Effects of Retrogressive Permafrost Thaw Slumping on Benthic Macrophyte and Invertebrate Communities of Upland Tundra Lakes

by

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Bsc. Hons., Universidade Federal do Rio Grande do Norte, 2005

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Supervisory Committee

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Abstract

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Global warming is forecast to cause significant thawing of the permafrost that surrounds lakes and rivers across the Arctic, with potential wide-scale effects on the water quality and biotic characteristics of these water bodies. The benthic environment is believed to be especially sensitive to permafrost-induced ecological change, and this has been the focus of recent field intensive research. Five lakes disturbed and three lakes undisturbed by retrogressive permafrost thaw slumps were sampled during late summer of 2006 to assess the potential effects of slumping on benthos. Water quality parameters, submerged macrophytes, benthic invertebrates, and sediment were collected. A significant difference ($p < 0.05$) between disturbed and undisturbed lakes was found for macrophyte, invertebrates, underwater light attenuation, and some sediment variables. The results suggest that thaw slumps can affect submerged macrophyte biomass, benthic invertebrate abundance, and also community structure in upland tundra lakes. Such differences between undisturbed and disturbed lakes are suggested to be related to changes in water column transparency, sediment nutrient availability, soil and terrestrial vegetation loading from the landscape, and changes in slope angle of the littoral zone.

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Chapter 1 : Introduction

The arctic region is considered especially sensitive to the impacts of global warming (ACIA, 2005) as evidenced by the increasingly presence of later freeze-up and earlier break-up of ice in rivers and lakes, retreat and disappearance of glaciers and ice caps in low-lying areas, reduction in snow-cover extent, increases in precipitation, reduction in sea-ice extent, permafrost degradation, and disappearance of lakes (Walsh *et al.,* 2005; Smith *et al*., 2005).

Changes in the extent of permafrost cover will have effects on the hydrological regime affecting freshwater bodies (Walsh *et al.,* 2005; Anisimov *et al.,* 2007). The permafrost is predicted to suffer a decrease of about 10 to 20% in areal extent, and change hundreds of kilometres in its southern limits to the north, likely causing lakes and wetlands to drain in some areas while creating new wetlands in others (Wrona *et al.,* 2005). Substances formed in the past from biological processes that are currently locked into the landscape (such as nitrates and phosphates) are predicted to be released to the environment (Davis, 2001; Kokelj & Burn, 2003; Wrona *et al.,* 2005).

Changes in the mechanical properties of frozen ground will increase the rate of down-slope movement, and collapse of slopes is projected for places that have been stable for thousands of years (Davis, 2001). An increase in the number of shoreline permafrost thaw slumps is expected to affect the functioning of high-latitude lakes primarily through changes in the water chemistry (Hobbie *et al*., 1999). In addition, these water bodies will be affected by changes in: runoff composition due to alterations in land cover, duration and magnitude of snow cover, UV radiation, water temperature, and available habitat (Arnell *et al.*, 1996).

An increase in nutrient input to freshwater bodies, in addition to other possible effects related to climate change variability (*e.g.* increase in degree-days, higher air/water temperatures, changes in landscape cover), will probably affect primary production (Wrona *et al.,* 2005), and be reflected consequentially in modification of food-web structures, biogeochemical cycles, and water quality. Some studies already highlight differences on water chemistry due to permafrost thaw slumping (Hobbie *et al.*, 1999; Kokelj *et al.*, 2005), which can be used as a proxy to understand the possible effects of large scale landscape permafrost thaw on freshwater environments. Such effects are predicted to be more frequent in a warming scenario and can affect primary production and food-web pathways in arctic freshwater systems (Hobbie *et al.*, 1999).

Benthic primary production has been considered a highly important component of overall primary production in arctic lakes (Sierzen *et al*., 2003) and climate change can have an impact on this biota. Thus, a better understanding of benthic biota and their relationship with physico-chemical variables is warranted. Benthic macrophytes and invertebrates require greater attention regarding the possible effects of these changes in freshwater bodies, as they are understudied and are important contributors to lake production (Vadeboncoeur *et al.*, 2002).

Taking the aforementioned in consideration, this thesis has two main objectives that will be addressed separately in the next chapters (3 and 4) written in journal style:

1) What is the effect of retrogressive permafrost thaw slumping on macrophyte biomass and community structure of upland arctic tundra lakes? What physico-

chemical variables are responsible in influencing the observed response patterns? (Chapter 3)

2) What is the effect of retrogressive permafrost thaw slumping on benthic invertebrate community structure of upland tundra lakes? Taking into consideration that macrophytes are believed to increase habitat complexity and food supply for zoobenthos, is there any relation between macrophyte biomass and invertebrate abundance in tundra lakes? What physico-chemical variables are related to benthic invertebrate community structure? (Chapter 4)

Chapter 2 provides general background information about the studied topic and a more detailed description of the study area. Chapter 5 contains general conclusions and a set of recommendations on future research.

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Chapter 2 : Theoretical Background

Lakes and ponds occupy large areas of the Arctic, and are partly or completely frozen most of the year depending on size and depth. Most of these lakes have clear water, are highly oligotrophic, and have low species richness (Stonehouse, 1989; Hershey *et al.*, 1999). In contrast, oxbow and other lakes formed on river plains are frequently muddy and well provided with minerals, but still have fewer species and lower productivity than similar lakes in temperate latitudes (Stonehouse, 1989).

Arctic lakes are generally characterized by the presence of low total dissolved salts and low decomposition rates, with a considerable amount of energy and nutrients locked in dead organic matter (Hobbie, 1980). In addition, seasonal changes in chemical and physical patterns of the water column, and fewer hours of solar radiation in the winter contribute to the low system productivity.

Production in arctic lakes is believed to be dominated by benthic organisms (Sierzen *et al.*, 2003), and interactions between benthic and pelagic organisms may dominate the food web (Hershey *et al.*, 1999). Benthos were considered the primary source of carbon for all species of benthic and pelagic adult fishes studied in oligotrophic lakes in Alaska, suggesting that benthic primary production is important due to the extreme oligotrophy and low planktonic productivity available to the consumers (Sierzen *et al.*, 2003). In the ultra-oligotrophic Char Lake (Northwest Territories -NWT), 80% of the annual photosynthesis was estimated to occur in the benthos (Welch & Kalff, 1974) and in one lake (lake-18, Tuktoyaktuk Peninsula, NWT), 50% of the carbon was produced by benthos, 20% by phytoplankton, and 30% by allochthonous material (Ramlal *et al.*, 1994).

Despite the fact that macrophytes can be a highly important component of benthic primary production, little is known about the environmental variables that affect macrophyte biomass production in arctic lakes. Light availability, nutrient content, lake morphology, slope, and sediment composition and availability of organic matter have all been found to contribute to macrophyte production and distribution in temperate lakes and may have the same importance in the Arctic. For example, slope is suggested to be a major variable that controls macrophyte biomass through its effects on sediment stability and deposition of fine nutrient-rich material (Duarte & Kalff, 1990). In addition, sediment has been recognized as a source of nutrient supply to submerged macrophytes, especially nitrogen, phosphorus, iron, manganese, and micronutrients (Barko *et al*., 1991; Jackson, 1998).

In arctic delta lakes, biomass of submerged macrophytes presented a diverse relationship with water transparency depending on the material that was causing the attenuation of light. Decreased bed illumination caused by suspended sediment in the water column was related to a decrease in macrophyte biomass, while other lakes with decreased bed illumination caused by colour material had higher macrophyte biomass, probably related to the decreased exposure to UV (Squires *et al.,* 2002). Organic matter and total nitrogen content in sediment were also found to be related to increased macrophyte biomass, being higher in lakes right along the delta which have high rates of organic and inorganic sedimentation, creating suitable substrate conditions for the growth of macrophytes (Squires & Lesack, 2003). Despite the high-latitude location, a higher biomass of submerged plants was observed in these lakes, compared to temperate lakes, and temperate and tropical floodplains (Squires & Lesack, 2003).

In addition to the contribution to benthic production, macrophytes have an important function in nutrient cycling and the structuring of arctic lake food webs (Kalff, 2001). Most of these plants are rooted and are a living link between sediment and the overlying water, acting as interceptors and modifiers of material flow from land to the open water (Carpenter & Lodge, 1986). In general, macrophytes influence the distribution and abundance of periphyton (algae attached to substrates), help to reduce shoreline erosion by decreasing wave energy, trap particles and nutrients creating a substrate for bacteria and periphyton growth, and serve as habitat and daytime refuge for a variety of organisms like zooplankton, fishes and benthic invertebrates (Kalff, 2001).

Benthic invertebrates are an important component of secondary production in temperate lake systems and are involved in the transfer of energy to upper trophic levels, but little is known about their status in arctic lakes. Consumption of a variety of food resources by these invertebrates leads to energy transfer from benthic and pelagic habitats to pelagic food webs (Stoffels *et al.*, 2005), and in some shallow temperate lakes their production is estimated to be 2-5 higher than zooplankton production (Wetzel, 2001). In the Arctic, inputs of terrestrial material have been suggested to be of great importance for zoobenthic communities of small oligotrophic lakes, contrary to the importance of pelagic production to zoobenthos that is mainly observed in eutrophic temperate lakes. Inputs of allochthonous DOC can favour bacterial production at the sediment-water interface, being later utilized by benthic invertebrates such as chironomids (Hershey *et al.*, 2006). In addition, benthic invertebrates are considered an index of potential fish productivity in lake systems (Rasmussen, 1988).

Various environmental factors are known to affect the composition and abundance of zoobenthic communities, including biotic relationships, and spatial and physico-chemical factors that are influenced by the presence of submerged macrophytes. In general, benthic invertebrates feed on particulate organic matter that grows or settles on the sediment (Rasmussen, 1988) such as algae, bacteria, and detritus that can be altered by the presence of submerged macrophyte beds (Beaty *et al.*, 2006). Epipelic algae that grow on macrophytes, in addition of being a food source for zoobenthos also leach dissolved organic matter, having a positive influence on benthic microbes that are also consumed by the invertebrates (Beaty *et al.*, 2006).

Since zoobenthos are positively affected by the presence of submerged macrophytes, most lake physico-chemical characteristics affecting benthic primary production are also related to zoobenthic communities. Water physico-chemical changes have been related to modifications in zoobenthic composition (Heino, 2000). Calcium in the water column has been related to productivity of macrophytes and is believed to limit the distribution of a variety of molluscs and crustaceans due to changes in salt-balance mechanisms and accumulation of Ca for shell formation and cuticle growth (Rasmussen, 1988). Higher water temperatures stimulate plant growth in the littoral zone favouring invertebrate communities (Moore, 1981), and also increases growth and development rates of invertebrates **(**Plane & Downing, 1989).

Water transparency has a positive effect on invertebrate production as it favours benthic primary production (Moore, 1981). Relative abundance of vascular and non-vascular macrophytes and presence of microbial mats are related to oxygen levels in the sediment, which can ultimately affect zoobenthic communities. Non-vascular macrophytes cannot oxygenate sediment (Waters & San Giovanni, 2002), while microbial mats respiration will determine if sediment will be oxic or anoxic, thus affecting solubility and availability of metals and nutrients to benthic primary producers (Kalff, 2001)

Littoral slope and fetch affect macrophytes and zoobenthos by influencing sediment particle size composition and retention of inorganic and organic material (Stoffels *et al.*, 2005; Rasmussen & Kalff, 1987). Steep slopes have reduced ability to retain the fine nutrient-rich sediments that are more beneficial to benthos, and also affect biota by slumping and side-movement of the sediment (Duarte & Kalff, 1986; Rasmussen & Kalff, 1987; Rasmussen, 1988). In addition, presence of high levels of organic matter (OM) can limit nutrient uptake, and macrophyte growth can be disrupted by the presence of phytotoxic compounds produced during anaerobic decomposition (Barko *et al.*, 1991). High OM content also increases sediment packing, influencing sediment-oxygen content and zoobenthic community structure composition through changes to more anoxic tolerant groups such as chironomids and oligochaetes (Vos *et al.,* 2004).

