metal toxicity, associated with Al and Fe ions, may also have influenced the chydorid communities in this study. Although extremely high concentrations of total monomeric Al and Fe were recorded during this study, the concomitant increase in TDOC is likely to have mediated the toxic potential associated with such ions, as it is recognised that the complexation with DOM controls the speciation, toxicity and bioavailability of metal ions (Bidoglio and Stumm, 1994). However, it is possible that metal toxicity was the main determinant responsible for only two individuals of a single species (*A. guttata*) recorded from GC1. The highest concentration of Fe (4620 ug l^{-1}), as well as a very high concentration of total monomeric Al (347.60 ug l^{-1}), were both recorded from this lake. Al toxicity is known to occur for zooplankton, with losses of Na and chloride (Cl) being the causes of death (Havas, 1985; Gensemer and Playle, 1999). Similarly, Fe is known to be toxic at such high concentrations (Biesinger and Christensen, 1972).

Proximity to the sea is known to impact upon chydorid communities due to the influence of marine derived ions (Fryer, 1980). The increased species richness of the granite lakes is most likely due to the elevated pH, alkalinity and Ca concentrations associated with marine sea-salt inputs, as pH has been shown to

influence chydorid species richness (Walseng and Karlsen, 2001). The increased abundance of *A. harpae* in the granite lakes is also likely explained by the higher pH of these lakes. Conversely, the increased abundance of *A. excisa* in the sandstone lakes may be explained by the lower pH of these lakes as this species is known to be more tolerant of acidic conditions in comparison with other chydorid species (Fryer, 1968). The low Ca content of *A. excisa* (Shapiera et al., 2011), may also have enabled this species to better cope with lower Ca concentrations of the sandstone lakes.

4.6. Conclusions

By investigating catchments subject to solely forestry-derived disturbance, this study has demonstrated that conifer plantation forestry has a profound impact on the chydorid communities of blanket bog lakes in Ireland. Previous studies on the impact of catchment forestry operations on lake biota have shown conflicting results, due to the background environmental variation (Paterson et al., 1998). Also, chemical inputs from other non-forestry catchment land uses, such as agriculture (Lepistö et al., 2001), make determining the biological effect of forestry more difficult. There have been a number of studies demonstrating the potential eutrophication effects of forestry on lakes, primarily in Canada and Finland (Kortelainen and Saukkonen, 1998; Carignan et al., 2000; Bredesen et al., 2002). However, the majority of studies in western Europe have focused in the past on the acidification and potential Al toxicity effects of forestry (Ormerod et al., 1989; Kelly-Quinn et al., 1996; Pühr et al., 2000). The increased Al recorded in the impacted lakes does not appear to be the dominant driver of chydorids, although it possibly accounts for the very low numbers of individuals recorded from a single clearfell lake. This study has shown that eutrophication appears to be the dominant driver underlying biological changes, rather than any impact of increased acidity. The impact of forest fertilisation is likely to increase in coming years as plantation forestry continues to grow globally, while still maintaining its dependence on fertilisers to produce a viable crop (Smethurst, 2010). Such a trend is likely to lead to further eutrophication of surrounding water bodies.

Questions remain as to the source of nutrients recorded in this study, the mechanisms responsible for their release, and potential mitigation strategies. Current

forestry best management practices, including drain-blocking and installing buffer strips (Broadmeadow and Nisbet, 2004), have been shown to be relatively inefficient at preventing the efflux of chemical compounds from forestry operations (Prepas et al., 2001). Clearly further research is needed to determine the source and also the best management strategies for reducing the runoff of plantation forestry-derived nutrients to receiving waters.

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Chapter 5

Macroinvertebrate assemblages of peatland lakes: Assessment of conservation value with respect to anthropogenic land-cover change



Cordulia aenea (Linnaeus) (the Downy Emerald) adult (**top**) and larva (**bottom**). This research was the first to record the larva of this species in Ireland. These photographs were kindly supplied by Robert Thompson.

5.1. Summary

Small blanket bog lakes can contain many rare and threatened aquatic invertebrate species. Their conservation value, however, is threatened throughout Europe by peat extraction and particularly conifer afforestation, which can compromise the physico-chemical habitat quality of peatland lakes through excessive inputs of forestry-derived dissolved and particulate substances. The effect of conifer plantation forestry on the conservation value of these habitats was quantified by comparing the hydrochemistry and assemblages of aquatic Coleoptera, Heteroptera and Odonata of replicate lakes across three distinct catchment land uses: i) unplanted blanket bog only present in the catchment, ii) mature conifer plantation forests only present in the catchment and iii) catchments containing mature conifer plantation forests with recently clearfelled areas. All three catchment land uses were replicated across regions of sedimentary and igneous geology. Lakes with afforested catchments, in both geologies, had elevated concentrations of plant nutrients, total dissolved organic carbon (TDOC) and heavy metals, the highest concentrations being recorded from lakes with catchment clearfelling. Coleoptera and Heteroptera assemblages responded strongly to forestry-mediated changes in water chemistry, whereas Odonata assemblages responded more to catchment geology – geology being confounded by altitudinal differences among lakes. The greatest species-quality scores (SQS) and species richness were recorded from the clearfell lakes. Three of the four International Union for the Conservation of Nature (IUCN) nationally red-listed species recorded during this study were, however, absent from clearfell lakes. The findings of this study demonstrate that plantation forestry can have a profound impact on the aquatic macroinvertebrate assemblages and conservation value of

small blanket bog lakes. Despite indices such as SQS scores and species richness appearing to reveal a beneficial response of blanket bog lake communities to habitat deterioration, they mask that certain ‘emblematic’ species are being severely negatively impacted by the disturbance caused by plantation forestry.

5.2. Introduction

Despite their relatively small global areal extent, freshwaters support a disproportionately large number of species in comparison with other ecosystems (Dudgeon et al., 2006). The value of small standing water bodies for biodiversity has gained increasing recognition, both nationally (Gioria et al., 2010) and internationally (Nicolet et al., 2004; Oertli et al., 2005). In northern Europe, however, the conservation value of small standing water bodies on blanket bog has not been widely recognised (Maitland, 1999). Such habitats are a characteristic feature of northern latitude blanket bog habitat (Lindsay et al., 1988), and are noted as having high aquatic Coleoptera and Odonata species richness (Downie et al., 1998). They are also the preferred habitat for many rare and threatened species (Preston and Croft, 1997; Drinan et al., 2011). Although the conservation value of blanket bog is recognised internationally, being listed under Annex I of the EU Habitats Directive (European Commission, 1992), major knowledge gaps remain in terms of the physico-chemical and biological characteristics of standing water bodies associated with this habitat in Britain and Ireland (Maitland, 1999; Curtis et al., 2009).

Blanket bog has a maritime distribution globally (Proctor, 2006), and although common in Britain and Ireland, is rare in a global context (Tallis, 1998). Many blanket bogs have been severely impacted by human disturbance. Drainage and fertilisation associated with agricultural reclamation, peat extraction, overgrazing by sheep, burning, wind farm infrastructure and extensive conifer afforestation have all resulted in the degradation of bog habitat (Holden et al., 2004),

such that few peatlands remain unimpacted in many European countries (Joosten and Clarke, 2002; Chapman et al., 2003).

The use of peatlands for conifer plantation forestry has a long history and began as early as the 17th century when it was realised that “after a fen or bog soil had been drained...it could profitably be used for forest growth” (Gadd, 1773, cited in Paavilainen and Päivänen, 1995). During this time, Russia and many of the Baltic countries extensively drained peatlands for forestry (Paavilainen and Päivänen, 1995). Currently, 25% of the Finland’s forested land consists of drained peatland (Laiho et al., 1998). In Scotland, where the greatest extent of British peatland is located (Milne and Brown, 1997), 25% of Caithness and Sutherland peatlands have been affected by afforestation (Ratcliffe and Oswald, 1988). Similarly, an estimated 27% of Irish blanket bog has been afforested (Conaghan, 2000).

Forest activities within a catchment, including afforestation, draining, thinning, clearfelling, reforestation and forest road construction can affect the hydrochemistry and, thereby, the ecological state of receiving lakes by increasing loadings of plant nutrients, humic substances and sediment (Rask et al., 1998; Carignan and Steedman, 2000; Watmough et al., 2003). The majority of studies investigating the impact of such hydrochemical change on aquatic biota have focused primarily on running waters, with many studies finding little or no forestry impact (Liljaniemi et al., 2002; Gravelle et al., 2009; Heino et al., 2009; McKie and Malmqvist, 2009). Others, however, have shown that chironomid larvae and shredder abundance increases and that acid-sensitive species of Trichoptera and Ephemeroptera decline in abundance and diversity (Death et al., 2003; Kiffney et al., 2003; Martel et al., 2007; Kreutzweiser et al., 2008, 2010).

The fewer studies examining forestry impacts on standing water biota have been carried out primarily on smaller temporary ponds (Jeffries, 1991; Palik et al. 2001; Hanson et al., 2009, 2010) and pools (Standen, 1999), with less on larger lakes (Rask et al., 1993, 1998; Sahlén, 1999; Scrimgeour et al., 2000). The majority of these lentic studies have revealed only a slight impact of forestry, although Sahlén (1999), studying the impact of forestry on Odonata in boreal forest lakes, found that clearfelling resulted in a decrease in dragonfly species richness. Apart from this latter study, this current study is the only one in the author's knowledge to investigate the impacts of catchment forestry on lake aquatic Coleoptera, Heteroptera and Odonata assemblages.

Aquatic macroinvertebrate communities are often used to assess the conservation value of various freshwater habitats (Palmer, 1999; Briers and Biggs, 2003; Chadd and Extence, 2004). For lentic habitats, aquatic Coleoptera, Heteroptera and Odonata are the most widely used, as they are usually the most speciose taxonomic groups, their ecology and national distributions are well documented, and they are found in a wide variety of habitats (Savage, 1982; Foster et al., 1992; Fairchild et al., 2000; Sahlén and Ekestubbe, 2001; Bilton et al., 2006). The majority of species from these taxa are also predators, the number of which is reported to be an important indicator of environmental quality for a given site (Davis et al., 1987). All three groups also tend to respond in a predictable manner to lake physico-chemical environmental variation (Macan, 1954; Nilsson et al., 1994; D'Amico et al., 2004; Foote and Hornung, 2005).

The objective of this study was to investigate the effect of conifer plantation forestry on the conservation value of lakes in blanket bog catchments in Ireland using aquatic macroinvertebrates. The aquatic Coleoptera, Heteroptera and Odonata

assemblages were used to compare the conservation values of lakes subject to catchment afforestation with lakes of undisturbed, unplanted blanket bog.

5.3. Materials and methods

5.3.1. Site description

The 26 study lakes studied in this chapter are the same as those studied in chapters 3 and 4 (described in Section 3.3.1.1.). The granite lakes were situated at lower altitude and in closer proximity to the coast than the sandstone lakes. This variation in geographic location and geological setting was reflected in the hydrochemistry of the study lakes, with the granite lakes containing higher concentrations of marine-derived ions, notably sodium (Na), chloride (Cl), magnesium (Mg) and sulphate (SO₄) (Drinan et al., 2013a). The deposition of marine-derived ions in Irish lakes has been shown to decrease with increasing distance inland from the coast (Aherne and Farrell, 2002).

Fish populations in all study lakes were assessed using the methods outlined in chapter 2 (described in section 2.3.1.). Fish were recorded from four of the twelve lakes underlain by sandstone and in eight of the fourteen lakes underlain by granite (Table 5.1). Fish populations in all lakes were extremely low. Eel (*Anguilla anguilla* Linnaeus), three-spined stickleback (*Gasterosteus aculeatus* Linnaeus) and brown trout (*Salmo trutta* Linnaeus) were the most common. One lake contained a small population of perch (*Perca fluviatilis* Linnaeus).

Table 5.1. Study lakes containing fish populations.

Geology	Catchment land use	Lake	Fish
Sandstone	Blanket bog	SB1	Absent
		SB2	Absent
		SB3	Absent
		SB4	Present
		SB5	Present
		SB6	Present
	Mature plantation	SM1	Absent
		SM2	Absent
		SM3	Absent
	Clearfell	SC1	Absent
		SC2	Absent
		SC3	Present
Granite	Blanket bog	GB1	Absent
		GB2	Present
		GB3	Present
		GB4	Present
		GB5	Absent
		GB6	Present
		GB7	Absent
	Mature plantation	GM1	Present
		GM2	Present
		GM3	Absent
		GM4	Present
	Clearfell	GC1	Present
		GC2	Absent
		GC3	Absent

5.3.2. Littoral macroinvertebrate sampling

Littoral macroinvertebrates were sampled in April, June and September 2009 using two methods: activity traps and multihabitat sweeps. Ten baited activity traps similar to those used by Downie et al. (1998) were deployed to sample the mobile predatory species in each lake. The traps were of a submerged funnel and bottle design, with the funnel inserted into the bottle. The aperture diameter of the circular entrance was 22 mm, and the wider funnel opening was 100 mm in diameter. The total length of the trap was 230 mm. Traps were submerged and placed in all available mesohabitats per lake (submerged, floating and emergent aquatic vegetation, mineral benthic

substrate and peat bank) and remained *in situ* for three consecutive days during each sampling date. Multihabitat sweeps were used for less mobile species and were taken using a standard 1 mm mesh size pond net (frame size 0.20 x 0.25 m). The four-minute sampling time was divided equally among the proportions of different mesohabitats present in each lake. Macroinvertebrate samples were preserved using 70% ethanol. All macroinvertebrate individuals were identified to the lowest practical taxonomic level and were identified using standard identification keys (Hammond, 1983; Friday, 1988; Savage, 1989; Nilsson and Holmen, 1995).

5.3.3. Assessment of conservation value

The conservation value of each lake was assessed using species-quality scores (SQS), similar to Foster et al. (1992). SQS were calculated using the number of hectads (10 x 10 km square) of the Irish National Grid that each individual species of aquatic Coleoptera, Heteroptera and Odonata have been recorded since 1950. These data were provided in appropriate checklists for all species recorded (National Biodiversity Centre, 2011; Nelson, B.H., *pers. comm.*). The counts for species were split into ‘octaves’, i.e. categories of abundance in which the least occurrence doubled from 1 record to records of 512 or more hectads (Table 5.2). The species scores for each category were then assigned scores in a geometric series, with 1 point for the commonest species and 10 points for the least common.

Species richness was calculated as the cumulative number of species recorded at a specific lake over the entire sampling period. The occurrence of species of national conservation interest was also noted for all sites, with these species being

Table 5.2. Development of species-quality scores (SQS) for Irish aquatic Coleoptera, Heteroptera and Odonata.

Number of hectad occurrences (data up to 2011)	Species-quality scores (SQS)
1	10
2 – 3	9
4 – 7	8
8 – 15	7
16 – 31	6
32 – 63	5
64 – 127	4
125 – 255	3
256 – 511	2
> 512	1

listed as either near threatened, vulnerable, endangered or critically endangered in Irish Red Lists for aquatic Coleoptera (Foster et al., 2009) and Odonata (Nelson et al., 2011). The conservation status of Irish aquatic Heteroptera, however, has yet to be assessed using the International Union for the Conservation of Nature (IUCN) regional criteria.

5.3.4. Water chemistry sampling

Water samples were taken from the littoral zone of each lake at a similar depth (0.6 m) and distance (7 m) from shore, bimonthly for 12 months, beginning in March 2009. Water samples were collected in acid-washed polypropylene bottles, stored at 4°C in a cooler box and transported to the laboratory for analysis within 24 hours after collection. Conductivity, dissolved oxygen and temperature were measured on site using WTW portable meters. Ten water chemistry parameters were analysed: pH, total dissolved organic carbon (TDOC), total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), ammonia, calcium (Ca), iron (Fe), total

monomeric aluminium (tot.Al) and chlorophyll *a*. Methods for water chemistry analyses are described in chapter 2 (Section 2.3.2.).

5.3.5. Statistical analyses

Non-metric multi-dimensional scaling (NMDS) analysis was performed, using PC-ORD (version 6; MjM Software, Gleneden Beach, Oregon), to determine among-lake patterns in the aquatic macroinvertebrate assemblages, as it can be used with non-normal and zero rich data (McCune and Grace, 2002). The multihabitat sweep and activity trap data were pooled for these analyses. NMDS ranks points in low-dimensional space such that the relative distances apart of all points are in the same rank order as the relative dissimilarities of the samples (Clarke and Warwick, 2001). The ordination was based on a Bray-Curtis dissimilarity matrix with varimax rotation. Significance of the axes was determined using Monte Carlo simulation using 999 permutations. Species abundances were averaged over the sampling period, and $\log(x + 1)$ transformed to reduce the impact of dominant species on the analyses. Species comprising of less than 5% abundance of any individual community were excluded from the analyses. Singletons, species occurring only once, were also removed (McCune and Grace, 2002). The three separate groups were ordinated in bi-plots and correlated to environmental variables. The final solution for each analysis was based on 999 permutations.

The Multi-Response Permutation Procedure (MRPP) (PC-ORD 6), a non-parametric multivariate procedure used for testing differences among groups, was performed to test for significant among-lake differences in assemblages with respect to catchment land use (blanket bog, mature plantation and clearfell), geology and

fish presence/absence. The MRPP analysis was based on a Bray-Curtis dissimilarity matrix using abundance data. The MRPP test returns a test statistic T that describes the separation among groups (the more negative T is, the stronger the separation) (McCune and Grace, 2002). The effect size is provided by the chance-corrected within-group agreement (A). A describes within-group homogeneity, compared with random expectation. $A = 1$ when all items are identical within groups ($\delta = 0$), $A = 0$ when heterogeneity within groups equals expectation by chance, and $A < 0$ when there is more heterogeneity within groups than expected by chance.

Analysis of variance (ANOVA) was performed using PASW Statistic 17, to test for significant among-lake differences in SQS and other community metrics with respect to catchment land use and geology. Prior to performing ANOVAs, normality and homogeneity of variances were tested using Kolmogorov-Smirnov and Levene's tests, respectively. The ANOVA models were calculated on the basis of Type III sums of squares to take the unbalanced design into account. Significant results were tested for pair-wise comparisons by *post-hoc* Bonferroni tests. Dependent variables were transformed where necessary to fulfil the requirements of the parametric tests.

5.4. Results

5.4.1. Aquatic Coleoptera, Heteroptera and Odonata assemblages

A total of 111 species of aquatic Coleoptera, Heteroptera and Odonata were recorded across all the 26 lakes (Table 5.3). Species richness per lake varied from 18 – 60 (median 31.5) across all lakes. Coleoptera was the most species-rich group recorded in any one lake (mean = $55.9\% \pm 1.7$ S.E.), followed by Heteroptera (mean = $24.5\% \pm 1.2$ S.E.) and Odonata (mean = $19.5\% \pm 1.8$ S.E.). The Dytiscidae was the dominant family of Coleoptera (42 species), while Corixidae (19 species) and Coenagrionidae (4 species) were the most dominant for the Heteroptera and Odonata, respectively. In total, 12,068 individuals were recorded over the entire sampling period, 53% of which were Coleoptera adults, 28% were Heteroptera adults and 19% were Odonata larvae.

Table 5.3. List of aquatic macroinvertebrate species recorded from all lakes over the sampling period (lc: least concern, NT: Near Threatened, and EN: Endangered).

Order	Species	SQS	IUCN Assessment	Blanket bog													Mature plantation								Clearfell					
				SB1	SB2	SB3	SB4	SB5	SB6	GB1	GB2	GB3	GB4	GB5	GB6	GB7	SM1	SM2	SM3	GM1	GM2	GM3	GM4	SC1	SC2	SC3	GC1	GC2	GC3	
Coleoptera	<i>Gyrinus aeratus</i> Stephens	4	lc			+				+					+															
	<i>Gyrinus marinus</i> Gyllenhal	4	lc				+																		+					
	<i>Gyrinus minutus</i> Fabricius	4	lc			+	+		+	+	+	+		+	+	+		+	+	+	+	+		+	+	+		+		
	<i>Gyrinus substriatus</i> Stephens	2	lc	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+				+		+		+		
	<i>Gyrinus urinator</i> Illiger	6	NT																						+					
	<i>Haliphus confinis</i> Stephens	4	lc	+																										
	<i>Haliphus fulvus</i> (Fabricius)	3	lc					+	+	+		+		+	+	+		+												
	<i>Haliphus lineatocollis</i> Mannerheim	2	lc	+											+	+	+		+			+								
	<i>Haliphus ruficollis</i> (De Geer)	2	lc	+				+														+								
	<i>Noterus clavicornis</i> (De Geer)	2	lc				+			+															+					
	<i>Hygrobia hermanni</i> (Fabricius)	5	lc		+				+																+					
	<i>Agabus affinis</i> (Paykull)	3	lc										+												+					
	<i>Agabus arcticus</i> (Paykull)	6	NT	+	+	+												+	+											
	<i>Agabus bipustulatus</i> (Olivier)	1	lc	+	+	+	+	+	+		+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+		
	<i>Agabus nebulosus</i> (Forster)	3	lc			+	+	+							+	+									+					
	<i>Agabus sturmi</i> Gyllenhal	2	lc	+	+	+			+								+	+		+			+		+	+	+	+		
	<i>Agabus unguicularis</i> (Thomson)	4	lc														+													
	<i>Ilybius aenescens</i> Thomson	4	lc			+	+	+	+	+	+	+					+		+		+	+	+	+	+	+	+	+		
	<i>Ilybius ater</i> (De Geer)	3	lc																						+		+	+		
	<i>Ilybius fuliginosus</i> (Fabricius)	2	lc						+	+								+	+	+	+				+	+	+	+		
	<i>Ilybius guttiger</i> (Gyllenhal)	4	lc			+	+	+									+		+	+	+			+	+	+	+	+		
	<i>Ilybius montanus</i> (Stephens)	4	lc															+	+	+			+	+		+				
	<i>Ilybius quadriguttatus</i> (Lacordaire)	3	lc			+											+							+				+		
	<i>Colymbetes fuscus</i> (Linnaeus)	3	lc	+		+	+	+	+								+	+			+			+	+	+		+		
	<i>Rhantus exsoletus</i> (Forster)	3	lc				+	+	+			+	+	+				+	+	+		+	+	+	+	+	+	+		
	<i>Rhantus frontalis</i> (Marsham)	4	lc			+		+																+	+					
	<i>Rhantus grapii</i> (Gyllenhal)	5	lc																							+				
	<i>Rhantus suturellus</i> (Harris)	5	lc															+		+										
	<i>Lioporus haemorrhoidalis</i> (Fabricius)	4	lc																					+	+					
	<i>Acilius canaliculatus</i> (Nicolai)	5	lc			+																			+					
	<i>Acilius sulcatus</i> (Linnaeus)	4	lc	+	+	+				+		+		+	+		+	+	+	+		+		+			+	+		
	<i>Dytiscus lapponicus</i> Gyllenhal	7	NT	+	+												+		+											
	<i>Dytiscus marginalis</i> Linnaeus	3	lc					+	+									+	+		+	+		+	+	+	+	+		
	<i>Dytiscus semisulcatus</i> Müller	3	lc	+	+	+	+	+	+								+		+	+		+		+	+		+			
	<i>Hydaticus seminiger</i> (De Geer)	4	lc			+	+																	+	+		+			
	<i>Graptodytes pictus</i> (Fabricius)	3	lc																			+					+			
	<i>Hydroporus erythrocephalus</i> (Linnaeus)	2	lc	+		+			+	+						+		+	+		+					+	+	+		

Table 5.3. (cont.) List of aquatic macroinvertebrate species recorded from all lakes over the sampling period (lc: least concern, NT: Near Threatened, and EN: Endangered).

Order	Species	SQS	IUCN Assessment	Blanket bog													Mature plantation								Clearfell					
				SB1	SB2	SB3	SB4	SB5	SB6	GB1	GB2	GB3	GB4	GB5	GB6	GB7	SM1	SM2	SM3	GM1	GM2	GM3	GM4	SC1	SC2	SC3	GC1	GC2	GC3	
Coleoptera	<i>Hydroporus gyllenhalii</i> (Schödte)	2	lc		+	+	+				+			+	+		+	+	+	+	+			+	+	+	+			
	<i>Hydroporus incognitus</i> Sharp	3	lc			+	+									+		+					+		+	+	+	+		
	<i>Hydroporus melanarius</i> Sturm	5	lc		+																		+			+	+	+		
	<i>Hydroporus obscurus</i> Sturm	3	lc	+		+	+		+		+	+	+	+	+	+	+	+	+		+	+	+		+			+		
	<i>Hydroporus palustris</i> (Linnaeus)	2	lc	+		+		+								+		+							+	+	+			
	<i>Hydroporus planus</i> (Fabricius)	2	lc						+																+	+	+			
	<i>Hydroporus pubescens</i> (Gyllenhal)	2	lc	+	+	+	+	+	+	+	+		+	+	+	+	+	+		+	+	+		+	+	+		+		
	<i>Hydroporus tristis</i> (Paykull)	3	lc	+	+		+		+						+	+	+			+	+		+	+	+	+	+	+		
	<i>Hygrotus impressopunctatus</i> (Schaller)	4	lc																						+					
	<i>Hygrotus inaequalis</i> (Fabricius)	2	lc		+	+		+	+		+						+	+	+							+		+		
	<i>Hyphydrus ovatus</i> (Linnaeus)	3	lc					+		+	+			+							+			+		+	+	+		
	<i>Nebrioporus assimilis</i> (Paykull)	4	lc						+	+	+	+	+	+	+	+					+									
	<i>Porhydrus lineatus</i> (Fabricius)	3	lc			+												+									+			
	<i>Stictotarsus duodecimpustulatus</i> (Fabricius)	3	lc								+		+			+				+										
	<i>Stictonectes lepidus</i> (Olivier)	3	lc		+				+								+													
	<i>Laccophilus minutus</i> (Linnaeus)	3	lc	+		+			+	+	+								+								+			
	<i>Helophorus aequalis</i> Thomson	3	lc					+	+							+									+					
	<i>Helophorus brevipalpis</i> Bedel	1	lc					+	+	+						+		+	+	+			+	+		+	+			
	<i>Helophorus flavipes</i> Fabricius	3	lc		+	+	+	+	+					+			+	+			+		+	+	+	+	+	+		
	<i>Helophorus minutus</i> Fabricius	4	lc					+	+												+									
	<i>Anacaena globulus</i> (Paykull)	2	lc	+	+	+		+	+	+	+		+			+	+	+	+	+	+	+	+	+	+	+	+	+		
	<i>Anacaena lutescens</i> (Stephens)	2	lc													+	+			+						+	+	+		
	<i>Enochrus affinis</i> (Thunberg)	4	lc				+					+				+				+				+		+	+	+		
	<i>Enochrus coarctatus</i> (Gredler)	3	lc				+																			+				
	<i>Enochrus fuscipennis</i> (Thomson)	4	lc				+						+			+														
	<i>Enochrus ochropterus</i> (Marshall)	4	lc										+			+														
	<i>Helochaetes punctatus</i> Sharp	5	lc														+													
	<i>Hydrobius fuscipes</i> (Linnaeus)	2	lc					+												+		+				+				
	<i>Laccobius bipunctatus</i> (Fabricius)	3	lc																							+				
	<i>Coelostoma orbiculare</i> (Fabricius)	3	lc																							+				
	<i>Oulimnius tuberculatus</i> (Müller)	3	lc								+					+														
	<i>Dryops luridus</i> (Erichson)	3	lc								+					+												+		
	<i>Donacia clavipes</i> Fabricius	6	lc																					+						
	<i>Donacia crassipes</i> Fabricius	6	lc										+																	
	<i>Donacia impressa</i> Paykull	5	lc																							+				
	<i>Donacia obscura</i> Gyllenhal	7	lc						+												+					+				
	<i>Donacia thalassina</i> Germar	4	lc													+					+		+		+					

Table 5.3. (cont.) List of aquatic macroinvertebrate species recorded from all lakes over the sampling period (lc: least concern, NT: Near Threatened, and EN: Endangered).

Order	Species	SQS	IUCN Assessment	Blanket bog														Mature plantation								Clearfell					
				SB1	SB2	SB3	SB4	SB5	SB6	GB1	GB2	GB3	GB4	GB5	GB6	GB7	SM1	SM2	SM3	GM1	GM2	GM3	GM4	SC1	SC2	SC3	GC1	GC2	GC3		
Hemiptera- Heteroptera	<i>Velia caprai</i> Tamanini	4	lc	+	+	+			+	+	+	+		+	+	+			+	+	+	+	+				+	+	+		
	<i>Gerris lacustris</i> (Linnaeus)	4	lc					+		+					+				+		+	+	+	+	+	+	+	+			
	<i>Nepa cinerea</i> Linnaeus	3	lc								+	+	+	+	+	+	+		+	+		+	+	+		+		+	+		
	<i>Hydrometra stagnorum</i> (Linnaeus)	4	lc									+							+							+					
	<i>Notonecta glauca</i> Linnaeus	4	lc	+			+	+	+	+								+	+		+	+		+	+	+	+	+	+		
	<i>Notonecta obliqua</i> Gallen	5	lc	+			+						+		+			+	+	+	+		+			+	+	+	+		
	<i>Arctocoris germari</i> (Fieber)	5	lc				+								+				+									+	+		
	<i>Callicorixa praeusta</i> (Fieber)	4	lc				+	+	+	+	+							+			+		+	+	+	+	+	+	+		
	<i>Callicorixa wollastoni</i> (Douglas & Scott)	6	lc	+	+			+				+						+							+	+	+	+	+		
	<i>Corixa affinis</i> Leach	7	lc				+																								
	<i>Corixa dentipes</i> (Thomson)	5	lc										+		+						+		+	+	+						
	<i>Corixa panzeri</i> (Fieber)	6	lc				+													+											
	<i>Corixa punctata</i> (Illiger)	4	lc				+												+						+	+		+	+		
	<i>Cymatia bondsdorffii</i> (Sahlberg)	4	lc				+					+	+	+		+		+	+		+	+	+	+	+	+	+	+	+		
	<i>Glaenocoris propinqua</i> (Fieber)	7	lc	+	+	+					+	+	+					+	+	+	+				+				+		
	<i>Hesperocoris castanea</i> (Thomson)	5	lc					+	+	+	+	+	+	+	+	+		+	+	+	+		+	+	+	+	+	+	+		
	<i>Hesperocoris linnaei</i> (Fieber)	5	lc				+											+	+	+	+		+	+	+		+	+	+		
	<i>Hesperocoris sahlbergi</i> (Fieber)	5	lc					+	+															+	+	+	+	+	+		
	<i>Sigara concinna</i> (Fieber)	6	lc					+															+								
	<i>Sigara distincta</i> (Fieber)	4	lc				+				+	+			+				+			+		+	+	+	+	+	+		
	<i>Sigara dorsalis</i> (Leach)	4	lc																							+	+	+	+		
	<i>Sigara limitata</i> (Fieber)	10	lc																								+				
	<i>Sigara nigrolineata</i> (Fieber)	5	lc				+																			+					
	<i>Sigara scotti</i> (Douglas & Scott)	4	lc	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
	<i>Sigara semistriata</i> (Fieber)	5	lc																							+		+			
Odonata	<i>Coenagrion puella/pulchellum</i> (Linnaeus/Vander Linden)	2	lc					+							+	+	+			+			+	+		+	+	+			
	<i>Enallagma cyathigerum</i> (Charpentier)	1	lc	+	+	+		+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
	<i>Ischnura elegans</i> (Vander Linden)	1	lc				+							+	+	+	+			+		+		+	+		+	+			
	<i>Pyrrhosoma nymphula</i> (Sulzer)	1	lc	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
	<i>Lestes sponsa</i> (Hansemann)	2	lc				+						+	+	+			+		+	+	+	+	+	+	+	+	+			
	<i>Aeshna grandis</i> (Linnaeus)	2	lc											+		+				+			+	+	+		+	+			
	<i>Aeshna juncea</i> (Linnaeus)	1	lc	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
	<i>Brachytron pratense</i> (Müller)	3	lc												+					+	+	+		+		+		+			
	<i>Cordulia aenea</i> (Linnaeus)	8	EN								+	+	+	+	+					+	+										
	<i>Libellula quadrimaculata</i> Linnaeus	1	lc				+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
	<i>Sympetrum danae</i> (Sulzer)	2	lc					+	+		+						+		+					+	+						
	<i>Sympetrum striolatum</i> (Charpentier)	1	lc					+								+	+				+										

5.4.1.1. Coleoptera ordination

MRPP analysis of Coleoptera assemblages revealed significant differences with respect to both catchment land use and geology, but not fish (Table 5.4). NMDS of lake Coleoptera assemblages indicated that a solution incorporating two axes, with a final stress of 0.17, was most appropriate (Monte Carlo test). NMDS axis 1 separated lake assemblages with respect to catchment land use and NMDS axis 2 with respect to geology (Fig. 5.1). Assemblages from forestry-affected lakes, particularly clearfell lakes, were associated with elevated concentrations of TDOC, total monomeric Al, TP, Fe, TN, chlorophyll *a*, ammonia, SRP and reduced dissolved oxygen levels (Fig. 5.1). Assemblages from the lower altitude granite lakes were associated with higher pH, temperature, conductivity and Ca concentrations (Fig. 5.1).

Clearfell lake assemblages were characterised by larger species, notably *Dytiscus marginalis* Linnaeus, *Ilybius ater* (De Geer), *Rhantus exsoletus* (Forster), *Ilybius guttiger* (Gyllenhal) and *Noterus clavicornis* (De Geer) (Fig. 5.1). Blanket bog lake assemblages were characterised by smaller species, notably *Nebrioporus assimilis* (Paykull), *Hydroporus erythrocephalus* (Linnaeus) and *Gyrinus aeratus* Stephens. The separation between geologies appeared to be driven by the higher altitude sandstone lakes containing greater abundances of *Acilius sulcatus* (Linnaeus), *Dytiscus lapponicus* Gyllenhal and *Agabus arcticus* (Paykull), while the lower altitude granite lakes contained greater abundances of *Enochrus fuscipennis* (Thomson), *Stictotarsus duodecimpustulatus* (Fabricius) and *Haliphus fulvus* (Fabricius) (Fig. 5.1). One lake (GB4) scored highly negatively on this axis because it contained far fewer species in comparison with other lakes.

Table 5.4. Results of multiple-response permutation procedures (MRPP) to test for differences in aquatic macroinvertebrate assemblages across lakes of contrasting catchment land use (blanket bog, mature plantation and clearfell), geology and fish presence/absence (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 3).

Group	Factor				A	T	p
Coleoptera	Catchment land use				0.193	-5.589	<0.001
	<u>Pair-wise comparisons</u>						
		Blanket bog	v	Mature plantation	0.105	-3.272	0.008
		Blanket bog	v	Clearfell	0.198	-5.684	<0.001
		Mature plantation	v	Clearfell	0.116	-2.474	0.010
	Geology				0.119	-5.042	0.001
Heteroptera	Fish				0.043	-1.835	0.054
	Catchment land use				0.217	-5.358	<0.001
	<u>Pair-wise comparisons</u>						
		Blanket bog	v	Mature plantation	0.047	-1.339	0.099
		Blanket bog	v	Clearfell	0.240	-5.982	<0.001
		Mature plantation	v	Clearfell	0.207	-3.542	0.009
Odonata	Geology				0.081	-2.908	0.012
	Fish				0.018	-0.644	0.226
	Catchment land use				0.045	-1.192	0.121
	Geology				0.064	-2.451	0.025
	Fish				0.002	-0.093	0.388

Singificant terms are emboldened.