Despite all the evidence showing a relationship between submerged macrophyte biomass and benthic invertebrates, mostly in temperate lakes, there are contradictions as some studies highlight lower invertebrate abundance in areas with macrophyte presence while others relate the opposite (Ságová-Marecková, 2002). However, a possible explanation is that as the submerged macrophyte biomass increases, a higher number of invertebrates will associate with it (*i.e.* epiphytic) and not with the sediment (*i.e.* benthic) (Diehl & Kornijów, 1998; Kalff, 2001). Changes in macrophyte biomass can also affect different species to varying degrees. For example, increases in epiphytic algae related to submerged macrophytes negatively affect benthic collector-suspension feeders (*e.g.* chironomids larvae) due to reduced supply of fresh and dead planktonic algae under the macrophytes (Kornijów & Moss, 1998).

Although well known relationships between macrophytes and macroinvertebrates exist, they are mainly observed in lakes and ponds containing fish (Diehl & Kornijów, 1998) and in temperate zones. Rennie & Jackson (2005) found increased zoobenthic abundance accompanying increased macrophyte habitat complexity only in lakes with fish present when compared to lakes without fish. As documented, invertebrate abundance, biomass and diversity were observed to be influenced by variables that control macrophyte habitat complexity such as macrophyte biomass, number of species and plant surface area (Rennie & Jackson, 2005), and thus contradictions in previous studies may be related to the absence of fish communities.

Benthic invertebrates, therefore, perform important ecosystem and community functions in lakes and can be an important source of food to fish at different ontogenetic stages, influencing the structure of fish communities in temperate lakes (Diehl & Kornijów, 1998; Kalff, 2001). However, despite the clear importance of benthic invertebrates and macrophytes to lake food webs, few studies have dealt with benthic and pelagic food web-related or limnological aspects of arctic freshwater ecosystems (*e.g*. Hobbie, 1964; Schindler *et al.,* 1973; Stanley & Daley, 1976; Hobbie *et al*., 1999; Levine & Whalen, 2001; Lim *et al.*, 2001; Michelutti *et al,* 2002; Kokelj *et al.,* 2003; Thompson *et al., in prep.*).

2.1 Study Area

The studied lakes are located around Inuvik and Richards Island (Northwest Territories, Canada), and span a narrow latitudinal gradient between 68º56' and 69º25' N. A few limnological-related studies have been performed in the selected study location and around the nearby Tuktoyaktuk Peninsula. These have addressed a diverse range of subjects including lake water physico-chemical characterization in upland and delta lakes, the study of impacts of shoreline permafrost slumping on water column physico-chemical characteristics and biota, and other permafrost-related research (*e.g.* Ramlal *et al*., 1994; Pientiz *et al*., 1997; Squires *et al.,* 2002; Squires & Lesack, 2003; Kokelj & Burn, 2003, 2005; Kokelj *et al.,* 2005; Thompson *et al*., 2008.).

The region east of the Mackenzie Delta has a variety of drained lakes and small lakes that are poorly hydraulically connected (Kokelj *et al*., 2005). Richards Island alone contains over 1200 lakes that cover approximately 24% of the area, with many having less than 5 m depths in the central region (Burn, 2002). The presence of continuous permafrost around these lakes constrains the hydrological connection between freshwater systems and most streamflow occurs during the warm months, with the dominant hydrological events occurring during the spring snowmelt freshet when the active layer begins to develop for the summer period (Pientiz *et al*., 1997).

These lakes occur in non-bedrock areas (marine sediments- colluvial deposits, moraine, rolling, hummocky) that commonly have an ice-rich zone at the top of the permafrost table, formed from downward moisture movement from the active layer (up to 130cm) at the end of summer and upward moisture movement from underlying permafrost over winter. The seasonal leaching from thawed soils and ionic movement resultant from thermal induced moisture migration creates a solute enriched zone in the near-surface permafrost (Kokelj & Burn, 2003; 2005).

Early-summer air temperatures are characterized by a steep gradient between Inuvik and Richards Island, which is also reflected by changes in vegetation from boreal forest near Inuvik to shrub tundra at less than 30 km north of the city. Such differences occur because the sea ice pack at the Beaufort Sea decreases the temperature near the coast, with recorded mean annual temperatures around -10.5ºC near Tuktoyaktuk and -9.7ºC around Inuvik. Annual precipitation also differs between both areas with higher snowfall around Inuvik (~ 160cm) than near the coast (< 100cm), and higher atmospheric loading of Cl^- and Na^+ near the coast (Kokelj *et al.,* 2005; Burn, 2002; Pientiz *et al*., 1997).

Ice cover on lakes typically forms around early October and lasts until June, although somewhat longer deviations characterize lakes near the coast because of the chilling effect of the coastal climate. During the winter, water freezes to the bottom in shallow areas of most lakes (Burn, 2002). During the ice-free season, they are mainly fed by low-solute surface and sub-surface runoff from snowmelt and precipitation that pass through the nutrient-poor active layer (Kokelj *et al*., 2005).

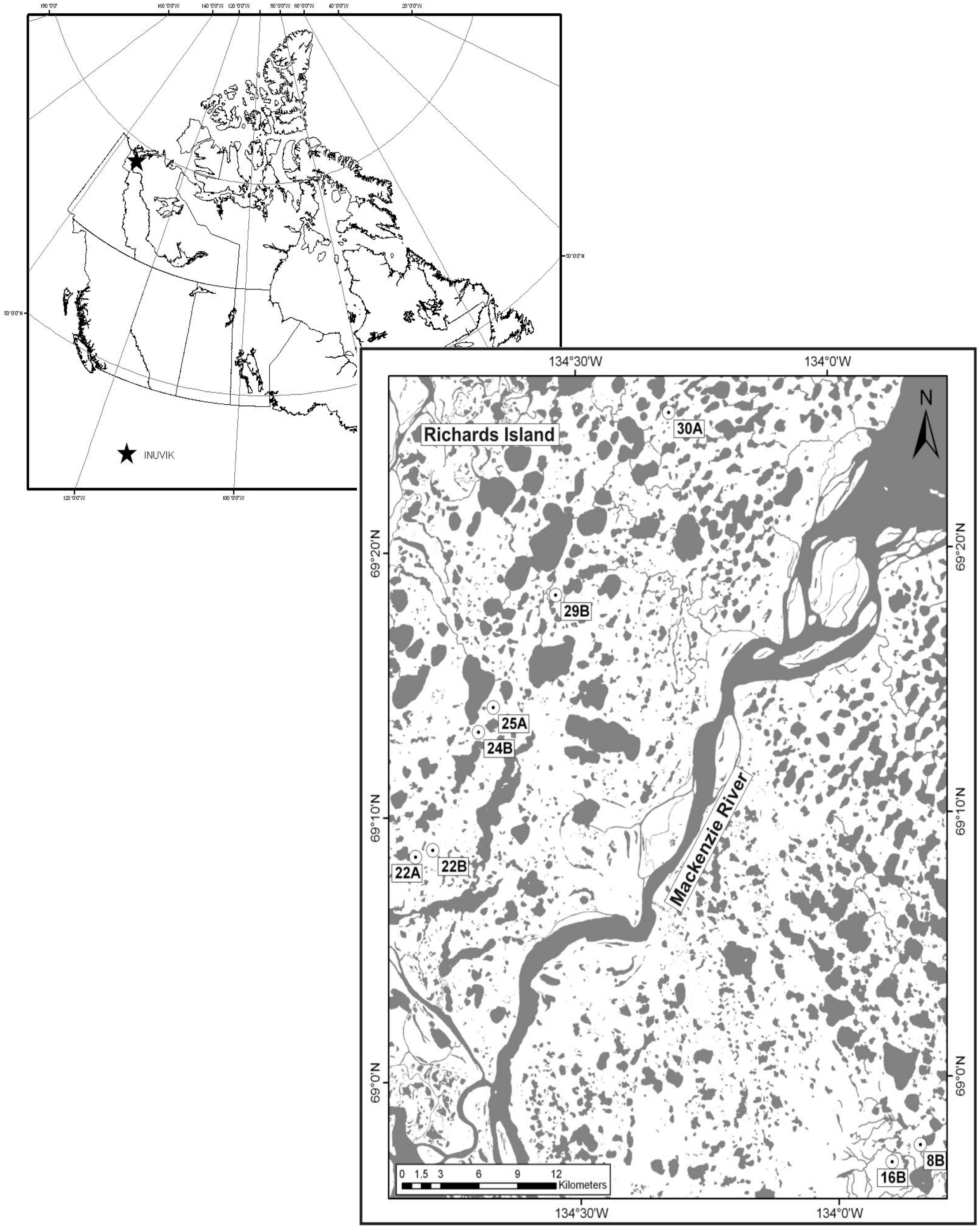

Figure 2-1: Geographic location of the studied lakes. Undisturbed lakes: 22A, 25A, 30A; disturbed lakes: 16B, 8B, 22B, 24B, 29B. Source: Natural Resources Canada/CanVec (www.geogratis.gc.ca)

For this study, three undisturbed lakes and five lakes disturbed by retrogressive permafrost thaw slumping were selected around the described area after an extensive selection process that involved various steps (Fig 2.1). Primarily, a database including water-column quality data from 60 lakes surveyed in 2005 (Thompson *et al.*, *in prep.*) was scanned for the exclusion of lakes considered outliers (*i.e.* extreme values of chemical variables). After, only lakes located north of the tree line and out of areas with disturbance were selected (*e.g.* fire), since one of the main concerns for proper selection was to minimize the potential variation due to landscape-type and latitude. It has been previously shown that water-column physico-chemical parameters varied by latitude in lakes surveyed between 60º37'N and 69º35'N around the studied area and were probably due to differences in bedrock geology and catchment vegetation (Pienitz *et al.*, 1997). Also, catchment area, lake area, and lake volume data were utilized in a Cluster Analysis to identify undisturbed and disturbed lakes that had similar physical characteristics. Finally, field logistics were taken into consideration since the study sites could only be reached practically by air during the ice-free season.

Thus, the eight selected lakes were all located within a ~53 km latitudinal range, in areas with similar catchment characteristics and north from the boreal forest to shrub tundra transition (most southerly lake about 30 km from the transition zone). In general, undisturbed lakes had a mean depth of 2.9 m (1.9 m to 3.76 m) and a mean catchment-area: lake-area ratio (Ca:La) of 4.8 (4.3 to 5.1).The comparable statistics for the disturbed lakes were 3.5 m (2.4 m to 4.5 m) and Ca:La of 4.0 (2.4 to 5.0), although these lakes also tended to have some deep holes adjacent to the slump zone. More information about the studied lakes is provided in the following chapters.

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Chapter 3 : Effects of retrogressive permafrost thaw slumping on sediment chemistry and benthic macrophyte communities of upland tundra lakes

Abstract

Global warming is predicted to cause changes in permafrost cover and stability in the arctic region. Ionic concentrated zones in regions of ice-rich permafrost are a reservoir of chemicals that can be potentially transferred to lakes and rivers during permafrost degradation such as retrogressive thaw slumping. Input of enriched runoff (e.g., SO_4^{-2}, Ca^{+2}) from permafrost thaw runoff, and sediment and vegetation from the landscape, possibly create a totally different lake environment that affects lake production. Benthos are believed to be especially sensitive to permafrost-induced ecological change, and this has been the focus of field intensive research. Five disturbed lakes and three undisturbed by retrogressive thaw slumps were sampled during late summer of 2006 to assess the potential effects of slumping on sediment chemistry, underwater light availability, and macrophyte biomass and community structure. Water quality parameters, submerged macrophytes and sediment were collected and significant differences ($p<0.05$) between disturbed and undisturbed lakes were found for macrophyte biomass, underwater light attenuation, and some sediment variables. It is suggested that enriched runoff chemistry may alter nutrient availability at the sediment-water interface and also the degradation of organic material affecting lake transparency and submerged macrophyte communities. The results suggest that thaw slumps can affect food-web in tundra lakes through an increase in benthic production.

Keywords: Tundra lakes; Sediment chemistry; Macrophytes; Permafrost thaw.

3.1 Introduction

Extensive evidence of a warming climate has been found in the arctic region (Wrona *et al*., 2005; Anisimov *et al*., 2007). Examples include indications of later freeze-up and earlier break-up of ice in rivers and lakes, retreat and disappearance of glaciers and ice caps, reduction in snow cover extent, increases in precipitation, reduction in sea-ice extent, permafrost degradation, and disappearance of lakes (Smith *et al*., 2005; Walsh *et al.,* 2005; Wrona *et al*., 2005; Anisimov *et al*., 2007).

With respect to permafrost, changes in the mechanical properties of frozen ground will increase the rate of down-slope movement, and collapse of slopes is projected for places that have been stable for thousands of years (Davis, 2001). An increase in the frequency and number of permafrost slumping events is expected to affect the functioning of high-latitude freshwater ecosystems through changes in the water chemistry (Hobbie *et al*., 1999).

Landscape-related disturbance is projected to increase nutrient input to freshwater systems in addition to other environmental effects related to climate change, thereby affecting primary and secondary production, modifying food-webs, and altering biogeochemical cycles and water quality (Wrona *et al.,* 2005). A few studies have already highlighted differences in water chemistry related to permafrost thaw slumping (Hobbie *et al*., 1999; Kokelj *et al*., 2005).

Considering that benthic primary and secondary production can be important components of the overall production in arctic lakes (Sierszen *et al.,* 2003; Rautio & Vincent, 2007), a more comprehensive understanding of the effects of permafrost thaw on the benthos is needed. Among the benthic biota, a special focus should be placed on macrophytes as they contribute significantly to primary production, increase habitat heterogeneity (being beneficial to benthic invertebrates and fishes), and are involved in other important in-lake processes (Vadeboncoeur *et al.*, 2003; Barko & James, 1998). Macrophytes have the ability to physically inhibit sediment resuspension, sequester nutrients, reduce phosphorus mobility, and modify predator-prey relationships among pelagic organisms (Vadeboncoeur *et al.*, 2003). In conjunction with allochthonous inputs from surrounding terrestrial systems and sedimented plankton, macrophytes are an important energy source for benthic secondary production (Schindler & Scheuerell, 2002). Since most macrophytes are rooted, they are considered a living link between sediment and the overlying water column, acting as interceptors and modifiers of material flow from land to the open water (Carpenter & Lodge, 1986). Macrophytes also influence the distribution and abundance of periphyton, reduce shoreline erosion through their effect on reducing wave energy, and serve as habitat and daytime refuge for a variety of organisms, such as zoobenthos, pelagic zooplankton, fishes, and waterfowl (Kalff, 2001).

Many variables have been considered important for macrophyte production. These include underwater light availability, water nutrient content, lake morphology, littoral slope, sediment composition and organic matter content (*e.g.* Duarte & Kalff, 1986; Barko *et al.,* 1991; Jackson *et al.*, 1993; Anderson & Kalff, 1998; Havens, 2003). Slope is also suggested to be a major variable controlling macrophyte biomass through its effects on physical characteristics of the sediment, and thereby affecting the stability and the deposition of fine nutrient-rich material (Duarte & Kalff, 1986).

In addition to being used as physical attachment, sediment has been recognized as a source of nutrient supply to submerged macrophytes (Barko *et al.*, 1991; Jackson, 1998), especially nitrogen, phosphorus, iron, manganese, and other micronutrients. Some of these elements tend to co-precipitate and are frequently present in low concentrations on oxygenated surface waters (Barko *et al*., 1991). Other evidence of the use of sediment by macrophytes for nutritional purposes is that phosphorus in the water column is frequently considered limiting, making sediment a potential supplier of this and other elements (Jackson, 1998). Sediment composition also has an influence on macrophyte growth. Sandy sediments usually have low nutrient content with fertility depending on nutrient input from groundwater, while organic ones exhibits a quite low nutrient concentration on the basis of sediment volume (Barko *et al.,* 1991).

Very little, however, is known about the environmental variables that affect the community structure and production of macrophytes in arctic tundra lakes. The objective of this study is to investigate the influence of retrogressive permafrost thaw slumps on sediment chemistry and related water parameters on the distribution, biomass and community structure of macrophytes as a proxy to the possible effects of large scale permafrost thaw on arctic freshwater systems. This study focused on investigating the hypothesis that retrogressive thaw slumping can produce significant differences in sediment chemistry and submerged macrophyte community structure between lakes disturbed and not disturbed by such slumping.

3.2 Lakes Selection and Sampling Methods

A set of lakes were selected between Inuvik and Richards Island (N.W.T, Canada) based on lake/catchment characteristics, water quality data from a 60 lake survey

(Thompson *et al.*, *in prep.*), and constraints of field logistics. A final subset of 3 lakes not affected by retrogressive thaw slumping (undisturbed or *U* lakes) and 5 lakes affected (disturbed or *D* lakes) were selected for detailed study (Figure 3-1, Table 3-1).

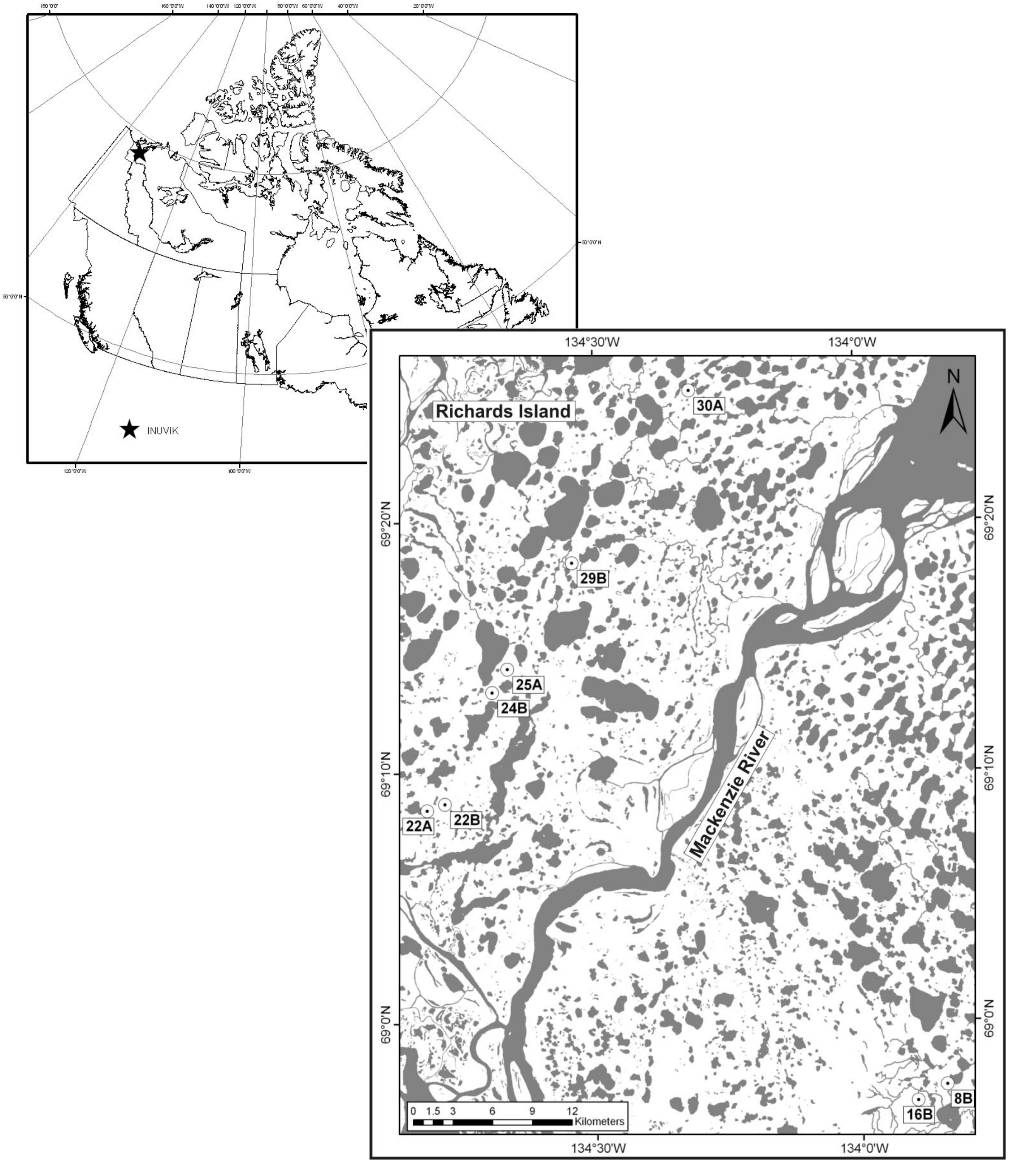

Figure 3-1: Geographic location of studied lakes. Source: Natural Resources Canada/CanVec (www.geogratis.gc.ca)

Table 3-1: Lake attributes summary table. Lake area (La), catchment area: lake area (Ca: La) ratio, catchment area: lake volume (Ca: Lv) ratio, maximum depth (Z_{max}), mean depth (Z_{mean}), lakes (*U*= undisturbed, *D*= disturbed), number of lakes (N), mean, standard deviation (S.D), minimum and maximum values (Min and Max).

Lakes		La (m^2)	Ca:La	Ca:Lv	Z_{max} (m)	Z_{mean} (m)
U lakes	Mean	40,100	4.78	1.77	7.30	2.88
N= 3	S.D	19,419	0.44	0.14	2.88	0.92
	Min.	18,700	4.28	1.61	4.20	1.92
	Max.	56,600	5.11	1.88	9.90	3.76
D lakes	Mean	76,380	3.99	1.15	9.54	3.48
N= 5	S.D	40,514	1.18	0.63	4.33	0.80
	Min.	35,500	2.41	0.66	5.30	2.44
	Max.	142,900	5.04	2.01	16.80	4.52

Disturbed lakes were sampled in two areas: one located at the opposite side (*Do*) of the physical disturbance caused by the slump, and another in an area adjacent (*Da*) to the slump and thus more directly physically affected by the disturbance. This allowed for testing whether disturbance had a localized effect in disturbed areas compared to the ones that were more distant (*Do*) (Figure 3-2). Stratified radial transects starting from the shoreline towards the center of the lake were used as the main sampling unit (replicate) in the present study, and were distributed to encompass the different areas of each lake. Taking into consideration the focus on the littoral benthos, sampling points were randomly placed in 1, 2 and 3-metre depth strata along the transects, yielding a maximum of 9 sample points (3 depths x 3 transects) in undisturbed lakes and a maximum of 18 sample points in disturbed lakes (9 in each disturbance zone - *Do* and *Da)* (Figure 3-2). However, due to logistical constraints in the field, some variables could not always be sampled at all strata depths in all lakes.