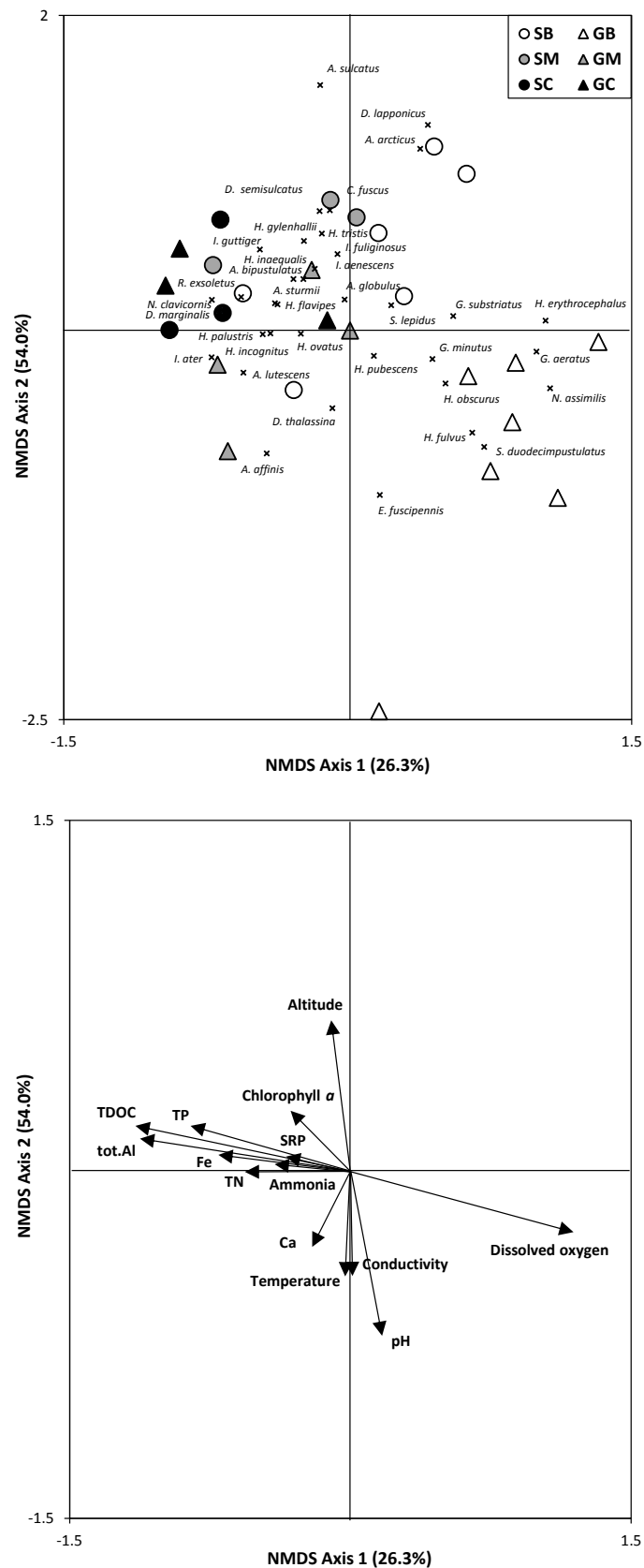


Figure 5.1. Non-metric multi-dimensional scaling (NMDS) analysis of aquatic Coleoptera assemblages in each of the 26 study lakes, including lake and species scores (top) and environmental variables (bottom). Only environmental variables significantly correlated with either axis 1 or 2 are displayed (geology: S = sandstone and G = granite; catchment land use: B = blanket bog, M = mature plantation and C = clearfell).

5.4.1.2. Heteroptera ordination

MRPP analysis of Heteroptera assemblages, as for the Coleoptera, revealed significant differences with respect to both catchment land use and geology, but not fish (Table 5.4). NMDS of lake Heteroptera assemblages required two axes to reduce stress to a minimal level – final stress 0.21 (Monte Carlo test). NMDS axis 1 separated lakes with respect to geology and NMDS axis 2 with respect to catchment land use (Fig. 5.2). Assemblages from forestry-affected lakes, particularly clearfell lakes, were associated with elevated concentrations of TDOC, Fe, TP, SRP, TN, chlorophyll *a*, Ca and ammonia and reduced dissolved oxygen levels (Fig. 5.2). Assemblages from the lower altitude granite lakes were associated with higher conductivity and temperature (Fig. 5.2).

Clearfell lake assemblages were characterised by greater abundances of *Sigara semistriata* (Fieber), *Hesperocorixa linnaei* (Fieber), *Hesperocorixa sahlbergi* (Fieber), *Corixa punctata* (Illiger) and *Callicorixa praeusta* (Fieber) (Fig. 5.2). The assemblages of the blanket bog and mature plantation lakes were somewhat similar, and contained fewer species in comparison with the clearfell lakes. The only species which displayed a greater preference for these lakes were *Arctocorisa germari* (Fieber), *Glaenocorisa propinqua* (Fieber) and *Velia caprai* Tamanini (Fig. 5.2). The separation in assemblages between geologies was less clear and was driven by the higher altitude sandstone lakes containing greater abundances of *Callicorixa wollastoni* (Douglas & Scott), while the lower altitude granite lakes contained greater abundances of *Nepa cinerea* Linnaeus and *Cymatia bonsdorffii* (Sahlberg) (Fig. 5.2).

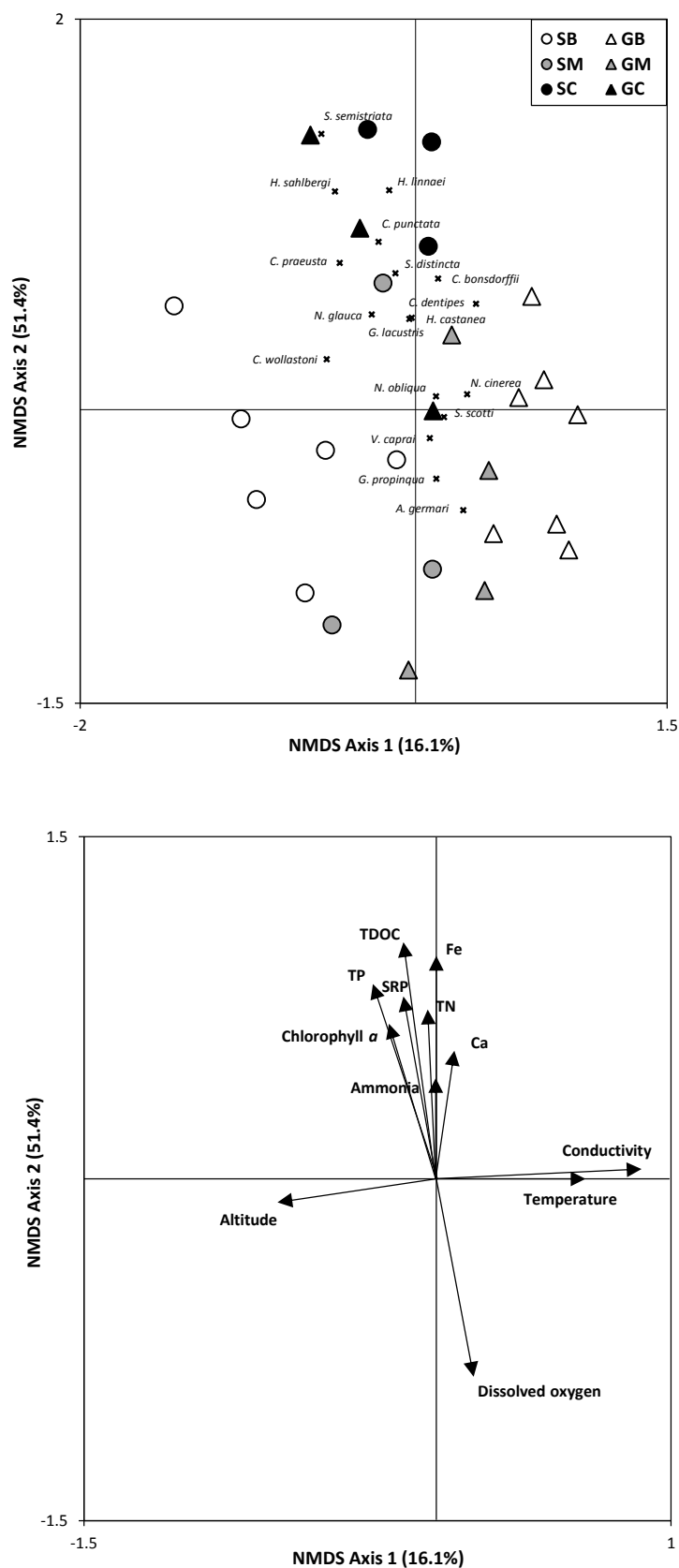


Figure 5.2. Non-metric multi-dimensional scaling (NMDS) analysis of aquatic Heteroptera assemblages in each of the 26 study lakes, including lake and species scores (top) and environmental variables (bottom). Only environmental variables significantly correlated with either axis 1 or 2 are displayed (geology: S = sandstone and G = granite; catchment land use: B = blanket bog, M = mature plantation and C = clearfell).

5.4.1.3. *Odonata* ordination

MRPP analysis of *Odonata* assemblages revealed significant differences with respect to geology, however, no significant differences were observed with respect to either catchment land use or fish (Table 5.4). NMDS of lake *Odonata* assemblages also required two axes to reduce stress to a minimal level – final stress 0.18 (Monte Carlo test). NMDS axis 1 separated lakes with respect to catchment land use and NMDS axis 2 with respect to geology (Fig. 5.3). Assemblages from a number of forestry-affected lakes were associated with elevated temperature, Fe, conductivity, Ca and TDOC concentrations and reduced dissolved oxygen levels (Fig. 5.3). Assemblages from the higher altitude sandstone lakes were associated with elevated dissolved oxygen concentrations (Fig. 5.3).

The separation in assemblages with respect to catchment land use was far less clear in comparison with that for geology. A number of mature plantation and clearfell lakes were characterised by greater abundances of *Brachytron pratense* (Müller), *Ischnura elegans* (Vander Linden), *Aeshna grandis* (Linnaeus) and *Lestes sponsa* (Hansemann) (Fig. 5.3). The assemblages of the blanket bog and mature plantation lakes were somewhat similar, and were characterised by greater abundances of *Enallagma cyathigerum* (Charpentier) (Fig. 5.3). The separation between geologies was driven by the higher altitude sandstone lakes containing far fewer species in comparison with the lower altitude granite lakes (Fig. 5.3). Only one species – *Sympetrum danae* (Sulzer) – displayed a preference for the higher altitude sandstone lakes (Fig. 5.3).

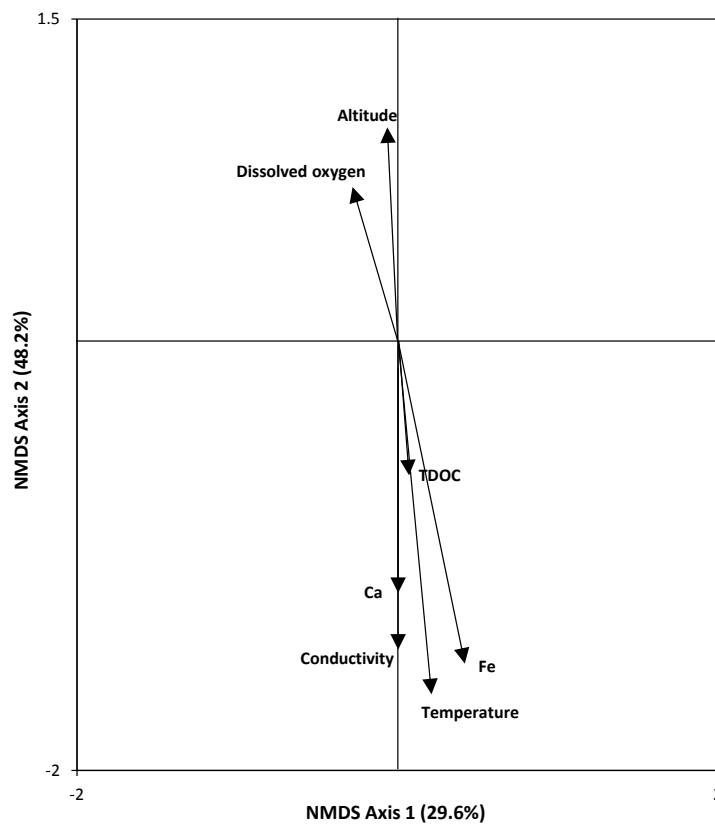
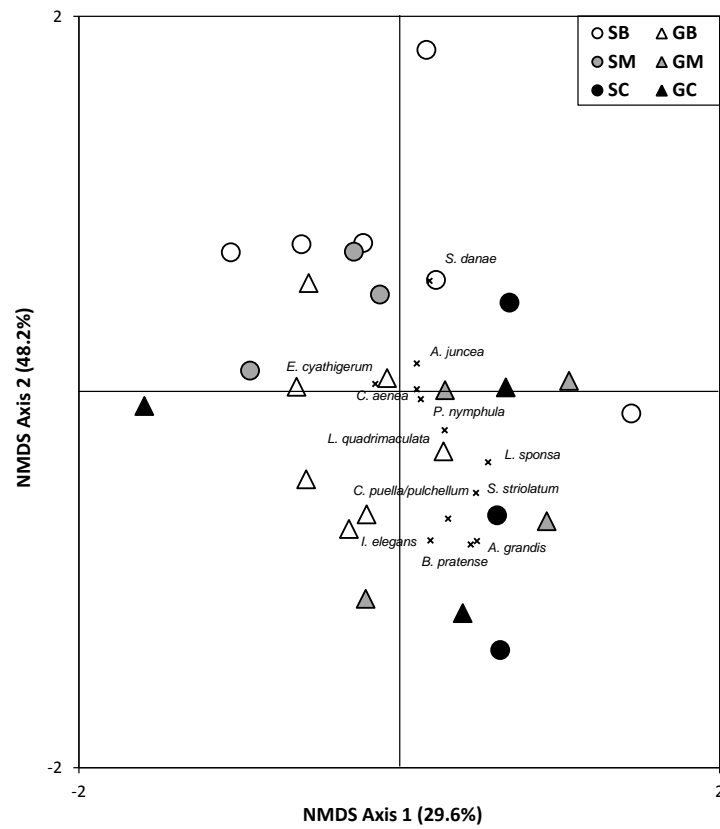


Figure 5.3. Non-metric multi-dimensional scaling (NMDS) analysis of Odonata assemblages in each of the 26 study lakes, including lake and species scores (top) and environmental variables (bottom). Only environmental variables significantly correlated with either axis 1 or 2 are displayed (geology: S = sandstone and G = granite; catchment land use: B = blanket bog, M = mature plantation and C = clearfell).

5.4.2. Conservation value: SQS, species richness and species rarity

SQS displayed a close association with species richness across all three macroinvertebrate groups (Fig. 5.4; Table 5.5). Coleoptera SQS, species richness and total abundance were all significantly higher in sandstone lakes (Fig. 5.4; Table 5.5). Catchment land use had no significant effect on any Coleoptera metric (Fig. 5.4; Table 5.5). Heteroptera SQS and species richness were significantly higher in clearfell lakes and total abundance significantly lower in mature plantation lakes (Fig. 5.4; Table 5.5). There was no significant effect of catchment geology on Heteroptera metrics. Odonata SQS, but not species richness, was significantly higher in granite lakes (Fig. 5.4; Table 5.5). Both SQS and species richness showed a significant interaction between geology and catchment land use, with clearfelling having contrasting effects between sandstone and granite geologies (Fig. 5.4; Table 5.5). Neither catchment land use nor geology had any significant impact on Odonata total abundance (Fig. 5.4; Table 5.5). Average lake SQS per species showed little variation across all lake types: SB (3.15 ± 0.12 S.E.), GB (2.99 ± 0.13 S.E.), SM (3.03 ± 0.03 S.E.), GM (2.96 ± 0.18 S.E.), SC (3.23 ± 0.02 S.E.) and GC (3.09 ± 0.06 S.E.).

Of the 111 species recorded during this study, 23 of these species were not recorded from any clearfell lake, 36 were not recorded from any mature plantation lake and 17 were not recorded from any undisturbed blanket bog lake. There were also a number of species which were only recorded from lakes in each of the three catchment land uses across both geologies (Table 5.6).

Three Coleoptera species recorded, *Gyrinus urinator* Illiger, *A. arcticus* and *D. lapponicus*, are listed as near threatened on the Irish Red List for aquatic

Coleoptera (Foster et al., 2009). *G. urinator* was recorded once from a clearfell lake, *A. arcticus* was recorded from three blanket bog and two mature plantation lakes, while *D. lapponicus* was recorded from two blanket bog and two mature plantation lakes. One Odonata species recorded, *Cordulia aenea* (Linnaeus), is listed as endangered on the Irish Red List for Odonata (Nelson et al., 2011). *C. aenea* was recorded from five blanket bog and two mature plantation lakes. Irish aquatic Heteroptera have yet to be assessed using the IUCN regional criteria, however, one corixid species – *Sigara limitata* (Fieber) – previously recorded from only a single hectad in Ireland, was recorded from a single clearfell lake (Table 5.3). Of the four species listed on Irish Red Lists, three species, *A. arcticus*, *D. lapponicus* and *C. aenea*, were not recorded from any clearfell lake.