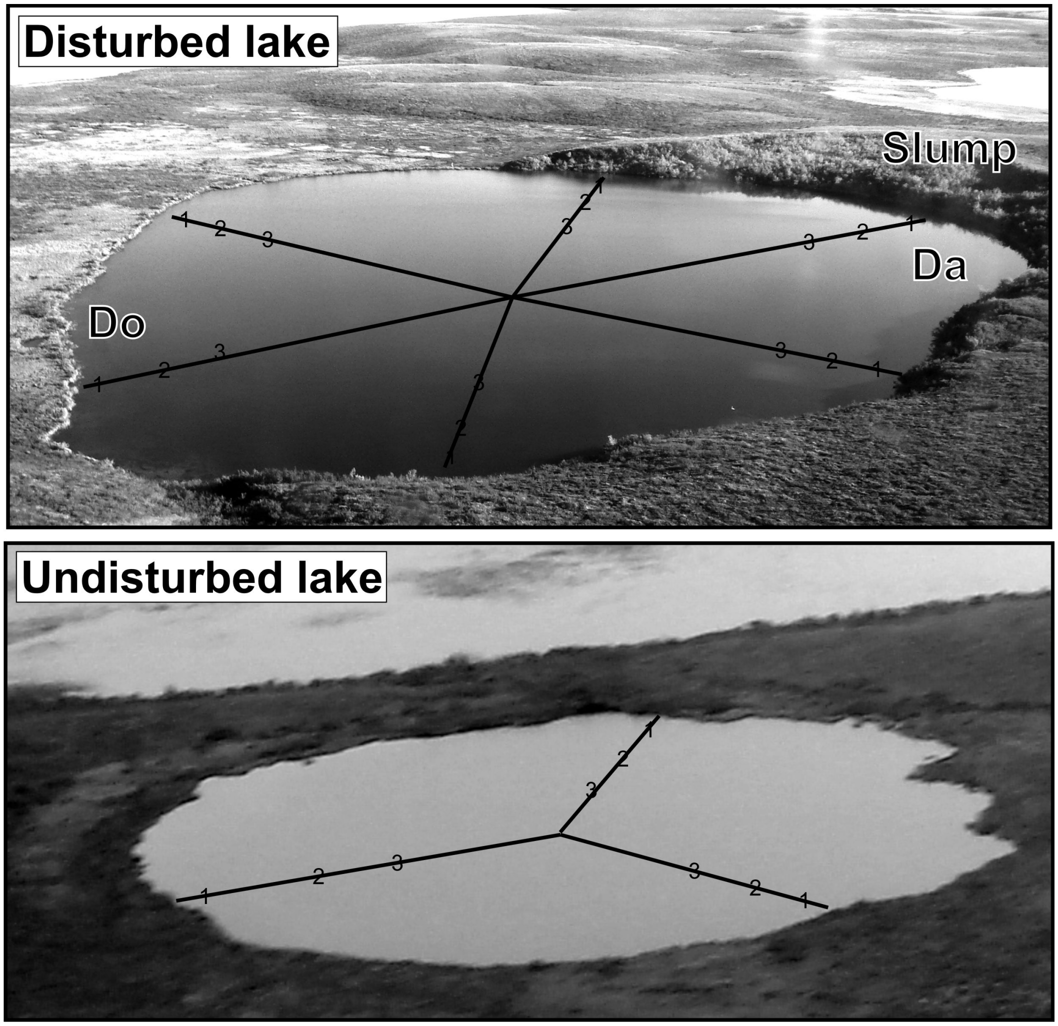

Figure 3-2: Schematic location of transect and sample points (1 to 3m depth) in undisturbed lakes (*U*), disturbed lakes (*D*), and sample location in *D* lakes (*Do* - opposite to the disturbance, *Da* – adjacent to the disturbance).

Between 26 August 2006 and 5 September 2006, samples of sediment, submerged macrophytes, and pelagic water were taken from the selected lakes. In addition, measurements of underwater photosynthetic active radiation (PAR) (Li-cor LI-192) were taken at each of the transect points at the near surface and approximately 0.6m depth, always before reaching the top of macrophytes**.** The results were used to calculate the underwater light attenuation coefficient (K_d) at each point in accordance with Kalff (2001).

It is worth noting that although the calculation of K_d are one time measurements, in conjunction with field work visual observations, they can still provide a general indication of the underwater light regimes.

Submerged macrophytes were collected at 1, 2 and 3-metre depths with a telescopic macrophyte sampler (Marshal & Lee, 1994) that covered an area of 0.164 m^2. In the laboratory, the above-ground plant portions were washed, separated and identified, then oven-dried to constant weight at 60ºC for dry-weight determination. Mosses were separated into live and dead parts, and only the live portion was utilized. Results were extrapolated to represent a total dry biomass per m^2. Identification of macrophytes was performed using Porsild & Cody (1980) and Cody (2000), and further validated by an expert in such procedures: Dr. Patricia Chambers of Environment Canada.

Sediment samples were collected immediately adjacent to the sampled macrophytes at 1 and 3- metre depths, with the use of a sediment corer (internal diameters of 5cm and 6.6cm; Universal gravity corer – Aquatic Research Instrument; punch core – manufactured at Environment Canada, Instrument Technology Shop, Saskatoon, Canada**).** Samples from the top 15 cm were transported to the laboratory, homogenized and separated into two fractions. One fraction was frozen, freeze-dried, and sent for analysis of recoverable metals (i.e. environmentally available) and nutrients at the Environment Canada National Laboratory for Environmental Testing (NLET), in Burlington, Canada (Table 3-2). The remaining fraction was oven-dried and burned for calculations of loss of ignition content (as a measure of organic matter content) in accordance with Hakanson & Jansson (1983).

Water physico-chemical parameters were collected at the deepest point in each lake previously determined from bathymetric surveys. A handheld multiparameter Y.S.I (model

556) was used to collect pH, temperature, and conductivity data. In addition, pelagic water samples were collected and sent to the NLET lab for analysis of particulate organic carbon (POC), dissolved phosphorus (DP), orthophosphate (OP), total phosphorus (TP), ammonium (NH_3N), nitrite-nitrate (NO_3NO_2), total dissolved nitrogen (TDN), particulate organic nitrogen (PON), and total nitrogen (TN).

Table 3-2: List of key nutrient, metals and metalloids analyzed from sediment samples.

Carbon (organic/inorganic)	Sodium (Na)	Potassium (K)	Arsenic (As)
Nitrogen (organic)	Zinc (Zn)	Calcium (Ca)	Beryllium (Be)
Phosphorus (inorganic)	Cooper (Cu)	Magnesium (Mg)	Bismuth (Bi)
Phosphorus (P)	Nickel (Ni)	Iron (Fe)	Cadmium (Cd)
Manganese (Mn)	Molybdenum (Mo)	Cobalt (Co)	Gallium (Ga)
Antimony (Sb)	Lanthanum (La)	Chromium (Cr)	Aluminium (Al)
Thallium (Tl)	Lithium (Li)	Strontium (Sr)	Rubidium (Rb)
Uranium (U)	Lead (Pb)	Vanadium (V)	Barium (Ba)

3.2.1 Statistical Analyses

Figure 3-3 and 3-4 summarize the logic-model and steps used to analyze the data. Initially, all the variables were tested for normality using a Kolmogorov-Smirnov (K-S) test ($p<0.05$) (Figures 3-3, 3-4; step 1a) and, when necessary, $\log_{10}$ transformed (Figure 3-3; step 2a) to meet the assumptions of parametric testing. General Linear Model (GLM) regressions were performed to test for differences in sediment chemistry between undisturbed (*U*) and disturbed (*D*) lakes, using depth as a covariate (Figure 3-3; step 3aa).

In cases where a significant difference ($p < 0.05$) between disturbed and undisturbed lakes was found, a subsequent GLM with a Bonferroni simultaneous *a posteriori* test between lake/disturbance location (*U, Do* – opposite to slump, *Da* – adjacent to slump) and depth was performed (Figure 3-3; step 4aa). These analyses were used to ascertain whether the differences were related to in-lake processes (*Do* vs. *Da*) versus between-lake (*U* vs. *Da*, *U* vs. *Do*) processes and physical proximity to the disturbance.

Since some sediment variables and macrophyte biomass data were not normally distributed even after transformation, the non-parametric Kruskal-Wallis test was used in these cases (Figure 3-3; steps 3a, 4a; and Figure 3-4; steps 2a, 3a). As water nutrient data were only collected at one station per lake, differences between undisturbed and disturbed lakes were analyzed using one-way Analysis of Variance (ANOVA). All the analyses were performed with MINITAB 13.1 (Minitab Inc., 2000).

From the available sediment variables, macronutrients (nitrogen, phosphorus, potassium, calcium, magnesium, carbon) and micronutrients (iron, manganese, zinc, copper, nickel, cobalt, and molybdenum) that are considered important for plant growth (Schulze *et al.*, 2005) were selected for ordination analysis (Figure 3-3; step 1b) performed with

CANOCO 4.5 software (ter Braak & Šmilauer, 2002). Sediment variables were log transformed (log (x+1)) and analyzed by Detrended Correspondence Analysis (DCA), detrending by segment. Detrending by segment assesses the heterogeneity in the taxa data through evaluation of the length of the community composition gradient (Lepš & Šmilauer, 2003). This analysis was performed to decide if a unimodal (Correspondence Analysis - CA, Canonical Correspondence Analysis - CCA) or linear analysis (Principal Component Analysis - PCA, Redundancy Analysis - RDA) would work better with the sediment data. Since the community composition gradient was < 1 (Figure 3-3; step 2b), the linear technique of Principal Component Analysis was employed as suggested in Lepš & Šmilauer (2003) (Figure 3-3; step 3b).

PCA ordination with sediment data had the objective of examining the distribution of sample points on the ordination space based on their nutrient content. To address this objective, the scaling focus was on inter-sample distance (scaling type 1), and sediment data scores were divided by the standard deviation so that the variables with large variance would not dominate the ordination. Sediment data were centered (weighted by its variance) and standardized since not all variables had the same measurement unit. Broken-stick model calculations (following Legendre & Legendre, 1998) were used to evaluate if the variability explained by individual axes were non-random, interpretable variations in the sediment data (Lepš & Šmilauer, 2003). Other approaches, such as calculating the threshold values based on the total variability divided by the number of axes, are known to overestimate the number of interpretable ordination axes (Lepš & Šmilauer, 2003).

Macrophyte taxa composition was also analyzed with ordination techniques, and a direct gradient analysis was performed since the objective was to investigate the macrophyte community response in relation to sediment chemistry variables and coefficient of underwater light attenuation (K_d). Only macrophyte samples that matched sediment chemistry (1 and 3 m) and K_d data were utilized on the analysis (Figure 3-4; step 1b). Data from lake 22B were not included in this analysis because macrophyte sampling was not performed due to high moss biomass that was not efficiently sampled by the equipment. Similarly, lake 16B data were not included due to the absence of sediment chemistry data. Hence, the final analysis included data from three undisturbed and three disturbed lakes. In addition, a nominal variable representing physical disturbance, which can be potentially disadvantageous to plant establishment and growth, was included to represent the higher input of sediment at the disturbed sites observed during sampling periods. Sites near the disturbance (*Da*) were assigned a value of 1, while the other sites (*U* and *Do*) were given a value of 0 during analysis.

Macrophyte taxa data were log (x+1) transformed and analyzed by DCA (detrending by segment) to determine if a unimodal (CA, CCA) or linear analysis (PCA, RDA) was most suitable to analyze the data (Figure 3-4; step 2b). As the largest value for the gradient was 5.7 (high > 4), a unimodal technique was chosen (Figure 3-4; step 3b). However, since unimodal techniques are not suitable for application to data containing many empty sample records (records with no taxa present), the linear type of canonical ordination was employed (RDA - Redundancy Analysis) as suggested by Lepš & Šmilauer, 2003 (Figure 3-4; step 4b).

The analysis was scaled on inter-taxa correlation (scaling type 2) with taxa-scores divided by the standard deviation, and centered by taxa. An RDA with forward selection was performed to investigate if all variables were significant and forward manual selection with a Monte Carlo permutation test was performed (199 permutations) to opt for the variables.

After the selection, a RDA with the chosen variables was repeated to test the significance of the first and of all canonical axes together with a Monte Carlo permutation test with unrestricted permutations (199 times) applied under the reduced-model, following ter Braak & Šmilauer, 2002. Also, constrained sample scores from the first axis were extracted and used in a similar RDA analysis to test the significance of the second axis.

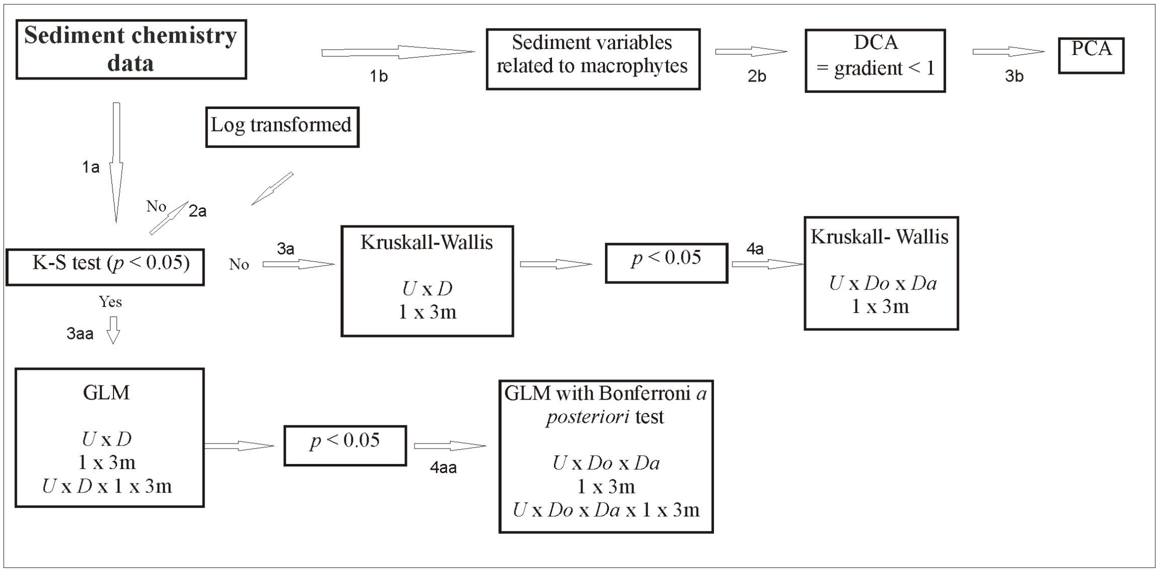

Figure 3-3: Schematic diagram representing the statistical steps followed with analysis of sediment chemistry data (referred in methods section). General linear model (GLM), Kolmogorov- Smirnov normality test (K-S), detrending correspondence analysis (DCA), principal component analysis (PCA), undisturbed (*U)* and disturbed (*D)* lakes, and opposite (*Do*) and adjacent (*Da*) areas to the disturbance in *D* lakes.

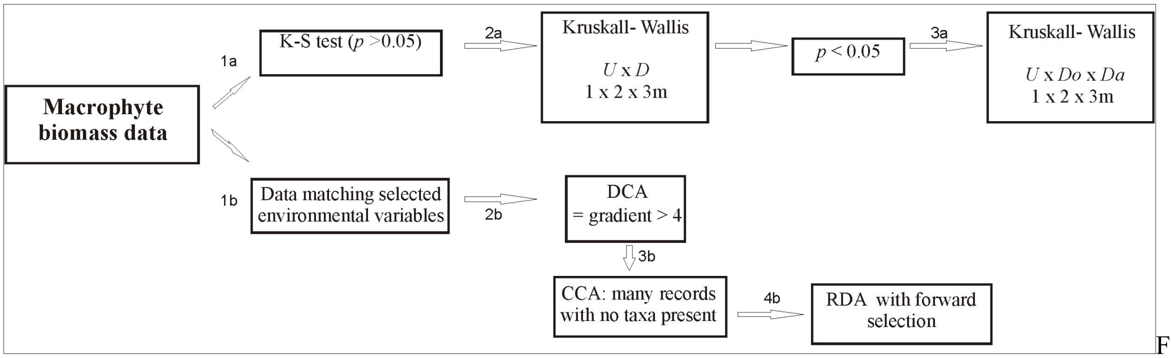

Figure 3-4: Schematic diagram representing the statistical steps followed in the analysis of macrophyte biomass data (referred in methods section). Kolmogorov- Smirnov normality test (K-S), detrending correspondence analysis (DCA), canonical correspondence analysis (CCA), redundancy analysis (RDA), undisturbed (*U)* and disturbed (*D)* lakes, and opposite (*Do*) and adjacent (*Da*) areas to the disturbance in *D* lakes.

3.3 Results

3.3.1 Water column

ANOVA tests for water nutrient data between undisturbed (*U*) and disturbed (*D*) lakes revealed no significant differences ($p > 0.05$) for the following constituents: POC, DP, OP, TP, NH_3N, NO_3NO_2, TDN, PON, and TN. However, pH (mean = 7.6 in *U* vs. 8.19 in *D*) and specific conductivity (mean = 128.6 in *U* vs. 516.7 µS/cm in *D*) were significantly different ($p < 0.05$) (Table 3-3).

Underwater light attenuation (K_d) in the littoral zone was significantly different ($p < 0.05$) between *U* and *D* lakes with higher median values in *U* lakes (1.40 in *U* and 1.02 in *D*). However, between disturbance proximity (*Do* and *Da*) no difference was observed for K_d values ($p > 0.05$) (Table 3-4).

Table 3-3: Descriptive statistics of water-column variables in undisturbed (U) and disturbed (D) lakes: number of samples (N), minimum (Min.) and maximum (Max.) values, mean and standard deviation (S.D). All chemical values in mg/L, specific conductivity in µS/cm, and temperature in ºC. Anova results between U and D lakes: F- statistics and p- values and degrees of freedom (DF). * indicates significant values at $p < 0.05$.

	Undisturbed lakes (U)					Disturbed lakes (D)					Anova U x D	
Variable	N	Min.	Max.	Mean	S.D	N	Min.	Max.	Mean	S.D	F (DF=1)	p
DP	3	0.007	0.016	0.010	0.005	5	0.004	0.008	0.006	0.002	3.16	0.126
NH_3N	3	0.014	0.020	0.016	0.003	5	0.014	0.025	0.018	0.004	0.48	0.515
NO_3NO_2	1	0.002	0.002	0.002	-	3	0.002	0.006	0.004	0.002	0.58	0.527
OP	3	0.000	0.001	0.000	0.000	5	0.000	0.001	0.001	0.000	1.41	0.281
POC	3	0.363	0.682	0.521	0.160	5	0.194	2.710	0.860	1.077	0.27	0.619
PON	3	0.055	0.107	0.081	0.026	5	0.021	0.313	0.111	0.129	0.15	0.710
TN	3	0.446	0.655	0.535	0.108	4	0.305	0.537	0.419	0.096	2.28	0.191
TP	3	0.014	0.037	0.024	0.012	5	0.007	0.027	0.017	0.009	0.96	0.365
TDN	3	0.424	0.530	0.462	0.059	5	0.292	0.408	0.371	0.049	5.55	0.057
pH	3	7.501	7.744	7.600	0.127	5	7.947	8.355	8.197	0.160	29.79	0.002*
Temperature	3	9.901	10.620	10.167	0.394	5	8.457	10.823	9.882	0.889	0.26	0.626
Specific conductivity	3	114.50	135.75	128.58	12.2	3	308	870	517	247	7.07	0.045*

Table 3-4: Summary of light attenuation coefficients (K_d) at the littoral zone of undisturbed (U) and disturbed (D) lakes. Number of samples (N), minimum (Min.) and maximum (Max.) values, median, and first and third quartiles (Q_1, Q_3). Kruskal-Wallis test results between K_d in undisturbed (U) and disturbed (D) lakes, and opposite (Do) and adjacent areas (Da) to the disturbance in D lakes. H-statistics, p- values, and DF (degrees of freedom) displayed. * indicates significant at $p < 0.05$.

		N	Min.	Max.	Median	Q_1	Q_3
U		20	0.87	2.14	1.40	1.23	1.87
D		47	0.49	1.87	1.02	0.89	1.23
	Do	21	0.64	1.87	1.09	0.94	1.26
	Da	26	0.49	1.77	0.99	0.89	1.22

Comparisons	U x D	U x Do x Da	Do x Da	U x Do	U x Da
p- value	0.000*	0.000*	0.48	0.002*	0.000*
H-statistics (DF)	16.34 (1)	16.77 (2)	0.5(1)	9.96 (1)	14.87 (1)

3.3.2 Sediment

GLM tests revealed significant differences ($p < 0.05$) in only seven sediment variables between undisturbed (*U*) and disturbed (*D*) lakes. Mg and Ca means showed highly significant differences ($p < 0.01$), with higher values in *D* lakes (Ca= 4.85g/kg in *U* vs. 9.44g/kg in *D*, and Mg= 5.74 g/kg in *U* vs. 7.35g/kg in *D*) (Table 3-5).

Organic C and N, As, Ni, and Zn were also significantly different between *U* and *D* lakes ($p < 0.05$). However, the highest mean values for these variables consistently occurred in undisturbed (*U*) lakes. The mean values of each of the variables for *U* and *D* were 7.29% and 4.90% of organic C, 0.61% and 0.34% of organic N, 0.02 and 0.015 g/kg of As, 0.052 and 0.041 g/kg of Ni, and 0.137 and 0.106 g/kg of Zn respectively (Figure 3-3;Table 3-5). Although a significant difference ($p < 0.05$) between 1 m and 3 m depths was observed for most of the sediment variables studied, no interaction between depth and *U*/*D* lakes was observed.

Bonferroni *a posteriori* testing revealed no significant differences ($p > 0.05$) between in-lake disturbance regions (*Da* and *Do*) and between disturbed regions and *U* lake comparisons for As, Ni and Zn. Mg and Ca were not significantly different between *Da* and *Do*, but were significantly different ($p < 0.05$) between these regions and undisturbed lakes. In contrast, organic N content in *Da* (0.24%) was significantly different ($p < 0.05$) from *Do* (0.44%) and highly significantly different ($p < 0.01$) from undisturbed lakes (0.61%). Organic C was only significantly different ($p < 0.05$) between *Da* (3.46%) and *U* (7.29%) lakes (*Do* = 6.21%) (Table 3-6). These indicated that *Do*, a region within the disturbed systems, was similar to a “control” undisturbed lake for the variables organic N and C.

Table 3-5: General linear model (GLM) results from analyses with sediment data from undisturbed (*U*) and disturbed (*D*) lakes, with depth (1 and 3m) as co-variate. F-statistics, *p*- values, and degrees of freedom (in parenthesis) displayed. * indicates significant at $p < 0.05$.