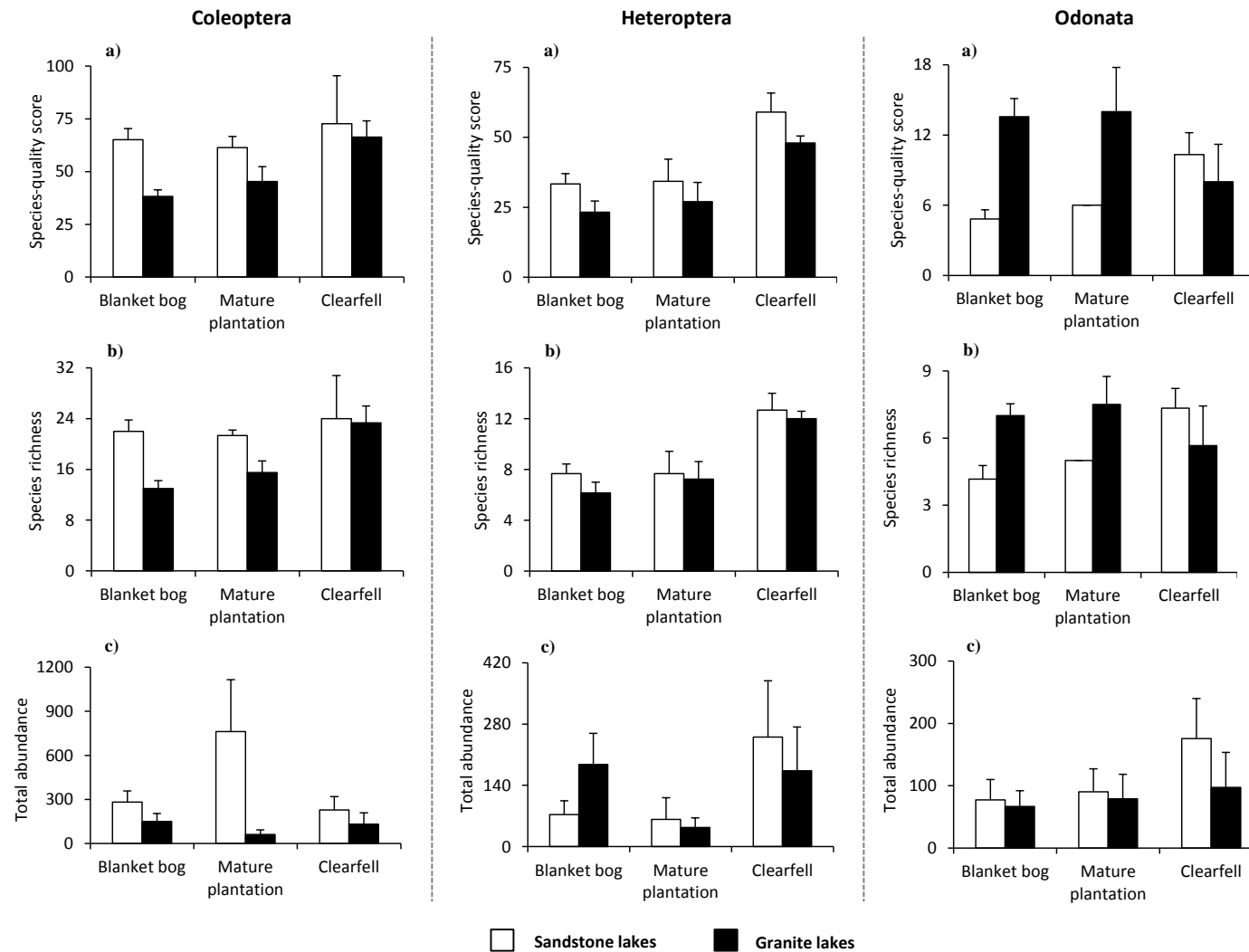


Figure 5.4. Comparison of mean a) SQS, b) species richness and c) total abundance for all three macroinvertebrate groups among the blanket bog, mature plantation and clearfell lakes across both geologies (sandstone and granite). Columns on each graph are mean values (± 1 S.E.) for each catchment land use calculated over the duration of the sampling period (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 3).

Table 5.5. Summary of 2 – way ANOVAs of aquatic Coleoptera, Heteroptera and Odonata SQS scores, species richness and total abundance, with catchment land use (blanket bog, mature plantation and clearfell) and geology (sandstone and granite) as main factors. Any two catchment land uses sharing a common letter are not significantly different.

		2 - way ANOVA			<i>post-hoc</i> Bonferroni tests			
			d.f.	<i>F</i>	<i>p</i>	Blanket bog	Mature plantation	Clearfell
Coleoptera	Species-quality score	Catchment land use	2, 20	2.489	0.108	-	-	-
		Geology	1, 20	6.219	0.022*	Sandstone > Granite		
		Interaction	2, 20	1.355	0.281	-	-	-
	Species richness	Catchment land use	2, 20	2.920	0.077	-	-	-
		Geology	1, 20	6.101	0.023*	Sandstone > Granite		
		Interaction	2, 20	1.882	0.178	-	-	-
	Total abundance	Catchment land use	2, 20	0.107	0.899	-	-	-
		Geology	1, 20	10.139	0.005**	Sandstone > Granite		
		Interaction	2, 20	1.900	0.176	-	-	-
Heteroptera	Species-quality score	Catchment land use	2, 20	9.038	0.002**	a	a	b
		Geology	1, 20	3.863	0.063	-	-	-
		Interaction	2, 20	0.063	0.939	-	-	-
	Species richness	Catchment land use	2, 20	9.963	<0.001***	a	a	b
		Geology	1, 20	0.825	0.375	-	-	-
		Interaction	2, 20	0.240	0.789	-	-	-
	Total abundance	Catchment land use	2, 20	5.511	0.012*	a	b	a
		Geology	1, 20	0.577	0.456	-	-	-
		Interaction	2, 20	1.311	0.292	-	-	-
Odonata	Species-quality score	Catchment land use	2, 20	0.100	0.905	-	-	-
		Geology	1, 20	7.096	0.015*	Granite > Sandstone		
		Interaction	2, 20	4.752	0.020*	-	-	-
	Species richness	Catchment land use	2, 20	0.692	0.512	-	-	-
		Geology	1, 20	2.513	0.129	-	-	-
		Interaction	2, 20	3.995	0.035*	-	-	-
	Total abundance	Catchment land use	2, 20	1.258	0.306	-	-	-
		Geology	1, 20	0.296	0.592	-	-	-
		Interaction	2, 20	0.607	0.555	-	-	-

Significant terms are emboldened. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Table 5.6. Species which were only recorded from lakes in each catchment land use (blanket bog, mature plantation and clearfell) across both geologies. The number of lakes in which each species occurred is listed in parentheses (n: SB = 6, GB = 7, SM = 3, GM = 4, SC = 3 and GC = 3).

	Blanket bog	Mature plantation	Clearfell
Sandstone	Coleoptera	Coleoptera	Coleoptera
	<i>Donacia obscura</i> (1)	<i>Agabus unguicularis</i> (1)	<i>Agabus affinis</i> (1)
	<i>Enochrus affinis</i> (1)	<i>Rhantus suturellus</i> (1)	<i>Anacaena lutescens</i> (1)
	<i>Enochrus coarctatus</i> (1)		<i>Donacia clavipes</i> (1)
	<i>Enochrus fuscipennis</i> (1)		<i>Donacia impressa</i> (1)
	<i>Gyrinus aeratus</i> (1)		<i>Donacia thalassina</i> (1)
	<i>Haliplus confinis</i> (1)		<i>Gyrinus urinator</i> (1)
	<i>Haliplus ruficollis</i> (2)		<i>Hygrotus impressopunctatus</i> (1)
	<i>Helophorus minutus</i> (2)		<i>Ilybius ater</i> (1)
	<i>Hydrobius fuscipes</i> (1)		<i>Liopterus haemorrhoidalis</i> (2)
Granite	<i>Hydroporus melanarius</i> (1)		Heteroptera
	<i>Nebrioporus assimilis</i> (1)		<i>Corixa dentipes</i> (3)
	Heteroptera		<i>Sigara limitata</i> (1)
	<i>Arctocorisa germari</i> (1)		<i>Sigara semistriata</i> (1)
	<i>Corixa affinis</i> (1)		Odonata
	<i>Corixa panzeri</i> (1)		<i>Brachytron pratense</i> (1)
	Odonata		
	<i>Sympetrum striolatum</i> (1)		
Granite	Coleoptera	Coleoptera	Coleoptera
	<i>Agabus affinis</i> (1)	<i>Agabus arcticus</i> (1)	<i>Coelostoma orbiculare</i> (1)
	<i>Donacia crassipes</i> (1)	<i>Enochrus ochropterus</i> (1)	<i>Enochrus coarctatus</i> (1)
	<i>Enochrus fuscipennis</i> (2)	<i>Graptodytes pictus</i> (1)	<i>Hydaticus seminiger</i> (1)
	<i>Gyrinus aeratus</i> (2)	<i>Haliplus lineatocollis</i> (1)	<i>Ilybius quadriguttatus</i> (1)
	<i>Haliplus fulvus</i> (5)	<i>Helophorus minutus</i> (1)	<i>Ilybius ater</i> (2)
	<i>Helochares punctatus</i> (1)	<i>Rhantus suturellus</i> (1)	<i>Laccobius bipunctatus</i> (1)
	<i>Helophorus aequalis</i> (1)	Heteroptera	<i>Porhydrus lineatus</i> (1)
	<i>Noterus clavicornis</i> (1)	<i>Corixa panzeri</i> (1)	<i>Rhantus grapii</i> (1)
	<i>Oulimnius tuberculatus</i> (2)		Heteroptera
Granite	Odonata		<i>Corixa punctata</i> (2)
	<i>Sympetrum danae</i> (1)		<i>Hesperocorixa linnaei</i> (1)
			<i>Hesperocorixa sahlbergi</i> (2)
			<i>Sigara dorsalis</i> (1)
			<i>Sigara semistriata</i> (1)

5.5. Discussion

5.5.1. The effect of conifer plantation forestry on the Coleoptera, Heteroptera and Odonata assemblages of blanket bog lakes

The findings of this study demonstrate that conifer plantation forestry has a major influence on the aquatic Coleoptera, Heteroptera and Odonata assemblages of blanket bog lakes. Forestry impacts were associated with marked changes in water chemistry, notably elevated concentrations of plant nutrients, heavy metals, TDOC and lower dissolved oxygen levels. For Coleoptera and Heteroptera, the effect of plantation forestry was most evident at the clearfell stage and was common to lakes across both geologies and regions. Odonata assemblages were influenced more by underlying geology (and associated altitude) than plantation forestry. pH did not show any association with forestry, and was not a major driver of macroinvertebrate assemblages. This was a surprising finding given the numbers of studies documenting the impact of plantation forestry-driven acidification on aquatic macroinvertebrates (Ormerod et al., 1993, 2004; Ormerod and Durance, 2009). Fish were also not a significant driver of assemblages for any of the three macroinvertebrate groups.

Changes in water chemistry, especially in relation to acidity and productivity, are known to influence the composition of lentic aquatic macroinvertebrate communities, although their response is highly variable and dependent upon a number of physical (e.g. lake morphometry, habitat complexity, etc.) and biotic (e.g. predation) factors which operate at different spatial scales (Friday, 1987; Brodersen et al., 1998; Heino, 2000; Brauns et al., 2007; Free et al., 2009; Heino, 2009;

McGough and Sandin, 2012). In comparison with acidity, there have been fewer studies investigating the influence of lake trophic on littoral macroinvertebrates (Heino, 2009). Many studies have struggled to find a consistent response of macroinvertebrate communities to trophic status due to other overriding environmental factors (Johnson and Goedkoop, 2002; White and Irvine, 2003; Brauns et al., 2007). Brodersen et al. (1998) is one of few studies, however, to document notable community change. This study found that chironomid abundance increased, while Shannon's diversity index and species richness of littoral macroinvertebrates decreased with increasing chlorophyll *a* concentrations in Danish lakes. Donohue et al. (2009a) also found that eutrophication reduced β -diversity of littoral macroinvertebrates at both local and regional scales. Similarly, Donohue et al. (2009b) showed that littoral macroinvertebrate communities associated with hard substrates responded to eutrophication.

Although terrestrial and aquatic physical habitat change may have influenced the assemblages in the study lakes, the variation in species composition of assemblages appears to be largely attributable to changes in lake water chemistry. The species which were characteristic of nutrient-enriched lakes in this study have also been reported to be associated with eutrophic conditions elsewhere. For example, Verberk et al. (2005), who studied the aquatic macroinvertebrate communities of a bog remnant in the Netherlands, found that *I. ater*, *I. guttiger* and *Rhantus* sp., characteristic of clearfell lakes in this study, were all associated with eutrophic water bodies. Verberk et al. (2001) also found that *N. clavicornis* and *Ilybius* spp. were associated with eutrophic water bodies in the same area. Similarly for Heteroptera, *C. praeusta*, *Sigara dorsalis* (Leach), *H. sahlbergi*, *H. linnaei* and *C. punctata*, which were more abundant in clearfell lakes, have all been shown to

have a preference for eutrophic habitats (Macan, 1954; Savage, 1989, 1994; Verberk et al., 2005). *C. praeusta* has also been found to be characteristic of nutrient-enriched water bodies elsewhere (Biesiadka and Szczepaniak, 1987; Nelson, 2000). In terms of the Odonata, the occurrence of larvae of *Brachytron pratense* (Müller) and *Ischnura elegans* (Vander Linden) in the more eutrophic forestry-affected lakes also reflects the preference of these species for more nutrient-rich waters (Nielsen, 1998; Nelson, 2000; Verberk et al., 2005).

Although not quantified during this study, it was noted that forestry-affected lakes, especially the clearfell lakes, were found to have large extensive *Sphagnum* mats encroaching inward from the littoral zone. This has been documented for lakes elsewhere which were subject to catchment afforestation (Raven, 1988). Microhabitat availability is known to influence Coleoptera, Heteroptera and Odonata assemblages (Savage, 1989; Nilsson et al., 1994; García-Avilés et al., 1996; Carchini et al., 2005; Honkanen et al., 2011). Similarly, the change in the surrounding riparian zone of the afforested lakes is another potential determinant of assemblage variation among lakes, especially for Odonata (Rith-Najarian, 1998; Corbet, 2006). Despite the data being limited to lake hydrochemistry, however, the concurrent shift in macroinvertebrate community composition towards an assemblage indicative of nutrient-enriched habitats, especially for the Coleoptera and Heteroptera, suggests that forestry-mediated eutrophication, rather than aquatic or terrestrial physical habitat changes, is the primary driver underlying such change. Previous work by the author on the same lakes used in this study has also demonstrated that a shift in littoral zooplankton community composition with respect to catchment plantation forestry was driven primarily by eutrophication (Drinan et al., 2013b).

Altitudinal differences over the range of this study have been shown to have a minimal influence on Coleoptera and Heteroptera assemblages (Eyre et al., 2006). Altitude had a greater influence on Odonata assemblages in the study lakes, however. The greater Odonata species richness of the granite lakes is likely due to their location at lower altitudes (mean 114 m \pm 15 S.E.) in comparison with the sandstone lakes (mean 298 m \pm 29 S.E.). Many Odonata species in Ireland occur very infrequently above altitudes of between 200 – 250 m (Nelson and Thompson, 2004). The inverse response of Odonata SQS and species richness to catchment clearfelling across the two geologies is also likely explained by the fact that the sandstone clearfell lakes were situated at a lower altitude (mean 199 m \pm 33 S.E.) in comparison with the mature plantation (mean 374 m \pm 5 S.E.) and blanket bog sandstone lakes (mean 309 m \pm 40 S.E.).

5.5.2. The effect of conifer plantation forestry on the conservation value of blanket bog lakes

Exotic conifer plantations are generally recognised as being less species rich in comparison with natural woodlands (Bremer and Farley, 2010). Despite this, however, many researchers have found that plantations can play a major role in conserving biodiversity and restoring forest species (Hartley, 2002; Carnus et al., 2006; Bockerhoff et al., 2008), including rare and endangered species (Bockerhoff et al., 2005; Pawson et al., 2010). Very little is known, however, about the impact of conifer plantation forestry on the species richness of aquatic fauna from lentic habitats. The results of this study demonstrate that species richness, known to be a function of both productivity and disturbance levels (Kondoh, 2001), was positively

associated with hydrochemical disturbance from conifer plantation forestry. Although it has been shown that species richness decreases as a habitat deteriorates from a natural state (plants: Clark and Tilman, 2008; mammals: Findlay and Houlihan, 1997; fish: Jones et al., 2004; insects: Scheffler, 2005), the results of this study seem to support the findings of others who have demonstrated that species richness increases with disturbance (Hamer et al., 1997; Willott et al., 2000; Liow et al., 2001). Increasing species richness with disturbance is in agreement with the ‘intermediate disturbance hypothesis’ (Connell, 1978), which states that low levels of disturbance leads to low diversity through competitive exclusion, while too much disturbance eliminates species incapable of rapid recolonisation.

Despite indices such as species richness and SQS appearing to reveal a beneficial response of blanket bog lake communities to habitat deterioration, they mask that certain ‘emblematic’ species (e.g. *C. aenea*) are being severely negatively impacted by the disturbance caused by plantation forestry. Previous research has shown that the rarest and most representative aquatic macroinvertebrate species of bog lentic habitats show a clear preference for undisturbed sites (van Duinen et al., 2003). In this study, many of the Coleoptera species which were only recorded from the undisturbed blanket bog lakes – *Nebrioporus* sp., *Stictonectes* sp., *Oulimnius* sp., *Enochrus* spp. – are known to be sensitive to trophic enrichment (Donohue et al., 2009b). Similarly, assessment of species rarity revealed that all but one of the four species listed on the Irish Red Lists for aquatic Coleoptera and Odonata were absent from all clearfell lakes. Both notable Coleoptera species recorded, *A. arcticus* and *D. lapponicus*, are usually restricted to undisturbed upland habitats in Ireland and are considered glacial relict species (McCormack, 2005). The preference of *C. aenea* for the undisturbed blanket bog lakes also suggests that this species is relatively

intolerant of habitat deterioration associated with forestry. Bog habitat-specialist species of Odonata have found to be most at risk from habitat disturbance in comparison with other Odonata species (Korkeamäki and Suhonen, 2002). Interestingly, the only Coleoptera listed on the Irish Red List which was restricted to a single clearfell lake was *G. urinator*, a species largely restricted to lowland, base-rich rivers and streams in Ireland (Foster et al., 2009).

5.5.3. The use of indices and metrics for the assessment of conservation value of freshwaters

The findings of this study leads to a pivotal question in terms of biological conservation value: is conserving higher biodiversity of greater significance than conserving rare species restricted to a particular habitat type? Increasing species richness is often a primary objective of conservation studies and it is also recognised that the protection of areas with high species richness is an efficient method to conserve overall biodiversity (Myers et al., 2000). However, the results of this study demonstrate that such an approach may undervalue populations of notable species which are habitat-dependent. The inadequacies of using a single index (e.g. species richness) to guide conservation policies for threatened and/or endemic species is known (Orme et al., 2005). Many studies have previously demonstrated that rare species often do not occur in locations with the highest species richness (Jetz and Rahbek, 2002; Stohlgren et al., 2005). Similarly, the use of metrics comparable to those used in this study, e.g. Community Conservation Index (Chadd and Extence, 2004), is likely to have yielded similar results as the calculation of such metrics is heavily dependent upon species richness and does not take into account the

autoecology of individual species. This was demonstrated in this study, whereby the increase in SQS, although suggestive of an increase in frequency of rarer taxa in the forestry-affected lakes, was shown to be solely attributable to the increased species richness of the forestry-affected lakes. A more comprehensive approach for conservation planning has been proposed by Fleishman et al. (2006). This study recommends the use of additional metrics and a greater knowledge of the basic life history of taxonomic groups, in conjunction with species richness, to establish more comprehensive conservation assessments and priorities. It seems more justified to place greater emphasis on the assemblage ‘distinctiveness’, the degree by which the assemblage represents a specific species pool as a part of a national or international ‘pool’ of organisms, as well as species rarity. The value of rarity for conservation assessment is already well recognised (Samu et al., 2008; Gauthier et al., 2010). In applying this approach, the conservation value of sites or habitats which are naturally depauperate (e.g. high altitude ponds) yet contain many rare or habitat-specific species, can be assessed more appropriately. Furthermore, such an approach would help to buffer against inappropriate conservation assessments based on estimates of species richness, an index which is inherently difficult to quantify owing to its dependency on area, scale and intensity of sampling, taxonomic grouping and survey methods (Fleishman et al., 2006).

5.6. Conclusions

Despite being thought to harbour many rare and endangered species (Maitland, 1999), as well as being a protected habitat type within the EU Habitats Directive (European Commission, 1992), small lakes in blanket bog catchments are generally little studied. In this study, the occurrence of a number of uncommon and rare aquatic macroinvertebrate species vindicates this claim. The results demonstrate the profound change in macroinvertebrate assemblage that this protected habitat is undergoing as a result of conifer plantation forestry operations. The hydrochemical and resulting biological effects of plantation forestry operations were evident at the mature plantation forest phase, but most distinct at the clearfell stage, with catchment clearfelling leading to the exclusion of three out of the four nationally red-listed species recorded during the study. Due to the lack of research effort, it seems very likely that many more rare species of aquatic macroinvertebrates remain unrecorded from similar blanket bog habitats elsewhere. However, many of these species may be lost due to the impact of peatland plantation forestry.

This result poses serious management implications for forest managers and policy makers in areas of peatland forestry worldwide, especially in northern and western Europe and Canada. The majority of European studies in the past have focused on the acidification and potential Al toxicity effects of forestry (Jeffries, 1991; Ormerod et al., 1993, 2004). However, the findings of this study suggest that eutrophication is likely to be the major determinant of ecological degradation of receiving standing waters associated with peatland conifer plantation forestry. Considering the need for fertiliser to produce economically viable plantation forest crops (Smethurst, 2010), coupled with the inefficiencies of peat soils in retaining

applied nutrients (Vuorenmaa et al., 2002), this ecological problem is likely to become more prevalent as plantation forestry continues to expand worldwide (FAO, 2010).

5.7. References

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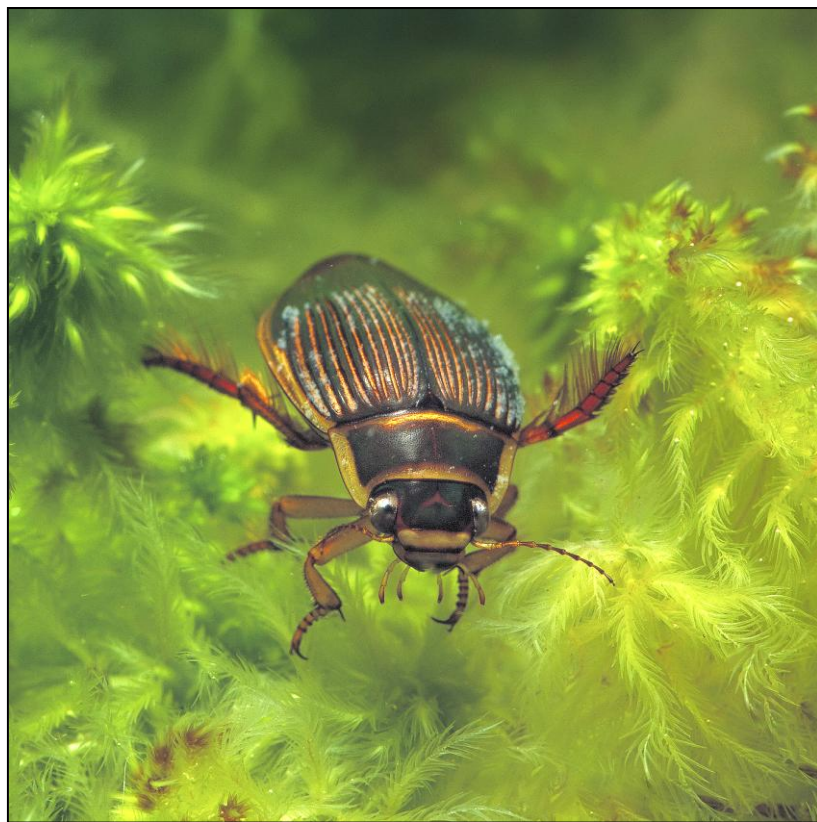
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Chapter 6

Influence of top-down versus bottom-up forces on the littoral macroinvertebrate communities of peatland lakes



Dytiscus marginalis Linnaeus (the Great Diving Beetle), an example of an invertebrate predator recorded during this study. This photograph was kindly supplied by Robert Thompson.

6.1. Summary

Much research effort has been invested into determining whether pelagic food webs are structured by bottom-up (resources) or top-down (consumer) forces. Far fewer studies, however, have investigated the same question in littoral food webs. In this study, the littoral macroinvertebrate communities of six blanket bog lakes were studied to determine the relative influence of forestry-mediated eutrophication and fish predation in determining littoral macroinvertebrate community structure and composition. Lakes were selected in a paired design (fish present/absent) across three bands of forestry-mediated nutrient status: i) low nutrients, ii) medium nutrients and iii) high nutrients. Littoral macroinvertebrate community structure and species turnover (β -diversity) varied significantly with respect to nutrient status, however, only community structure was significantly different with respect to fish. Community metrics, species richness and abundance, were higher in the nutrient-enriched lakes, however, fish had no discernible effect. Mobile (active) and benthic (sit-and-wait) predators, predominantly Coleoptera, Heteroptera and Odonata, were the groups which benefited most from nutrient enrichment in terms of taxon richness and abundance. Caseless Trichoptera were the only group to show a clear negative impact of nutrients, with their taxon richness and abundance both reduced in the nutrient-enriched lakes. Similarly this group, mainly the benthic predatory Polycentropodidae, was the only one to show a negative effect of fish. The response of the littoral macroinvertebrate communities was suggestive that forestry-mediated eutrophication was the main driver of community variation among lakes. This study demonstrates that plantation forestry-mediated bottom-up effects have a stronger influence on the littoral macroinvertebrates of peatland lakes in comparison with top-

down forces. The lack of a stronger influence of fish on littoral macroinvertebrates includes i) mesohabitat-mediated decoupling of predator-prey interactions, ii) anti-predatory adaptations of prey, iii) preferential consumption of alternative prey by brown trout (*Salmo trutta*) and iv) lack of benthivorous specialisation/foraging of brown trout in comparison with other fish species.

6.2. Introduction

The relative influences of resources (bottom-up forces) versus consumers (top-down forces) in structuring food webs have been a long-standing topic of research and debate in both terrestrial and aquatic ecology (McQueen et al., 1986; Power, 1992; Hunter and Price, 1992; Strong, 1992; Schmitz, 1993; Leibold et al., 1997; Polis, 1999). Bottom-up control operates when the biomass of organisms at any trophic level is dependent upon the productivity of their basal resources (McQueen et al., 1986; White, 1978). Top-down control operates when the abundance of the highest trophic level (e.g. carnivores) in a community controls the abundance of the mid trophic level (e.g. herbivores), relieving the lowest trophic level (primary producers) from predatory control (Hairston et al., 1960; Fretwell, 1977; Oksanen et al., 1981), this being termed a ‘trophic cascade’ (Paine, 1980; Carpenter et al., 1985). Both top-down and bottom-up forces can operate simultaneously in determining community structure (Mittelbach, 1988; McQueen et al., 1989).

In aquatic food webs it has been argued that the top-down effects of fish have a stronger influence on community structure, especially for pelagic food chains (Carpenter et al., 1985, 1987; Carpenter and Kitchell, 1988; Hansson and Carpenter, 1993; Brett and Goldman, 1996, 1997; Jeppesen et al., 1997). In general, these studies have found that predation by zooplanktivorous fish results in reduced zooplankton biomass which in turn leads to increased phytoplankton biomass. The strength of such top-down trophic cascades is thought to be dependent on the number of food web links – the predator influence being stronger in food webs with an even number of links (Persson et al., 1988).

Predator-driven impacts have also been investigated for littoral macroinvertebrate food webs, with many studies revealing a strong impact of fish on littoral macroinvertebrates. Many of these studies have been carried out in small-scale experiments which are spatially and temporally constrained (Brönmark et al., 1992; Diehl, 1992; Martin et al., 1992; Brönmark, 1994; Zimmer et al., 2000; Nyström et al., 2001), however, others have documented community-wide changes due to fish predation in whole-lake experiments (Carlisle and Hawkins, 1998; Svensson et al., 1999; Leppä et al., 2003; Potthoff et al., 2008; Schilling et al., 2009a, 2009b; Martínez-Sanz et al., 2010). The main findings of these latter studies is that the abundance of certain taxa, mainly large and mobile predatory taxa such as Coleoptera, Heteroptera and Odonata, as well as Chironomidae, Ceratopogonidae and Sphaeriidae, is negatively associated with fish biomass. There have, however, been many studies which have found little or no impact of fish predation on benthic macroinvertebrates (Thorp and Bergey, 1981; Hanson and Leggett, 1986; Cobb and Watzin, 1998; Wissinger et al., 2006).

Increased nutrient supply would be expected to influence macroinvertebrate community structure via increased production and altered physical habitat, with the resulting variation in biotic interactions causing a change in the flux of energy throughout the food web (Rawcliffe et al., 2010). Despite the number of findings which demonstrate a strong top-down effect of fish in controlling littoral macroinvertebrate community structure, few studies have tried to evaluate the relative influences of both bottom-up (nutrients) and top-down (fish predation) forces in lakes. Although whole-lake studies using such a design have been carried out on planktonic communities, only one study in the author's knowledge has considered littoral macroinvertebrates (Beresford and Jones, 2010). This study,

which was carried out in lowland artificial lakes, found fish to be the dominant driver in determining macroinvertebrate community structure, irrespective of lake nutrient status. In this study, the relative influences of trophy (forestry-mediated) and predators (fish) on the littoral macroinvertebrate communities of natural peatland lakes will be quantified.

Peatland forestry operations are regularly associated with the leaching of plant nutrients, major ions, humic substances and sediment to receiving lake water bodies (Rask et al. 1998; Carignan and Steedman, 2000; Carignan et al., 2000; Watmough et al., 2003; Kreutzweiser et al., 2008). Such inputs can lead to profound changes in lake hydrochemistry, with forestry-mediated eutrophication being documented for many peatland lakes (Planas et al., 2000; Prepas et al., 2001; Bredesen et al., 2002). The few studies which have investigated the biological impacts of such chemical inputs in lakes, in comparison with streams, have revealed only slight biological responses (Rask et al., 1993, 1998; Scrimgeour et al., 2000). However, recent work by the author has revealed that such hydrochemical impacts can lead to profound changes in littoral zooplankton communities, with these changes being consistent with eutrophication (Drinan et al., 2013).

Eutrophication is known to cause significant changes in littoral macroinvertebrate communities (Donohue et al., 2009a), with many macroinvertebrate taxa having well-defined tolerances with respect to lake trophic status (O'Toole et al., 2008; Donohue et al., 2009b). Despite this, however, the majority of studies hitherto have struggled to find a consistent community response to nutrient enrichment due to other overriding environmental factors (Brodersen et al., 1998; Tolonen et al., 2001; Johnson and Goedkoop, 2002; White and Irvine, 2003; Brauns et al., 2007). High spatial and temporal variability associated with

mesohabitat heterogeneity of lake littoral areas is considered to be one of the main factors underlying the non-predictable response of littoral macroinvertebrate communities to trophic change (White and Irvine, 2003). The overall response of the littoral macroinvertebrate communities to trophic change in these studies was that species diversity decreased, whilst the abundance of Orthocladinae and Chironomidae, as well as crustaceans, increased with increasing lake trophy.

Previous work by the author has demonstrated that the hydrochemical change associated with plantation forestry manifests a biological response via trophic change (Drinan et al., 2013). Considering this, the aims of this study were to determine whether or not the bottom-up (trophic) effects mediated by catchment plantation forestry have as strong an influence on littoral macroinvertebrate communities in comparison with the more commonly cited top-down (fish) effects.

6.3. Materials and methods

6.3.1. Site description

Potential study lakes, some known to contain fish populations and others known to be fishless, were identified in areas of blanket bog throughout the west of Ireland using ArcGIS (ESRI ArcMap v.9.3). Following this, a large number (> 30) of potential study lakes were hydrochemically assessed to determine the magnitude of forestry impact. From this larger group of lakes, six were selected for this study on the basis of forestry-mediated nutrient status, corresponding to low (Low), medium (Med) and high (High) nutrient status, and fish presence/absence (Fig. 6.1; Table 6.1). Two lakes were selected in each of these three bands, one containing a population of fish and one without a fish population (Table 6.1). The three fishless lakes selected were a subset of the 26 lakes studied in chapters 3 – 5 (described in Section 3.3.1.1.). The catchments of the low nutrient lakes were dominated by unplanted blanket bog, whereas the catchments of the medium and high nutrient lakes were dominated by closed-canopy conifer plantation forest (Table 6.1). Conifer plantation forests surrounding the lakes were dominated by sitka spruce (*Picea sitchensis* Bongard) with some lodgepole pine (*Pinus contorta* Douglas ex Loudon) present. A forestry database was provided by Coillte Teoranta, the Irish semi-state forestry body. Forestry operations were carried out to the current Irish forestry best management practices (Forest Service, 2000).

The plant species surrounding the low nutrient lakes were typical blanket bog species (Fossitt, 2000). These included purple moor-grass (*Molinia caerulea* (Linnaeus)), cross-leaved heath (*Erica tetralix* Linnaeus), deergrass (*Scirpus*

cespitosus Linnaeus), common cottongrass (*Eriophorum angustifolium* Roth), bog asphodel (*Narthecium ossifragum* (Linnaeus) Hudson) and white beak-sedge (*Rhynchospora alba* (Linnaeus) Vahl). Lake area ranged from 1.0 – 2.2 ha (mean = 1.5 ha) for the smaller fishless lakes, and from 16.8 – 34.5 ha (mean = 26.0 ha) for the larger fish lakes (Table 6.1). Mean depth ranged from 1.8 – 7.7 m (mean = 3.1 m) for all six lakes, while catchment area ranged from 9.3 – 30.0 ha (mean = 17.2 ha) for the smaller fishless lakes, and from 317.0 – 1629.4 ha (mean = 939.3 ha) for the larger fish lakes (Table 6.1). All lakes were underlain by igneous (granite) geology.

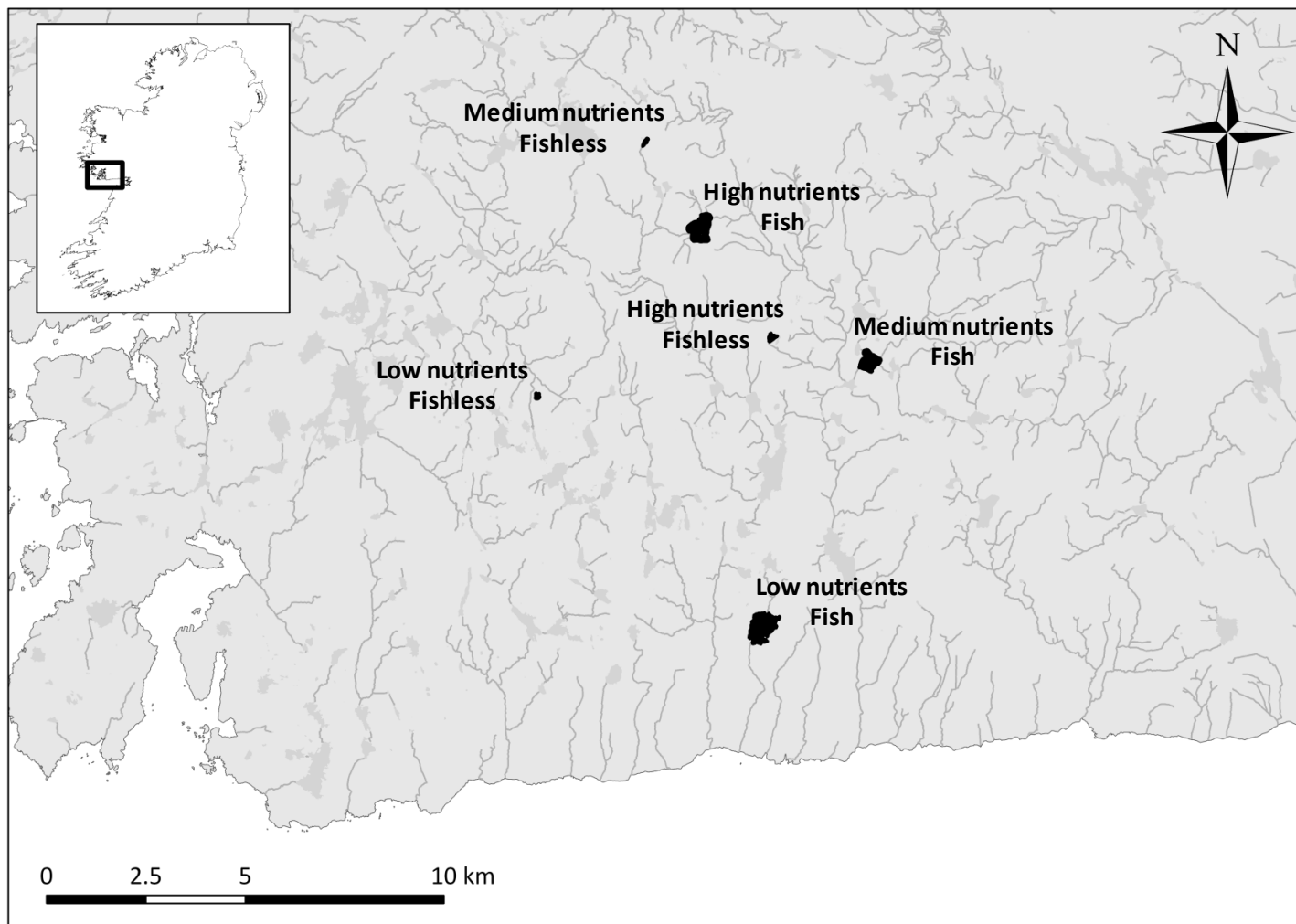


Figure 6.1. Map showing the location of the six study lakes in the west of Ireland.

Table 6.1. Geographic location, physico-chemical characteristics and catchment land use of the six study lakes. Blanket bog classification is based on Fossitt (2000) habitat classification scheme (Nutrient status: low, medium and high).