Comparisons	U x D		1m x 3m		U x D x 1m x 3m		higher
	p	F (1)	*p*	F (1)	*p*	F (1)	in:
Variables							
Mg	0.000*	21.97	0.001*	13.7	0.495	0.47	*D*
Ca	0.000*	43.72	0.573	0.32	0.589	0.29	*D*
Org N	0.010*	12.17	0.125	2.43	0.486	0.49	*U*
Org C	0.011*	7.04	0.382	0.78	0.352	0.88	*U*
As	0.016*	6.19	0.004*	9.12	0.074	3.32	*U*
Ni	0.036*	4.61	0.004*	8.92	0.223	1.52	*U*
Zn	0.040*	4.42	0.002*	10.62	0.341	0.92	*U*
Fe	0.084	3.11	0.000*	14.68	0.551	0.36	-
Mo	0.087	3.04	0.000*	13.95	0.149	2.15	-
P	0.116	2.55	0.001*	13.7	0.365	0.83	-
Inorg C	0.076	3.31	0.026*	5.30	0.096	2.89	-
Cd	0.137	2.28	0.036*	4.63	0.305	1.07	-
Rb	0.617	0.25	0.002*	10.20	0.910	0.01	-
Be	0.604	0.27	0.010*	7.10	0.991	0.00	-
Na	0.693	0.16	0.014*	6.85	0.592	0.29	-
U	0.376	0.80	0.045*	4.22	0.909	0.01	-
Ba	0.683	0.17	0.035*	4.68	0.830	0.05	-
Inorg P	0.395	0.73	0.043*	4.30	0.602	0.28	-
Tl	0.807	0.06	0.003*	9.98	0.836	0.04	-
Cr	0.834	0.04	0.004*	9.02	0.966	0.00	-
Cu	0.912	0.01	0.002*	10.7	0.416	0.67	-
V	0.939	0.01	0.002*	10.18	0.947	0.00	-
La	0.818	0.05	0.550	0.36	0.235	1.44	-
Ga	0.967	0.00	0.005*	8.73	0.951	0.00	-
Bi	0.556	0.35	0.038*	4.53	0.403	0.71	-
Li	0.517	0.42	0.004*	8.81	0.896	0.02	-
Sb	0.868	0.03	0.140	2.25	0.314	1.03	-
Pb	0.585	0.30	0.007*	7.94	0.963	0.00	-
K	0.837	0.04	0.002*	10.19	0.953	0.00	-
Al	0.756	0.10	0.003*	9.70	0.987	0.99	-

Table 3-6: General linear model (GLM) results from analyses with sediment data from undisturbed (*U*) lakes, and areas opposite (*Do*) and adjacent (*Da)* to the disturbance in *D* lakes, with depth (1 and 3m) as co-variate. F-statistics, *p*- values, and degrees of freedom (in parenthesis) displayed. * indicates significant at $p < 0.05$.

Comparisons	U x Do x Da		1m x 3m		U x Do x Da x 1m x 3m		Bonferroni simultaneous test
	p	F (2)	*p*	F (1)	*p*	F (2)	*p*
Variables							
Mg	0.000*	12.19	0.000*	19.70	0.141	2.04	*Do* (0.0022) and *Da* (0.0000) ≠ *U*
Ca	0.000*	26	0.503	0.46	0.655	0.43	*Do* (0.0000) and *Da* (0.0000) ≠ *U*
Org N	0.000*	9.91	0.220	1.54	0.542	0.62	*Da* ≠ *U* (0.0002) and *Da* ≠ *Do* (0.0344)
Org C	0.003*	6.51	0.647	0.21	0.452	0.81	*Da* ≠ *U* (0.0025)
As	0.046*	3.28	0.016*	6.22	0.115	2.26	-
Ni	0.053	3.11	0.011*	6.93	0.141	2.03	-
Zn	0.061	2.95	0.004*	9.14	0.252	1.42	-
Fe	0.050*	3.17	0.000*	14.67	0.068	2.84	-
Mo	0.153	1.95	0.001*	11.67	0.053	3.12	-
P	0.150	1.97	0.000*	13.95	0.248	1.43	-
Inorg C	0.089	2.56	0.209	1.63	0.037	3.59	-
Cd	0.287	1.28	0.057	3.80	0.582	0.55	-
Rb	0.014*	4.62	0.002*	11.06	0.123	2.19	-
Be	0.049*	3.20	0.009*	7.48	0.150	1.97	-
Na	0.132	2.17	0.061	3.80	0.559	0.59	-
U	0.224	1.54	0.050*	4.03	0.117	2.24	-
Ba	0.572	0.57	0.027*	5.16	0.244	1.45	-
Inorg P	0.061	2.96	0.010*	7.24	0.590	0.53	-
Tl	0.038*	3.49	0.002*	10.39	0.135	2.09	-
Cr	0.034*	3.61	0.003*	9.89	0.135	2.09	-
Cu	0.415	0.90	0.003*	9.59	0.139	2.05	-
V	0.042*	3.39	0.001*	11.36	0.119	2.22	-
La	0.962	0.04	0.312	1.04	0.376	1.00	-
Ga	0.031*	3.72	0.003*	9.60	0.145	2.01	-
Bi	0.053*	3.11	0.018*	5.94	0.116	2.25	-
Li	0.044*	3.32	0.003*	9.87	0.090	2.52	-
Sb	0.699	0.36	0.191	1.76	0.609	0.50	-
Pb	0.137	2.07	0.006*	8.31	0.121	2.20	-
K	0.049*	3.19	0.001*	11.32	0.122	2.20	-
Al	0.023*	4.05	0.002*	10.68	0.159	1.91	-

Kruskal-Wallis tests on Mn, Co, Sr, and ignition loss showed a significant difference ($p < 0.05$) between *U* and *D* lakes, and no difference between depths (Table 3-7). Median Mn concentrations varied from 0.83g/kg in *U* versus 0.42g/kg in *D* lakes; Co ranged from 0.015g/kg on *U* to 0.013g/kg on *D*; ignition loss varied from 13.26% on *U* to 9.67% on *D*; and Sr, the only of these variables with higher values in *D*, varied from 0.06g/kg on *U* versus 0.073g/kg on *D* (Figure 3-5).

Mn, Co and Sr were not significantly different between *Do* and *Da* regions ($p > 0.05$) but were different to the undisturbed lakes. Ignition loss results had a similar pattern as found from the Bonferroni test for organic C. The K-W test revealed that only *Da* was significantly different from *U* ($p < 0.05$). Correlation analysis showed a strong positive association between organic C and ignition loss ($r = 0.947$, $p < 0.01$).

Table 3-7: Kruskal-Wallis test results between sediment variables in undisturbed (*U*) and disturbed (*D*) lakes, and opposite (Do) and adjacent areas (*Da*) to the disturbance in D lakes. H-statistics, *p*- values, and degrees of freedom (in parenthesis) displayed. * indicates significant at $p < 0.05$.

Comparisons	*U* x *D* *p*	H (1)	*U* x *Do* x *Da* *p*	H (2)	*Do* x *Da* *p*	H (1)	*U* x *Do* *p*	H (1)	*U* x *Da* *p*	H (1)	
Variables											
Mn	0.000*	15.00	0.001*	15.01	0.960	0.00	0.001*	10.91	0.001*	12.04	*Do* and *Da* ≠ *U*
Co	0.016*	5.84	0.048*	6.06	0.588	0.29	0.046*	3.99	0.025*	4.99	*Do* and *Da* ≠ *U*
Sr	0.017*	5.68	0.058	5.68	0.946	0.00	0.032*	4.60	0.044*	4.06	*Do* and *Da* ≠ *U*
Ignition loss	0.017*	5.75	0.035	6.72	0.334	0.93	0.101	2.69	0.009*	6.74	*Da* ≠ *U*

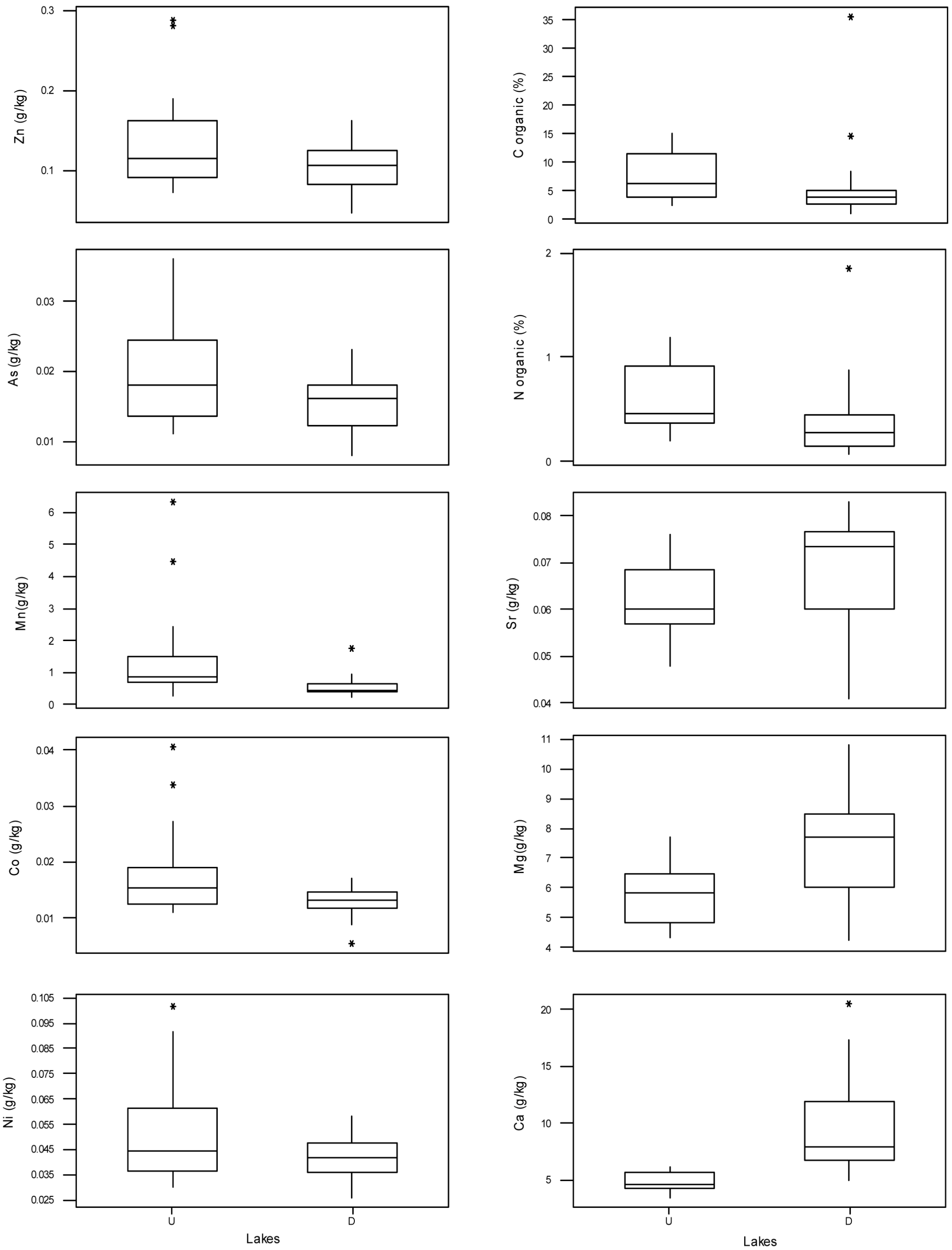

Figure 3-5: Box plots for sediment chemistry variables (Zn, As, Mn, Co, Ni, Sr, Mg, Ca, organic C and N) that were significantly different between undisturbed (*U*) and disturbed (*D*) lakes. Line inside boxes indicates median values, horizontal upper and lower lines indicate Q_1 and Q_3 values, vertical lines indicate upper and lower limit of values, and * indicates outliers.

Ordination analysis:

The first four axes of the PCA had eigenvalues of 0.462, 0.213, 0.109, and 0.048, explaining 83.1% of the total variability in the sediment data. Eigenvalues give a measure of importance of the ordination axis, expressed as the total of variability in the sediment data described by the corresponding axis (Jongman *et al.*, 1995; Lepš & Šmilauer, 2003). Broken–stick model calculations for the analysis with 16 sediment variables and 47 samples produced values of 0.211, 0.148, 0.117, and 0.096 for the first four axes. Based on these results, it was observed that only the first two axes described non-random variation in the data, since these were the only ones that exceeded the values predicted by the null model. The null model gives relative length values for the same number of pieces into which a stick with a unit length would separate when selecting the breaking points randomly (Lepš & Šmilauer, 2003). Thus, the first two axes of the PCA on sediment nutrient data explained 67.5% (eigenvalues of 0.462 and 0.213) of the variability in the sediment data.

As shown in Figure 3-6, there is an apparent separation of sample points from undisturbed lakes (*U*), from areas opposite to the disturbance (*Do*), and areas adjacent to the disturbance (*Da*) on D lakes. Samples from *U* lakes are positioned more closely to samples from opposite areas to the disturbance (*Do*). Samples from the adjacent areas to the disturbance (*Da*) are positioned more distant from samples from *U* lakes. In general, it can be observed that most of the samples located on the positive part of axis 2 are from *U* lakes, while the negative part of this axis is mostly formed by samples from areas opposite and adjacent to the disturbance in *D* lakes. The point located outside the highlighted groups represents data collected from a 1 m sample located at the area opposite to the disturbance

(*Do*) in lake 29B. This sample had the highest value of organic C (35%) from all data collected, contrary to the general pattern of higher organic levels present in *U* lakes.

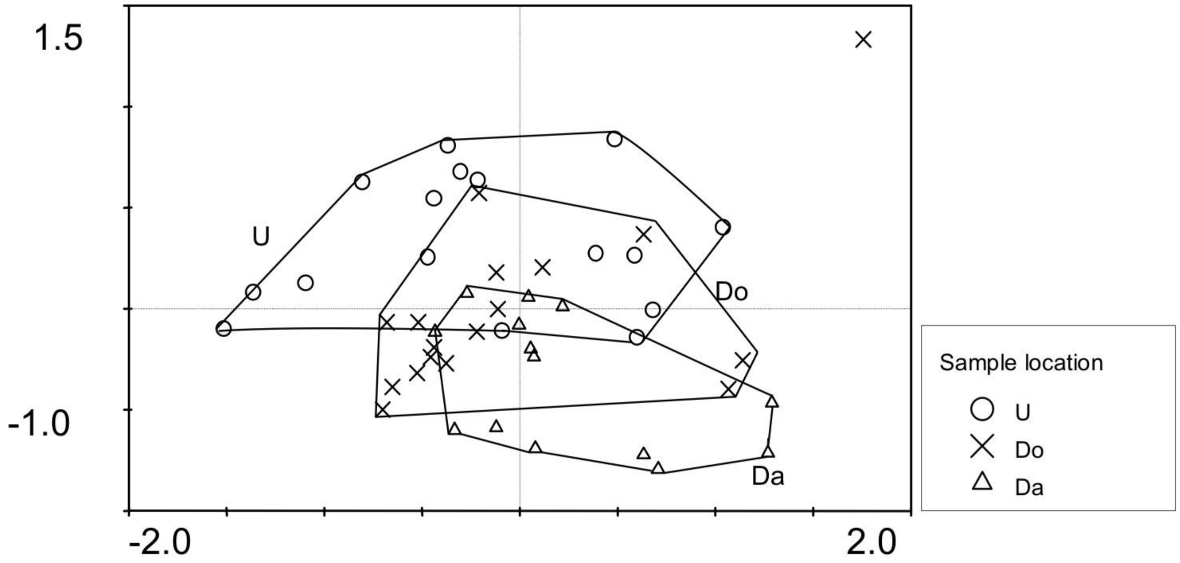

Figure 3-6: Sample scatter plot based on PCA with sediment nutrient data. Undisturbed lakes *(U)*, samples in opposite areas to the disturbance (*Do*) and adjacent to the disturbance (*Da*) in disturbed lakes. Axis 1 located at abscissa, and axis 2 at the ordinate.

The ordination diagram (Figure 3-7, Table 3-8) shows that axis one is dominated by Fe, Cu, Ni, P, Zn, K, and Co, with loadings between -1.39 to -1.25, and inorganic C contributing to the positive part of this axis with a loading of 0.55. Axis 2, seen as the one that mainly divides samples from undisturbed and disturbed lakes, is influenced by organic C and N, ignition loss, Mo and Mn (loadings of 1.93 to 0.89). Ca, inorganic P and Mg contributed to the negative portion of this axis with loadings of – 0.59, -1.25 and -1.28 respectively.

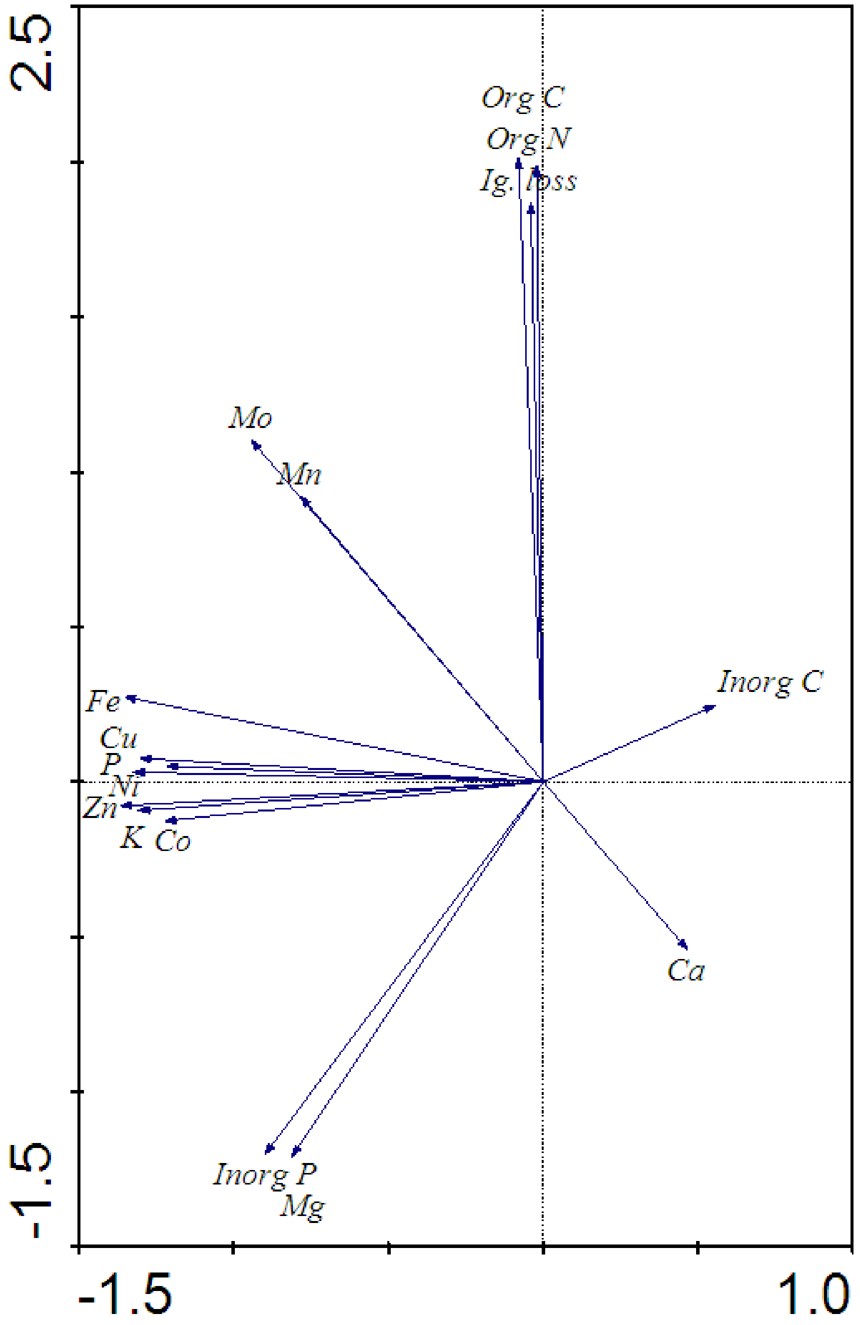

Figure 3-7: PCA distance biplot of sediment nutrient data (axis 1 is abscissa and axis 2 the ordinate).

Table 3-8: PCA ordination results: sediment chemistry variables scores on axes 1 and 2.

Variables	Loadings	
	Axis 1	Axis 2
Zn	-1.389	-0.1715
Fe	-1.3831	0.1777
Ni	-1.3512	-0.0619
Cu	-1.3138	-0.0071
K	-1.3051	-0.163
Co	-1.2616	-0.218
P	-1.2539	-0.0721
Mo	-1.0062	1.0393
Inorg. P	-0.8893	-1.2512
Mn	-0.8434	0.8904
Mg	-0.7725	-1.2844
Org. C	-0.2187	1.9389
Ig loss	-0.1161	1.6929
Org. N	-0.1037	1.9288
Ca	0.4986	-0.5944
Inorg. C	0.5537	0.2627

3.3.3 Macrophytes

Although the median values for total macrophyte biomass were the same at *U* and *D* lakes, the distributions were significantly different ($p < 0.01$) according to the Kruskal-Wallis test results, with higher values for *D* lakes. This can be explained by the observation that macrophytes were found more frequently in *D* lakes (44%) than in *U* lakes (11%). The biomass present in the *Do* region was significantly different from *Da* and *U* lakes ($p < 0.01$), while differences between *U* lakes and *Da* were not significant ($p > 0.05$) since both areas were virtually devoid of macrophytes (Table 3-9, 3-10). No significant difference was observed for macrophyte biomass between depths.

Table 3-9: Macrophyte biomass (g/m^2) summary data from all lakes, *U*, *D*, *Do*, and *Da*. Number of sample points (N), number and percentage of cases where macrophytes were present (N_p), minimum and maximum biomass (Min., Max.), median, and first and third quartiles (Q_1, Q_3).

Lakes/Areas	N	N_p and % presence	Min.	Max.	Median	Q_1	Q_3
All lakes	90	31 (34%)	0	705.50	0.0	0.0	19.21
Undisturbed lakes (*U*)	27	3 (11%)	0	24.27	0.0	0.0	0.00
Disturbed lakes (*D*)	63	28 (44%)	0	705.50	0.0	0.0	55.90
Opposite region (Do)	33	24 (72%)	0	705.50	28.7	0.0	104.10
Adjacent region (Da)	30	4 (13%)	0	76.22	0.0	0.0	0.00

Table 3-10: Kruskal-Wallis test results between macrophyte biomass in undisturbed (*U*) and disturbed (*D*) lakes, and opposite (Do) and adjacent areas (*Da*) to the disturbance in D lakes. H-statistics, *p*- values, and DF (degrees of freedom) displayed. * indicates significant at $p < 0.05$.

Comparisons	*U* x *D*	*U* x *Do* x *Da*	*Do* x *Da*	*U* x *Do*	*U* x *Da*
P - value	0.007*	0.000*	0.000*	0.000*	0.77
H-statistics (DF)	10.1 (1)	36.03 (2)	22.11 (1)	23.24 (1)	0.08 (1)

Figure 3-8 shows that macrophytes were more abundant in disturbed lakes. The highest mean biomass was found for mosses, followed by *Myriophyllum exalbescens* Fernald (Haloragaceae), *Potamogeton pectinatus* L. (Potamogetonaceae), and *Chara* spp (Characeae). *Ranunculus trichophyllus* Chaix (Ranunculaceae), *C. hermaphroditica* L. (Callitrichaceae), *Zannichellia palustris* L. (Zannichelliaceae), *Hippuris vulgaris* L. (Hippuridaceae), *Hippuris vulgaris* L. forma *fluviatilis* (Coss. & Germ.) Glück (Hippuridaceae), and *Potamogeton filiformis* Pers. (Potamogetonaceae), had mean abundances lower than 5g /m^2 (Table 3-11).