Lake code	Latitude/Longitude	Altitude (m)	Lake area (ha)	Mean depth (m)	Catchment area (ha)	% Blanket bog	% Afforested	TDOC (mg l ⁻¹)	TP (mg l ⁻¹)	SRP (mg l ⁻¹)	TN (mg l ⁻¹)	Ammonia (mg l ⁻¹)
Low Fishless	N 53° 19' 13.804" W 009° 25' 51.283"	93	1.2	2.4	12.2	100.0	0.0	7.11 (± 0.31)	0.011 (± 0.002)	0.001 (± 0.001)	0.566 (± 0.044)	0.018 (± 0.002)
Low Fish	N 53° 15' 58.634" W 009° 20' 56.165"	65	34.5	2.1	317.0	87.9	0.0	6.25 (± 0.87)	0.006 (± 0.001)	0.001 (± 0.001)	0.417 (± 0.012)	0.021 (± 0.006)
Medium Fishless	N 53° 22' 45.091" W 009° 23' 30.665"	233	1.0	2.3	9.3	2.2	97.8	11.16 (± 0.21)	0.016 (± 0.004)	0.001 (± 0.001)	0.576 (± 0.020)	0.027 (± 0.004)
Medium Fish	N 53° 19' 49.982" W 009° 18' 12.775"	64	16.8	7.7	1629.4	60.9	32.5	13.10 (± 2.24)	0.015 (± 0.002)	0.002 (± 0.001)	0.671 (± 0.086)	0.026 (± 0.005)
High Fishless	N 53° 20' 1.963" W 009° 20' 40.597"	85	2.2	1.8	30.0	2.2	97.9	26.18 (± 1.54)	0.038 (± 0.001)	0.004 (± 0.001)	1.181 (± 0.262)	0.052 (± 0.003)
High Fish	N 53° 21' 37.125" W 009° 22' 33.822"	105	26.6	2.2	871.4	18.5	77.6	15.83 (± 3.59)	0.038 (± 0.006)	0.002 (± 0.001)	0.772 (± 0.129)	0.034 (± 0.007)

6.3.2. Water chemistry sampling

Water samples were taken from the littoral zone of each lake at a similar depth (0.6 m) and distance (7 m) from shore in June, July and September 2010. Water samples were collected in acid-washed polypropylene bottles, stored at 4°C in a cooler box and transported to the laboratory for analysis within 24 hours after collection. Five chemistry parameters were analysed: total dissolved organic carbon (TDOC), total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN) and ammonia. Methods for water chemistry analyses are described in chapter 2 (Section 2.3.2.).

6.3.3. Littoral macroinvertebrate sampling

Littoral macroinvertebrates were sampled in June and September 2010 using two methods: multihabitat sweeps and activity traps. Multihabitat sweeps were used for less mobile species and were taken using a standard 1 mm mesh size pond net (frame size 0.20 x 0.25 m). The four-minute sampling time was divided equally among the proportions of different mesohabitats present in each lake (submerged, floating and emergent aquatic vegetation, mineral benthic substrate and peat bank). All mesohabitat sweep samples were processed separately for subsequent analyses. Ten baited activity traps similar to those used by Downie et al. (1998) were deployed to sample the mobile predatory species in each lake. The traps were of a submerged funnel and bottle design, with the funnel inserted into the bottle. The aperture diameter of the circular entrance was 22 mm, and the wider funnel opening was 100 mm in diameter. The total length of the trap was 230 mm. Traps were submerged

and placed in all available mesohabitats per lake and remained *in situ* for three consecutive days during each sampling date. Not all mesohabitats were present in all lakes. Macroinvertebrate samples were preserved using 70% ethanol. All macroinvertebrate individuals were identified to the lowest practical taxonomic level and were identified using standard identification keys (Hynes, 1967; Elliott and Mann, 1979; Hammond, 1983; Elliott et al., 1988; Friday, 1988; Savage 1989; Smith, 1989; Edington and Hildrew, 1995; Nilsson and Holmen, 1995; Elliott, 1996; Nilsson, 1996; Nilsson, 1997; Wallace et al., 2003).

Macroinvertebrates were categorised into six functional feeding groups according to Merritt and Cummins (1996) and Tachet et al. (2003). Functional feeding groups included gatherers, herbivore-piercers, mobile and benthic predators, scrapers and shredders. Mobile predators were defined as those who employ an active foraging mode in pursuit of prey, while benthic predators are sit-and-wait (ambush) predators. Personal judgement of the feeding habits of certain macroinvertebrate taxa was used if a species was assigned to more than one feeding group, or if the information for a genus or a species was unavailable in the literature.

6.3.4. Fish sampling

Salmonid populations were sampled in June and September 2010 following Inland Fisheries Ireland (IFI) protocol (based on European Committee for Standardization [CEN, 2005]). This method provides a whole-lake estimate for species occurrence and quantitative relative fish abundance expressed as catch-per-unit-effort (CPUE): $\Sigma (Y / L) / N$, where Y = number captured, L = area of net deployed and N = number of lifts of the net. The method involved dividing the lake into depth strata, with

random sampling being performed within each depth stratum. Sampling was carried out using multi-mesh gill nets which were 60 m long and 1.5 m deep, and were composed of 12 different mesh sizes ranging from eight to 50 mm mesh sizes, following a geometric series. Five gill nets were deployed in each lake during each sampling event. Furthermore, eel populations were sampled using fyke nets, two of which were deployed in each lake in September. All fish captured were frozen immediately after sampling.

6.3.5. Dietary analysis

Fish were slowly thawed in the laboratory and the stomach from each fish was excised and preserved using 70% ethanol until dietary analyses could be performed. All stomach contents were identified under a stereo binocular microscope to the lowest practical taxonomic level – order level for both terrestrial prey items and terrestrial prey items of aquatic origin (e.g. adult Diptera). Fragmented individuals were reconstructed where possible. Head and thoracic segments were also counted to accurately determine prey numbers. A total of 176 stomach contents, predominantly from brown trout, were examined from the three lakes containing fish populations.

6.3.6. Statistical analyses

Non-metric multi-dimensional scaling (NMDS) analysis was performed, using PC-ORD (version 6; MjM Software, Gleneden Beach, Oregon), to determine among-lake patterns in the littoral macroinvertebrate communities, as well as the fish stomach contents, as it can be used with non-normal and zero rich data (McCune and

Grace, 2002). NMDS ranks points in low-dimensional space such that the relative distances apart of all points are in the same rank order as the relative dissimilarities of the samples (Clarke and Gorley, 2006). The ordinations were based on a Bray-Curtis dissimilarity matrix with varimax rotation, using $\log(x + 1)$ transformed abundance data. Significance of the axes was determined using Monte Carlo simulation using 999 permutations. Taxa comprising of less than 3% abundance of any individual community/stomach content were excluded from all NMDS analyses. Singletons, taxa occurring only once, were also removed (McCune and Grace, 2002). The final solution for the NMDS analyses was based on 999 permutations.

The Multi-Response Permutation Procedure (MRPP) (PC-ORD 6), a non-parametric multivariate procedure used for testing differences among groups, was performed to test for significant among-lake differences in macroinvertebrate communities and fish stomach contents with respect to nutrient status (low, medium and high) and fish presence/absence. To determine the relative influence of both factors on macroinvertebrate community structure, two separate MRPP analyses were performed. One MRPP analysis was carried out using abundance data to assess the relative influences of both factors in determining community structure, while a second was carried out using binary (presence/absence) data to assess the relative influences of both factors in determining species turnover (β -diversity) among sites. β -diversity in this study was used to represent “the spatial turnover or change in the identities of species, as a measure of the difference in species composition either between two or more local assemblages or between local and regional assemblages” (Koleff et al., 2003). Both MRPP analyses were based on Bray-Curtis dissimilarity matrices. The MRPP test returns a test statistic T that describes the separation among groups (the more negative T is, the stronger the separation) (McCune and Grace,

2002). The effect size is provided by the chance-corrected within-group agreement (A). A describes within-group homogeneity, compared with random expectation. $A = 1$ when all items are identical within groups ($\delta = 0$), $A = 0$ when heterogeneity within groups equals expectation by chance, and $A < 0$ when there is more heterogeneity within groups than expected by chance.

The importance of prey categories in the diet was expressed as prey abundance defined as the percentage that a prey category comprised of the total number of all prey in the sample (Hyslop, 1980). The diversity of prey items ingested by fish was also compared among lakes.

6.4. Results

6.4.1. Littoral macroinvertebrate communities

A total of 136 macroinvertebrate taxa were recorded from the multihabitat sweeps and 64 from the activity traps across all lakes. Species richness per lake varied from 33 – 66 (median 60) across all lakes. Coleoptera was the most taxon rich group recorded from the multihabitat sweeps (mean = 28.6% \pm 2.1 S.E.), followed by Trichoptera (mean = 20.5% \pm 4.0 S.E.) and Diptera (mean = 14.0% \pm 1.6 S.E.) (Table 6.2). Coleoptera was also the most taxon rich group recorded from the activity traps (46.2% \pm 7.5 S.E.), followed by Heteroptera (mean = 20.3% \pm 6.4 S.E.) and Odonata (mean = 6.8% \pm 2.9 S.E.) (Table 6.3).

Table 6.2. Total taxon richness and mean abundances of macroinvertebrate groups (multihabitat sweep data) from the six study lakes, listed in decreasing order of total taxon richness (Nutrient status: low, medium and high).

Multihabitat sweep data	<u>Low</u>		<u>Medium</u>		<u>High</u>	
	Fishless	Fish	Fishless	Fish	Fishless	Fish
<u>Total taxon richness</u>						
Coleoptera	8	15	12	13	20	22
Trichoptera						
Caseless	6	8	4	4	3	1
Case-bearing	3	10	3	8	3	5
Diptera	5	5	8	6	9	7
Heteroptera	3	4	5	2	12	13
Odonata						
Anisoptera	1	4	4	2	5	2
Zygoptera	1	3	2	2	5	5
Other	2	5	3	4	3	3
Ephemeroptera	1	2	1	4	1	1
Gastropoda	0	1	0	5	0	0
Crustacea	0	1	0	2	1	1
Total	30	58	42	52	62	60
<u>Mean abundance (± 1 S.E.)</u>						
Coleoptera	5.9 (± 2.7)	4.9 (± 0.8)	3.3 (± 0.3)	4.8 (± 2.6)	8.9 (± 2.8)	12.5 (± 5.0)
Trichoptera						
Caseless	5.7 (± 0.6)	2.1 (± 2.1)	0.9 (± 0.4)	0.6 (± 0.5)	0.9 (± 0.9)	0.01 (± 0.1)
Case-bearing	0.3 (± 0.2)	4.9 (± 2.2)	0.7 (± 0.3)	1.8 (± 1.0)	3.6 (± 0.1)	4.1 (± 0.3)
Diptera (mainly Chironomidae)	16.8 (± 11.6)	18.7 (± 12.4)	31.7 (± 18.0)	12.2 (± 3.6)	24.3 (± 10.5)	53.0 (± 23.3)
Heteroptera	7.1 (± 4.8)	8.2 (± 5.9)	2.7 (± 0.8)	4.4 (± 1.3)	28.0 (± 5.4)	74.0 (± 48.0)
Odonata						
Anisoptera	0.1 (± 0.1)	0.3 (± 0.3)	2.8 (± 1.3)	0.6 (± 0.3)	1.1 (± 0.5)	1.4 (± 0.9)
Zygoptera	3.2 (± 1.3)	1.0 (± 0.7)	3.4 (± 0.3)	0.2 (± 0.1)	10.6 (± 0.2)	12.5 (± 5.5)
Other	2.0 (± 1.0)	9.4 (± 3.9)	1.7 (± 0)	16.0 (± 5.2)	22.9 (± 22.2)	6.0 (± 0.5)
Ephemeroptera	0.1 (± 0.1)	0.9 (± 0.9)	3.3 (± 1.5)	3.4 (± 0.9)	0.1 (± 0.1)	0.2 (± 0.2)
Gastropoda	0	7.0 (± 4.9)	0	0.5 (± 0.3)	0	0
Crustacea	0	1.6 (± 0.5)	0	9.0 (± 6.2)	3.7 (± 0.2)	91.4 (± 11.9)
Total	41.3 (± 19.1)	59.0 (± 16.4)	50.4 (± 14.5)	53.5 (± 3.6)	103.9 (± 21.6)	255.3 (± 14.6)

'Other' includes Hirudinae, Hydracarina, Oligochaeta, Plecoptera and *Sialis lutaria*.

Table 6.3. Total taxon richness and mean abundances of macroinvertebrate groups (activity trap data) from the six study lakes, listed in decreasing order of total taxon richness (Nutrient status: low, medium and high).

Activity trap data	<u>Low</u>		<u>Medium</u>		<u>High</u>	
	Fishless	Fish	Fishless	Fish	Fishless	Fish
<u>Total taxon richness</u>						
Coleoptera						
Dytiscinae	0	1	1	1	4	3
Colymbetinae	1	2	2	4	8	8
Hydroporinae	2	2	1	2	1	2
Heteroptera	4	2	0	1	3	4
Odonata						
Anisoptera	0	0	2	3	2	2
Zygoptera	0	0	1	0	1	0
Total	7	7	7	11	19	19
<u>Mean abundance (± 1 S.E.)</u>						
Coleoptera						
Dytiscinae	0	0.5 (± 0.5)	1.0 (± 1.0)	0.5 (± 0.5)	14.5 (± 12.5)	4.5 (± 3.5)
Colymbetinae	0.5 (± 0.5)	1.5 (± 1.5)	1.5 (± 1.5)	8.5 (± 8.5)	50.0 (± 16.0)	58.0 (± 28.0)
Hydroporinae	31.0 (± 27.0)	1.5 (± 1.5)	1.0 (± 1.0)	1.0 (± 1.0)	3.5 (± 2.5)	2.0 (± 2.0)
Heteroptera	26.5 (± 23.5)	1.5 (± 1.5)	0	0.5 (± 0.5)	16.5 (± 16.5)	19.0 (± 6.0)
Odonata						
Anisoptera	0	0	1.0 (± 1.0)	1.5 (± 1.5)	4.0 (± 1.0)	5.5 (± 3.5)
Zygoptera	0	0	0.5 (± 0.5)	0.0	2.0 (± 0)	0
Total	58.0 (± 50.0)	5.0 (± 2.0)	5.0 (± 5.0)	12.0 (± 12.0)	90.5 (± 48.5)	89.0 (± 24.0)

6.4.1.1. NMDS ordination – multihabitat sweep data

NMDS of the littoral macroinvertebrate communities multihabitat sweep data indicated that a solution incorporating three axes, with a final stress of 0.16, was most appropriate (Monte Carlo test). NMDS axis 1 distinguished macroinvertebrate communities with respect to fish and NMDS axis 2 with respect to nutrients (Fig. 6.2). The difference in macroinvertebrate communities among mesohabitats within lakes was, however, far less than overall community variation among lakes (Fig. 6.2). MRPP analysis further confirmed that both nutrients and fish had significant effects on littoral macroinvertebrate community structure (Table 6.4). However, only nutrients had a significant effect on β -diversity (Table 6.4). Mesohabitats had no significant effect on either community structure or β -diversity of the littoral macroinvertebrate communities (Table 6.4).

Fishless lakes tended to contain greater abundances of benthic predators such as *Pyrrhosoma nymphula* (Sulzer), Polycentropodidae and *Cordulia aenea* (Linnaeus), whereas the fish lakes tended to contain greater abundances of gatherers, shredders and scrapers, notably *Caenis horaria* (Linnaeus) and *Caenis luctuosa* (Burmeister), *Gammarus lacustris* Sars and *Lymnaea peregra* (Müller) (Fig. 6.2).

High nutrient lakes were characterised by greater abundances of mobile and benthic predators such as *Cymatia bonndorffii* (Sahlberg), *Hesperocorixa castanea* (Thomson), *Callicorixa praeusta* (Fieber) and Colymbetinae larvae, and the shredder *G. lacustris* (Fig. 6.2). The low nutrient lakes were characterised by greater abundances of the herbivore-piercers *Haliplus fulvus* (Fabricius) and *Sigara scotti* (Douglas and Scott), as well as the shredder *Sericostoma personatum* (Spence in

Kirby and Spence) (Fig. 6.2). Other than these few species, few others displayed a preference for low nutrient lakes.

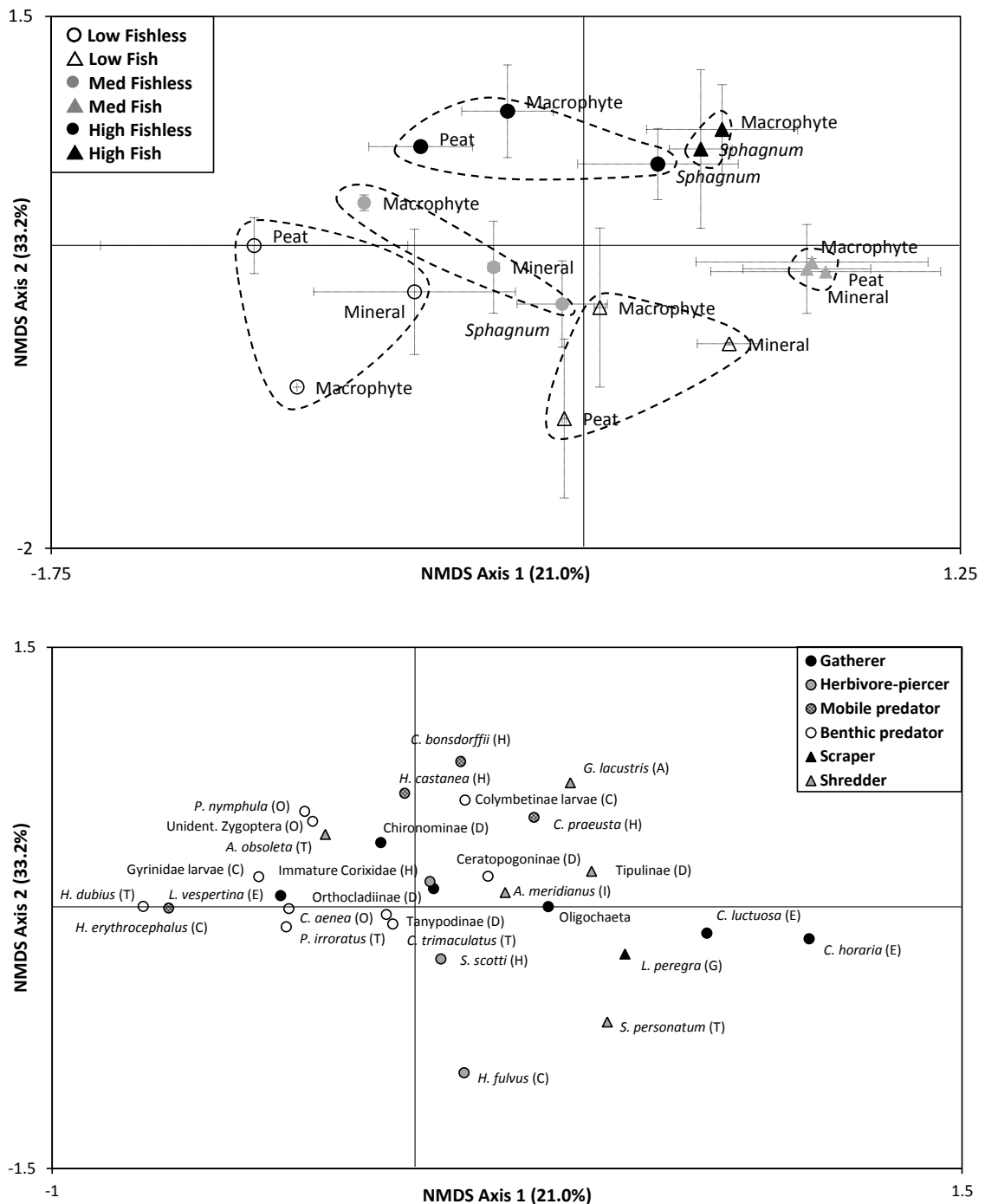


Figure 6.2. Non-metric multi-dimensional scaling (NMDS) analysis of multihabitat sweep data of the six study lakes, including lake scores (top) and taxon scores (bottom). Group centroids represent the mean mesohabitat scores (± 1 S.E.) over the entire sampling period (Nutrient status: low, medium and high). The class/order of taxa is given in parentheses.

Table 6.4. Results of multiple-response permutation procedures (MRPP) to test for differences in littoral macroinvertebrate community structure and species turnover (β -diversity) across lakes of contrasting nutrient status (low, medium and high) and fish presence/absence. Within-lake differences with respect to mesohabitat were also tested.

Multihabitat sweep data	Factor	<i>A</i>	<i>T</i>	<i>p</i>
i) Community structure	Nutrient status	0.027	-7.211	<0.001
	<u>Pair-wise comparisons</u>			
	Low v Medium	0.084	-2.929	0.011
	Low v High	0.211	-6.649	<0.001
	Medium v High	0.178	-5.310	<0.001
	Fish (presence/absence)	0.140	-7.012	<0.001
	Mesohabitat	0.040	-1.112	0.135
ii) β -diversity	Nutrient status	0.285	-2.912	0.007
	<u>Pair-wise comparisons</u>			
	Low v Medium	0.060	-0.546	0.270
	Low v High	0.359	-3.546	0.006
	Medium v High	0.199	-2.272	0.012
	Fish (presence/absence)	0.103	-1.563	0.074
	Mesohabitat	0.149	-1.699	0.058

Significant terms are emboldened.

6.4.1.2. NMDS ordination – activity trap data

NMDS of the assemblages captured in the activity traps indicated that a solution incorporating two axes, with a final stress of 0.09, was most appropriate (Monte Carlo test). Lake assemblages were clearly separated with respect to nutrients, but not the presence of fish (Fig. 6.3). This was confirmed by MRPP analysis, which showed that nutrients, but not fish, had a significant effect on assemblages captured in the traps (Table 6.5).

High nutrient lakes were characterised by greater abundances of larger Coleoptera including *Dytiscus marginalis* Linnaeus, *Colymbetes fuscus* (Linnaeus), *Acilius sulcatus* (Linnaeus), Dytiscinae larvae, as well as numerous *Agabus* spp. and *Ilybius* spp., the Heteroptera *C. bondsdorffii* and *C. praeusta*, and the Odonata *Libellula quadrimaculata* Linnaeus, *Sympetrum danae* (Sulzer) and *P. nymphula*

(Fig. 6.3). The few species characteristic of the low nutrient lakes included smaller Coleoptera, notably *Nebrioporus assimilis* (Paykull) and *Hydroporus erythrocephalus* (Linnaeus), as well as the Heteroptera *S. scotti*. *C. aenea*, *H. fulvus* and *Hydroporus palustris* (Linnaeus) were the only species which displayed a preference for the medium nutrient lakes (Fig. 6.3).

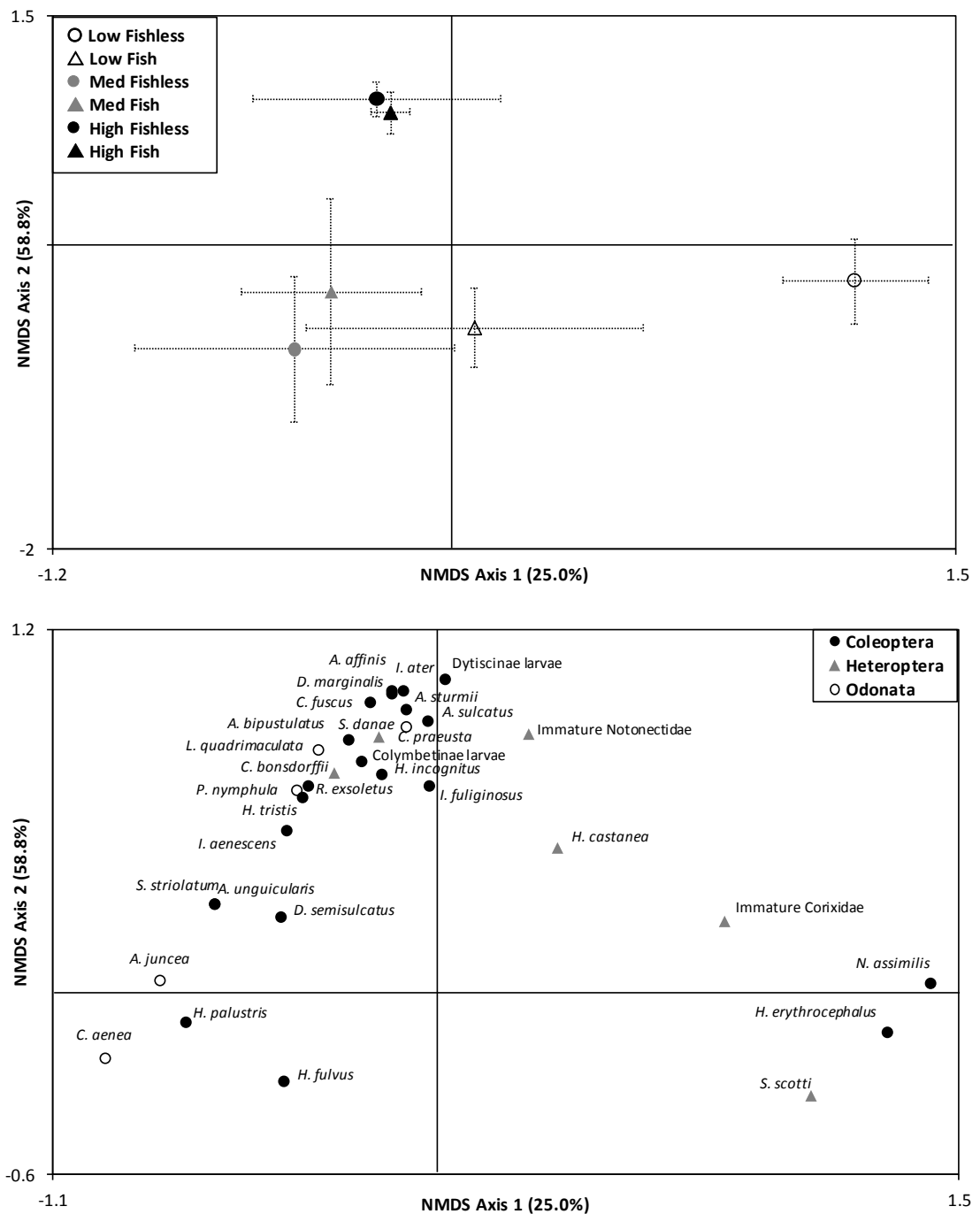


Figure 6.3. Non-metric multi-dimensional scaling (NMDS) analysis of macroinvertebrate assemblages captured in the activity traps from the six study lakes, including lake scores (top) and taxon scores (bottom). Group centroids represent the mean lake scores (± 1 S.E.) over the entire sampling period (Nutrient status: low, medium and high).

Table 6.5. Results of the multiple-response permutation procedure (MRPP) to test for differences in the assemblages captured in the activity traps across lakes of contrasting nutrient status (low, medium and high) and fish presence/absence.

Activity trap data	Factor	<i>A</i>	<i>T</i>	<i>p</i>
Assemblage captured	Nutrient status	0.417	-4.244	0.001
	<u>Pair-wise comparisons</u>			
	Low v Medium	0.208	-2.167	0.032
	Low v High	0.375	-3.461	0.009
	Medium v High	0.282	-2.914	0.012
	Fish (presence/absence)	0.019	-0.285	0.311

Significant terms are emboldened.

6.4.1.3. Community metrics

For multihabitat sweep data, total taxon richness and abundance were both highest in the high nutrient lakes, with little clear difference between low and medium nutrient lakes (Table 6.2). Fish had little clear impact on total taxon richness or total abundance, although total abundance was markedly higher in the nutrient-rich lake with fish (Table 6.2). For individual taxa, taxon richness of Coleoptera and Heteroptera was notably higher in the high nutrient lake, although again with little difference between low and medium nutrient lakes (Table 6.2). The abundance of Coleoptera, Heteroptera, Odonata, Diptera and Crustacea was also markedly higher in nutrient-rich lakes (Table 6.2). The presence of fish had little clear impact on the taxon richness or abundance of individual groups, although abundances of Heteroptera, Diptera and Crustacea were much greater in the high nutrient lake with fish (Table 6.2). Caseless Trichoptera (composed largely of benthic predatory Polycentropodidae) was the only group to show a clear negative impact of nutrients, with their taxon richness and abundance both lower in the nutrient-enriched lakes

(Table 6.2). Similarly, they were the only group to show a (somewhat) negative abundance trend with fish (Table 6.2).

The activity trap data (predatory macroinvertebrates) supported the findings of the multihabitat sweeps (Table 6.3). Taxon richness and total abundance were greatest in the high nutrient lake, with, as for multihabitat sweep data, little clear difference between the low and medium nutrient lakes (Table 6.3). Fish had no discernible effect on either total taxon richness or total abundance (Table 6.3). The Dytiscidae subfamilies showed contrasting patterns with respect to nutrients (Table 6.3). The larger Dytiscinae (size range: 12.0 – 38.0 mm) and Colymbetinae (size range: 6.0 – 18.0 mm) had greater taxon richness and abundance in the high nutrient lake, whereas the smaller Hydroporinae (size range: 1.5 – 6.0 mm) showed little clear pattern (Table 6.3). Neither Coleoptera nor Heteroptera showed any clear pattern with respect to fish (Table 6.3). Both taxon richness and abundance of Anisoptera, but not Zygoptera, increased with nutrients (Table 6.3). Similar to the Coleoptera and Heteroptera, fish had no discernible effect on Odonata (Table 6.3).

6.4.2. Fish CPUE

The CPUE for the three lakes containing fish populations varied somewhat among lakes: i) low nutrient lake: 1.22 (June) and 0.58 (September), ii) medium nutrient lake: 0.27 (June) and 0.49 (September) and iii) high nutrient lake: 1.50 (June) and 2.54 (September). Brown trout (*Salmo trutta* Linnaeus) were the most dominant species present; however, smaller populations of three-spined stickleback (*Gasterosteus aculeatus* Linnaeus) and eel (*Anguilla anguilla* (Linnaeus)) were also recorded.

6.4.3. Fish stomach contents

A total of 75 taxa were recorded from all fish stomach contents across all lakes. The diversity of prey items recorded from fish stomach contents was very similar across all lakes: low nutrient lake (mean = 3.87 ± 0.50 S.E.), medium nutrient lake (mean = 3.83 ± 0.46 S.E.) and high nutrient lake (mean = 4.09 ± 0.24 S.E.). The number of prey items ingested per fish per lake was markedly higher in the medium nutrient lake (mean = 229.6 ± 45.0 S.E.), in comparison with the low (mean = 30.1 ± 7.0 S.E.) and high nutrient lakes (mean = 44.2 ± 6.1 S.E.). Zooplankton, both littoral and pelagic, constituted the main prey type for fish across all lakes (Fig. 6.4). *Eurycercus lamellatus* (Baird) was the main littoral species recorded from the fish stomach contents, while *Daphnia* sp. was the main pelagic species recorded.

NMDS of the stomach contents indicated that a solution incorporating three axes, with a final stress of 0.15, was most appropriate (Monte Carlo test). There was a clear separation in fish dietary composition between the high nutrient lake and the two lower nutrient lakes (Fig. 6.5; Table 6.6). The stomach contents of fish from the high nutrient lakes were characterised by a greater abundances of Crustacea, Chironomidae, Trichoptera (both caseless and case-bearing), *Sialis lutaria* (Linnaeus) and Sphaeriidae, whereas the diets of fish in the low and medium nutrient lakes were characterised by greater abundances of aerial insects (both of terrestrial and aquatic origin), case-bearing Trichoptera, Heteroptera, *Daphnia* sp. and *G. aculeatus* (Fig. 6.5).

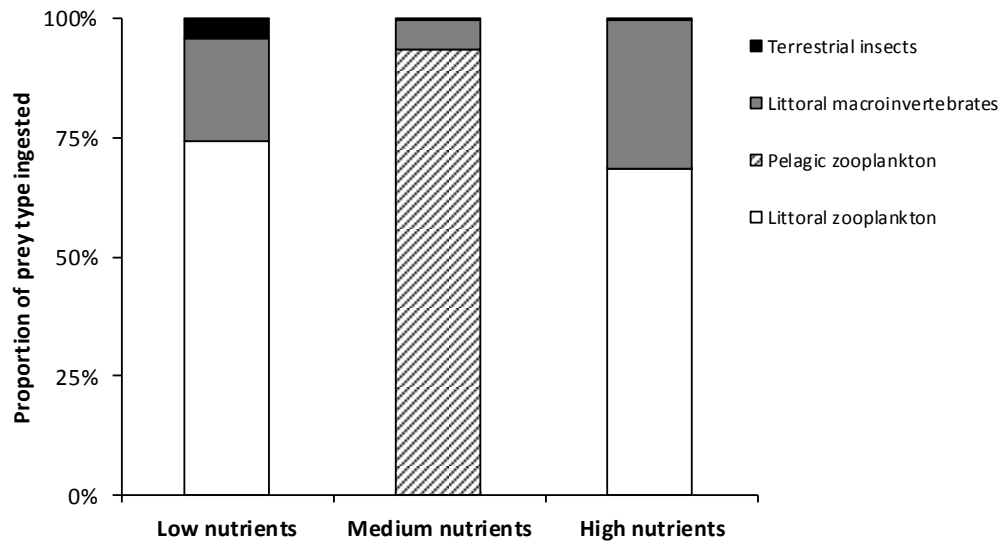


Figure 6.4. Proportional abundance of the different prey types ingested by fish in the three study lakes containing fish populations.

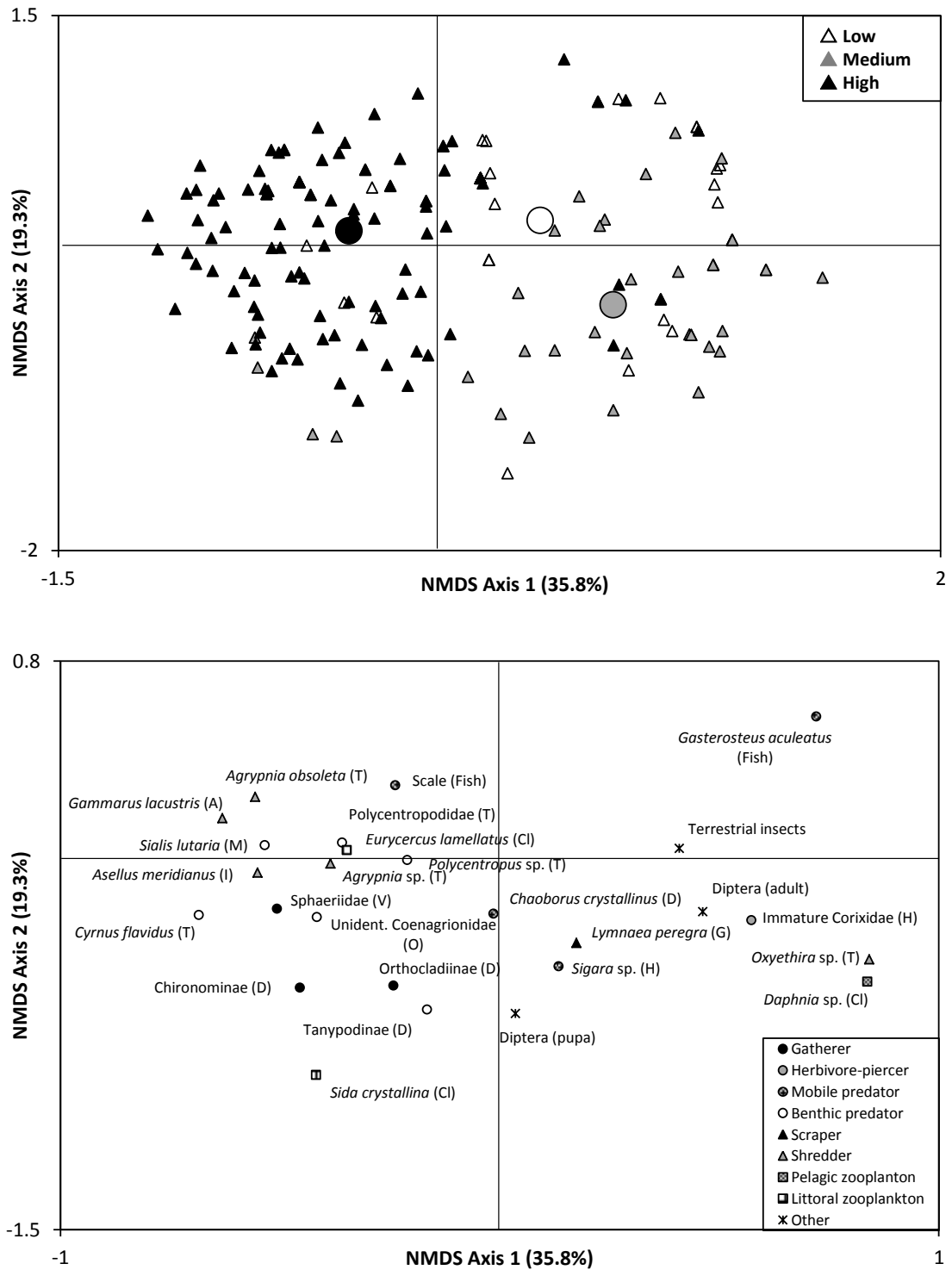


Figure 6.5. Non-metric multi-dimensional scaling (NMDS) analysis of fish stomach contents from the three lakes containing fish populations, including lake scores (top) and prey scores (bottom). Group centroids (circles) represent the mean lake scores (Nutrient status: low, medium and high). The class/order of taxa is given in parentheses.

Table 6.6. Results of the multiple-response permutation procedure (MRPP) to test for differences in the dietary composition of fish in lakes of contrasting nutrient status (low, medium and high).

Stomach content data	Factor		<i>A</i>	<i>T</i>	<i>p</i>
Dietary composition	Nutrient status		0.248	-53.331	<0.001
	<u>Pair-wise comparisons</u>				
	Low	v Medium	0.190	-20.067	<0.001
	Low	v High	0.069	-18.806	<0.001
	Medium	v High	0.253	-61.573	<0.001

Significant terms are emboldened.

6.5. Discussion

The findings of this study suggest that forestry-mediated eutrophication (bottom-up) has a stronger influence on littoral macroinvertebrate communities in comparison with fish (top-down). Despite the low number of lake replicates per treatment, coupled with the differences in fish densities among lakes, fish were nevertheless shown to have a minimal influence on the majority of macroinvertebrate species, including most mobile intermediate predators. Although many studies have shown that both forces can drive littoral macroinvertebrate communities, few have examined the relative strength of each force simultaneously in natural ecosystems. The findings of this study are somewhat surprising given the number of studies which have documented a strong top-down (fish) control on littoral macroinvertebrates communities (Carlisle and Hawkins, 1998; Svensson et al., 1999; Leppä et al., 2003; Potthoff et al., 2008; Schilling et al., 2009a, 2009b; Beresford and Jones, 2010; Martínez-Sanz et al., 2010).

Mobile and benthic predators, predominantly Coleoptera, Heteroptera and Odonata, and the shredders, *Asellus* and *Gammarus*, were the groups which appeared to benefit most from nutrient enrichment. Caseless Trichoptera, predominantly Polycentropodidae, was the only group to show a clear negative impact of nutrient enrichment. Similarly, this group was the only one to show a (somewhat) negative impact of fish. Overall, macroinvertebrate taxa were consumed in low numbers by fish in all lakes, with fish diets being dominated by littoral and pelagic zooplankton. Despite many studies documenting considerable within-lake variation in macroinvertebrate communities due to mesohabitat heterogeneity (Tolonen et al., 2001; White and Irvine, 2003; Brauns et al., 2007), such mesohabitat-mediated

community variation was not found in this study. This may possibly be due to the low number of available mesohabitats in these blanket bog lakes, however, further investigation is required to elucidate the exact determinant responsible for the lack of variation.

Distinguishing between the influence of habitat structure and nutrient enrichment in lakes is difficult, as these are often interrelated (Jeppesen et al., 2000), and it is likely that both factors contributed to the observed increase in macroinvertebrate abundance in this study. Many of the taxa associated with nutrient enrichment in this study are known to favour nutrient-rich habitats, thereby suggesting that forestry-mediated eutrophication, rather than habitat change, is the primary factor driving community change. For example, Coleoptera such as *Ilybius* spp., *Rhantus* sp., *Agabus* spp. and *C. fuscus*, characteristic of the high nutrient lakes in this study, are characteristic of eutrophic water bodies elsewhere (Verberk et al., 2001, 2005). Similarly, the Heteroptera *C. praeusta*, which was more abundant in the high nutrient lakes, is indicative of more eutrophic habitats (Savage, 1990, 1994). *Gammarus*, *Asellus* and Chironomidae are also known to show increased abundances in nutrient-enriched waters (Pinel Alloul et al., 1996; Brodersen et al., 1998; Rask et al., 1998; Donohue et al., 2009b). Furthermore, species which were more abundant in the low nutrient lakes in this study, including *Nebrioporus* sp., *L. peregra*, *Polycentropus* spp. and *Cyrtus trimaculatus* (Curtis), have all been shown to have a preference for oligotrophic conditions in other lakes (Brodersen et al., 1998; Tolonen et al., 2001).

Despite little difference in macroinvertebrate communities among mesohabitats, the high nutrient lakes contained a far greater biomass of *Sphagnum* in comparison with the low and medium nutrient lakes. An increase in *Sphagnum*

growth in peatland lakes which have forestry operations within their catchment has been previously documented (Raven, 1988). Dense macrophyte stands, such as large *Sphagnum* mats, are likely to have benefitted many taxa as they contain a higher number of available niches and a more abundant variety of food for benthic macroinvertebrates (Jones et al., 1998; Weatherhead and James, 2001). In addition, they ameliorate predation pressure from fish predators, as the predation efficiency of fish generally decreases in complex environments (Diehl, 1992; Diehl and Eklöv, 1995; Diehl and Kornijów, 1998; Tolonen et al., 2003). Combined, these factors often result in a higher diversity and abundance of benthic macroinvertebrates among macrophytes than on bare mineral benthos (Crowder and Cooper, 1982; Beckett et al., 1992; Diehl, 1992). Increased abundances of larger mobile taxa, such as Odonata, Corixidae and Dytiscidae, in dense macrophyte beds has previously been demonstrated (Nilsson et al., 1994; Nilsson and Söderberg, 1996; Heino, 2000; Tolonen et al., 2003), with Anisoptera in particular, displaying a strong affinity to *Sphagnum* habitats (Henrikson, 1993). Interestingly, many species which showed a preference for the mineral-dominated low nutrient lakes, particularly Polycentropodidae, also occur in streams (Edington and Hildrew, 1995). Their absence from the high nutrient lakes may reflect their requirement for higher dissolved oxygen concentrations which are unlikely to be present within dense *Sphagnum* mats.

The weaker impact of fish on macroinvertebrates, particularly mobile Coleoptera and Heteroptera predators, is surprising given that fish usually prefer larger, mobile prey which are more conspicuous to visual predators (McPeck, 1990a; Wellborn et al., 1996). The results of this study also contrast with other studies which document a general decrease in the abundance of larger and more active

individuals or species in the presence of fish (Henrikson, 1988; Bendell and McNicol, 1995; Wellborn et al., 1996; Fairchild et al., 2000; Zimmer et al., 2000; Tolonen et al., 2001; Schilling et al., 2009a, 2009b). In contrast to more specialised lake-dwelling fish such as perch (*Perca fluviatilis* (Linnaeus)) or roach (*Rutilus rutilus* (Linnaeus)) (Persson, 1987, 1991), salmonids such as brown trout are mostly generalist predators which lack the adaptations to strongly predate on littoral macroinvertebrates (Klemetsen et al., 2003). Many studies, however, have found that salmonids can exert strong impacts on macroinvertebrates in lakes (Carlisle and Hawkins, 1998; Schilling et al., 2009a, 2009b; Martínez-Sanz et al., 2010; de Mendoza et al., 2012). Most of these moreover have found the greatest impacts to be on large and mobile macroinvertebrates, particularly Coleoptera, Heteroptera, Odonata and Trichoptera. The only group to display sensitivity to fish predation in this study was the benthic predatory caseless Trichoptera, predominantly the Polycentropodidae. It seems very likely that the affinity of these species for mineral substrates (Heino, 2000; Tolonen et al., 2001), increased their risk of predation from fish due to the lack of refuge.

Other reasons for the lack of a stronger influence of fish on littoral macroinvertebrates in this study include i) anti-predatory adaptations of prey and ii) preferential consumption of alternative prey by brown trout. i) Aquatic insects exhibit a wide range of morphological, chemical and behavioural anti-predatory techniques to avoid being predated upon by fish (Peckarsky, 1982; Witz, 1990). For example, within the Odonata, reduced foraging activity (McPeck, 1990b), inconspicuous behaviour (Sternberg and Buchwald, 2000), night activity (Johansson, 1993), hiding (Sternberg and Buchwald, 1999), thanatosis (Sternberg and Buchwald, 2000), spines (Norling and Sahlén, 1997) and autotomy (Stoks, 1998) are all used by

the larvae of various species to avoid fish predation. For Coleoptera, chemoreception of predators is very well developed in many adult dytiscids (Hodgson, 1953; Åbjörnsson et al., 1997). Species of Ephemeroptera also use such non-contact chemical stimuli to avoid predators (Peckarsky, 1980). Chemical signals allow for species-specific identification of predators and they are also more persistent than mechanical signals (Dodson et al., 1994). Many adult aquatic Coleoptera and Heteroptera also produce noxious substances which make them unpalatable to fish (Peckarsky, 1982; Brönmark et al., 1984; Gerhart et al., 1991). ii) The heavy trout predation on zooplankton in this study, irrespective of the nutrient-mediated increase in available benthic macroinvertebrate prey, is likely to have relieved the littoral macroinvertebrates from fish predation pressure. This strong reliance on zooplankton is also likely to have prevented fish predators from developing a well-defined prey search image or preference for any one macroinvertebrate taxon.

6.6. Conclusions

The results of this whole-lake experiment, albeit lacking replication and being generally descriptive, have demonstrated that plantation forestry-mediated eutrophication outweighs the top-down predatory effects of fish in structuring littoral macroinvertebrate communities of peatland lakes. The lack of a stronger top-down control by fish (brown trout) on littoral macroinvertebrates, which has been shown to occur by many other studies, is likely due to the increased *Sphagnum* growth decoupling predator-prey interactions by providing greater refuge for prey. In addition, anti-predatory adaptations of prey, preferential consumption of alternative prey and the lack of a specialised feeding mode by brown trout on any given macroinvertebrate taxa are also likely to have reduced the magnitude of top-down forces on littoral macroinvertebrates.

Despite being claimed to have a minimal impact on the hydrochemistry of receiving waters (Nisbet, 2001), the findings of this study demonstrate that the chemical efflux associated with conifer plantation forestry is leading to profound changes in the biological communities of these rare, species-rich lentic habitats (Maitland, 1999). The likelihood of further habitat deterioration as a result of conifer plantation forestry is almost assured as plantation forestry continues to expand worldwide (FAO, 2010).

6.7. References

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Chapter 7

General Conclusions



Extensive clearfelling surrounding an upland blanket bog lake – Maghera Lough.

7.1. Blanket bog lake habitats

Despite blanket bog lakes being one of the rarest aquatic habitat types in western Europe, they are also one of the most understudied standing water habitats. The occurrence of a number of rare macrophyte and aquatic macroinvertebrate species, notably *Cordulia aenea* (Linnaeus), as well as a number of glacial relict Coleoptera species, demonstrates their importance for aquatic biodiversity (chapter 2). The difference in baseline physico-chemical and biological characteristics among the study lakes, as a result of underlying geology, altitude, proximity to the sea, lake morphology, etc., suggest that a single type-specific reference condition is unlikely to exist, and that much more research effort is required to provide a more accurate and comprehensive typology-based assessment of the reference conditions for this habitat type in Ireland and elsewhere.

7.2. Impacts of conifer plantation forestry on blanket bog lakes

As predicted from studies on streams, conifer plantation forestry does in fact lead to profound changes in the hydrochemistry of blanket bog lakes, irrespective of underlying geology, altitude or geographic location (chapter 3). Although present during the mature plantation phase, the findings of this study confirm that the strongest impacts are seen post-clearfell. The main changes in hydrochemistry were elevated concentrations of plant nutrients, heavy metals, total dissolved organic carbon (TDOC) and reduced dissolved oxygen concentrations in the forestry-affected lakes. The elevated concentration of TDOC in the stream from the clearfell site was also found to be more labile than that from the mature plantation and

undisturbed blanket bog streams, respectively. The finding that lake pH was seemingly unaffected by forestry operations was surprising given the number of studies reporting the acidification of surface waters draining conifer plantations.

The hydrochemical changes were associated with profound changes in the biological communities of the lakes (chapters 4 – 6). A shift in Chydoridae communities, from dominance of the larger-bodied *Alonopsis elongata* (Sars) in the nutrient-poor blanket bog lakes to the smaller-bodied *Chydorus sphaericus* (O. F. Müller) and other smaller species in the more nutrient-enriched forestry-affected lakes, indicated that eutrophication was the main driver of community change (chapter 4). A similar pattern of forestry-mediated eutrophication was seen for the littoral macroinvertebrates, particularly the Coleoptera, Heteroptera and Odonata, with an increase in diversity and abundance of species associated with nutrient enrichment (chapters 5 & 6). The weak pH response of lakes to plantation forestry was reflected in the biotic communities, with few, if any, low pH-tolerant taxa having higher abundances in the forestry-affected lakes. However, metal toxicity associated with the elevated concentrations of heavy metals in a single clearfell lake – GC1 – was likely responsible for the absence of chydorids. Overall, the changes in the invertebrate communities in the study lakes in response to catchment forestry provided a clear and unambiguous demonstration of the negative impacts of conifer plantation forestry on the ecological and conservation status of blanket bog lakes (chapters 4 – 6).

Within-lake habitat variation and among-lake differences in predator biomass may reasonably be expected to have strong impacts on invertebrate communities in lakes, given the wealth of literature demonstrating their potential as community drivers. The results of this study demonstrate that forestry-mediated nutrient

enrichment was a more powerful driver structuring communities than either of these two factors. Not only are nutrients the biggest global threat to the integrity to freshwaters, but they also have an overriding influence on invertebrate communities (chapter 6).

7.3. Implications of the study

The fact this study was carried out on lake ecosystems helped to provide a more integrated assessment of catchment chemical influxes associated with forestry operations, and its subsequent ecological impacts. This study is one of few to provide empirical evidence of the severe habitat deterioration of lakes as a result of catchment plantation forestry operations. Elucidating the contribution of plantation forestry to total catchment loadings of plant nutrients to receiving surface waters is often difficult due to other catchment land uses such as agriculture and human habitation. Although agriculture is the primary source of leached nutrients being received by Irish freshwater bodies, this study demonstrates that plantation forestry alone can lead to the eutrophication of lake water bodies.

One of the main implications of this study is that current Irish forestry best management practices, particularly at the clearfell stage, are grossly ineffective at preventing chemical runoff to receiving waters on peatland. Such runoff is leading to a clear reduction in both water quality and the ecological status of blanket bog lakes in Ireland. The extensiveness of conifer plantation forestry on peatlands in Ireland, in addition to the current harvestable age of many plantation forests, is likely to pose serious problems in the near future regarding Ireland's obligation under the EU Water Framework Directive (2000/60/EC) to protect, enhance and restore all water

bodies to ensure that at least ‘good status’ water quality is achieved by 2015. Subsequently, any failing under that Directive, is most likely going to lead to a shortcoming under the EU Habitats Directive (92/43/EEC) which seeks to ensure ‘favourable conservation status’ of any designated water-dependent habitat or species. This was highlighted in this study by the reduced abundance of IUCN nationally red-listed species in the forestry-affected lakes, primarily due to reduced water quality.

The replanting of clearfelled areas, usually required as part of a general felling licence under the Forestry Act, 1946, may also pose serious implications for the long-term ecological and conservation status of many blanket bog lakes in Ireland. Continuing plantation forest cover in a lake’s catchment will yield an on-going supply of plant nutrients over the forest cycle which could maintain eutrophic conditions for extended periods of time. Even if the clearfelled area was not to be replanted, instead left to recolonise naturally, there is still a threat of persistent eutrophication due to the internal recycling of phosphorus (P) which may have accumulated in the sediment over the previous forest rotation. Although certain lakes recover quickly following reductions in external inputs of nutrients, many other lakes do not. The exact causes of slow recovery, or nonrecovery, from eutrophication are multifaceted and are not yet fully understood. It is quite possible that even if current plantation forestry operations within blanket bog lakes catchments were to cease, these lakes could still take many years to recover to an undisturbed state.

7.4. Recommendations for further research

This study has highlighted a number of areas which require further research:

- This study has provided an insight into the ecology and conservation value of blanket bog lakes in Ireland. It is highly likely that comparable lakes in different regions throughout Ireland also harbour rare and IUCN nationally red-listed species. However, without further research many of these species may be lost due to habitat deterioration of the contiguous blanket bog habitat.
- Physical disturbance associated with catchment forestry activities, especially during clearfelling, is likely to be the primary release mechanism responsible for the runoff of chemicals to receiving waters. However, the exact source(s) of individual chemicals and their relative contributions remains a topic in need of research. Such information would help to better inform forestry practitioners and would enable the implementation of a more efficient management protocol ensuring the least possible quantity of chemicals being leached to surface waters.
- In light of the large body of research which has been published in the previous two decades regarding the subsidies of allochthonous carbon to lentic food webs and overall lake metabolism, it seems justified to invest more research effort into the source, relative quantity and biochemical lability of the TDOC being leached from conifer plantation forests into lake ecosystems. Increased catchment loadings of dissolved organic matter could be shifting forestry-affected lakes towards a net heterotrophic status, thereby fundamentally changing lake ecosystem functioning.

- It is clear from this study that clearfelling represents the most detrimental stage of the plantation forest cycle with respect to plant nutrient runoff. Forest managers and policy makers need to place greater emphasis on reducing this runoff from afforested catchments, especially given that plantation forests require fertilisers to yield commercially viable tree crops.
- Finally, considering that eutrophication was the main driver of community change in this study, it seems that the acidification effects of conifer plantation forestry on streams ecosystems are likely to be of minor importance in comparison with forestry-mediated eutrophication in lake ecosystems. This implies that greater emphasis should be placed on trophic, rather than acidification or metal toxicity, in future research into the biological impacts of conifer plantation forestry on surface freshwaters, especially for lakes.

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