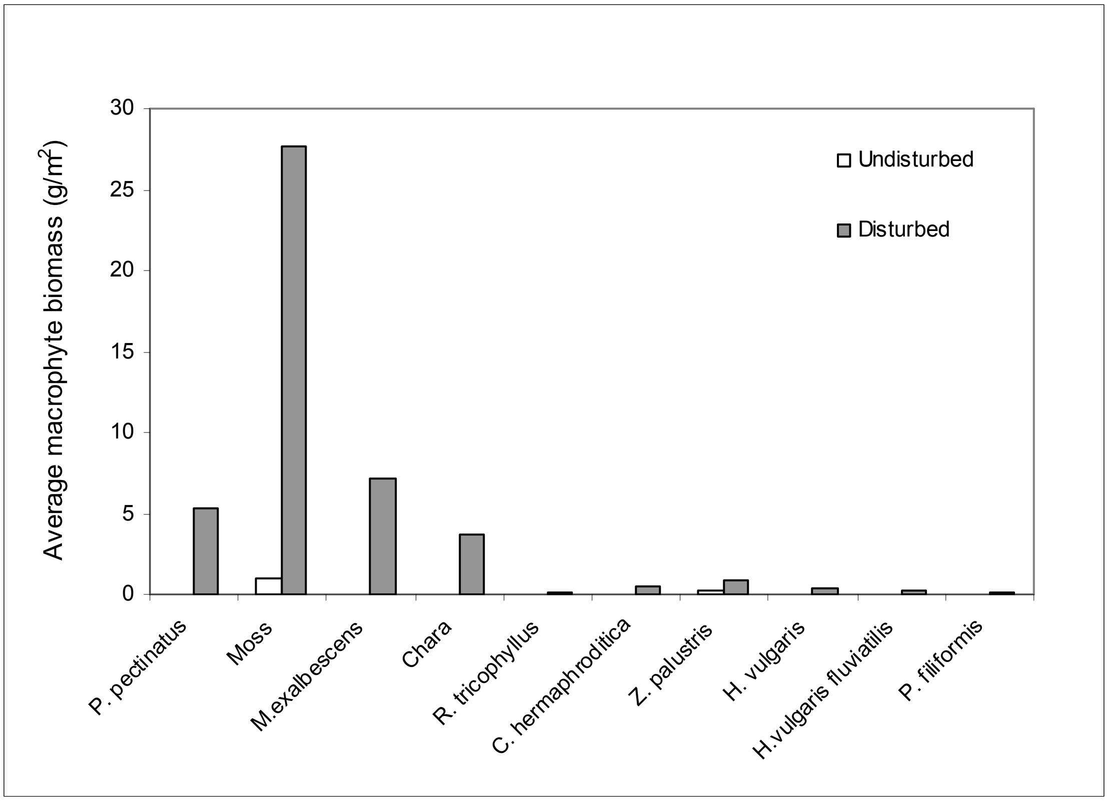

Figure 3-8: Macrophyte community composition in undisturbed (*U*) and disturbed (*D*) lakes.

Table 3-11: Macrophyte average biomass (g/m^2) separated by taxa and location (undisturbed lakes (*U*), opposite (*Do*) and adjacent areas to the disturbance (*Da*) in disturbed lakes). Lake/lake area, number of sampled sites (N), macrophyte taxa, macrophyte biomass (g/m^2), and number of sampled sites with presence of each taxon (N$_p$).

Lake/ lake area	*U*		*Do*		*Da*	
N	27		33		30	
	g/m^2	N$_p$	g/m^2	N$_p$	g/m^2	N$_p$
P. pectinatus	0.00	0	8.96	14	1.19	2
Moss	1.00	2	52.79	11	0.00	0
M. exalbescens	0 .00	0	10.37	9	3.52	4
Chara	0.02	1	6.98	3	0.00	0
R. trichophyllus	0.00	0	0.17	4	0.00	0
C. hermaphroditica	0.00	0	0.81	7	0.04	1
Z. palustris	0.25	1	1.68	1	0.00	0
H. vulgaris	0.02	1	0.74	3	0.02	1
H. vulgaris fluviatilis	0.00	0	0.39	2	0.00	0
P. filiformis	0.00	0	0.15	1	0.00	0

3.3.3.1 Ordination analysis:

Based on the RDA with forward selection, only the variable K_d was significant ($p<0.05$) to explain macrophyte taxa distribution, explaining 12.1% of its variability and having a correlation of 60.4%. Only the first of the four calculated axes is canonical, since only one constrained axis can be formed with one environmental variable. This axis was significant with a $P = 0.040$ (F = 2.3) (Table 3-12).

Table 3-12: Summary results of RDA with K_d versus Macrophyte taxa.

Axes	1	2	3	4	Total variance
Eigenvalues	0.121	0.286	0.257	0.145	1
Taxa-environment correlations	0.604	0.000	0.000	0.000	
Cumulative percentage variance:					
a) of taxa data	12.1	40.7	66.4	80.9	
b) of taxa-environment relation	100	0	0	0	
Sum of all:					
a) eigenvalues					1
b) canonical eigenvalues					0.121

In general, taxon-environment correlation can be inferred from the biplot observing the cosine of the angle between the arrow of taxa and the arrows of environment variables (Jongman *et al.*, 1995). The relationship can be assumed to be positive if the arrows of one determined taxon and environmental variable are pointing in the same direction. Consequently, opposite directions imply a negative correlation (Jongman *et al.*, 1995) (Figure 3-9).

In general, Moss and *R. trichophyllus* were the only taxa that had scores higher for axis 1 (0.52 and – 0.05 respectively), and K_d had a correlation value of 1 with this axis since it was the only environmental variable included. *R. trichophyllus* was related to the first axis on the analysis and is positively correlated to K_d, while Moss showed a negative correlation with K_d (Table 3-13, Figure 3-9).

Table 3-13: Taxon scores of RDA with macrophyte taxa data and environment variables.

Variables	Taxon scores	
	Axis 1	Axis 2
H. vulgaris	-0.1364	-0.3354
Z. palustris	-0.2495	0.2404
C. hermaphroditica	0.0612	-0.5914
M. exalbescens	-0.2006	-0.6674
P. pectinatus	0.028	-0.6979
R. trichophyllus	-0.0482	-0.0217
Chara	0.3584	0.6738
Moss	0.5178	0.255

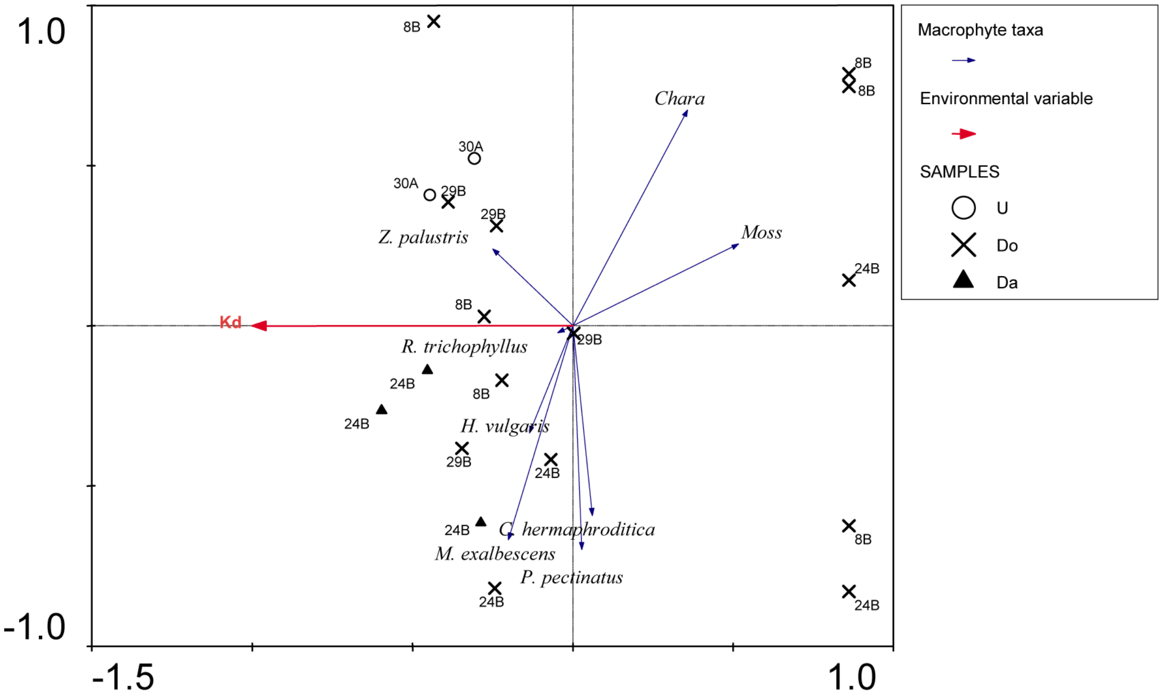

Figure 3-9: Taxon-environment correlation triplot from RDA summarizing differences in macrophyte composition along a littoral underwater coefficient of light attenuation (K_d) gradient. Numbers at the plot represent sample location where macrophytes were encountered: 30A- undisturbed lake, 8B, 24B and 29B - disturbed lakes. Axis 1 located at abscissa, and axis 2 at the ordinate.

3.4 Discussion

3.4.1 Water and Sediment

A variety of factors ranging from in-lake to landscape processes can influence benthic macrophyte communities. Regional geology, catchment size, and climate have a great influence on the way that freshwater bodies are physico-chemically and biologically characterized, and thus one of the main goals of this study was to control for as much as possible the amount of variability related to these factors. It has been previously shown that physico-chemical parameters of lake water were greatly influenced by latitude in surveys around the study area (between 60º37'N and 69º35'N), probably related to differences in bedrock geology and catchment vegetation (Pienitz *et al.*, 1997). Thus, the 8 lakes chosen for more detailed analysis were all located in a ~53 km latitudinal range in areas with similar catchment characteristics, which probably contributed to the lack of differences in water nutrient levels encountered between undisturbed (*U*) and disturbed (*D*) lakes. Hence, all differences found in macrophyte communities are therefore attributed to in-lake processes with influence of permafrost slumping in *D* lakes and not to broader landscape and/or climatic-related heterogeneity.

Conductivity and pH values were significantly higher in disturbed lakes, similar to the pattern observed in comparisons between undisturbed and disturbed lakes in the same geographical area by Kokelj *et al*. (2005). Higher ionic content in disturbed lakes was postulated to be the result of runoff passing through ionic-enriched zones in a permafrostdegraded catchment, while runoff in undisturbed lakes was derived from runoff passing through nutrient-poor organic soils underlain by permafrost.

The different light environment in the littoral zone of *D* lakes contradicts what would be expected in a scenario of physical disturbance of a lake shoreline with input of landscape material into the lake water. Littoral underwater light attenuation (higher in *U* lakes) was in accordance with findings from Kokelj *et al.* (2005), where undisturbed lakes had higher water colour and DOC (dissolved organic carbon) than disturbed ones, which translates into higher light attenuation. This difference could be the result of adsorption of organic compounds to more highly exposed mineral soils in disturbed catchment of *D* lakes, while coloured runoff in *U* lakes would be a result of water flux through the shallow organic soils in undisturbed catchments (Carey, 2003; Kokelj *et al.*, 2005; Thompson *et al.*, 2008). Also, higher ionic concentrations supplied to the lakes from the enriched slump runoff as shown in Kokelj *et al.* (2005) could be adsorbing to organic compounds in the water column, causing increased precipitates and clearing of the water column. For example, calcite crystals can form aggregates that play a role in the removal of nutrients and organic matter from the water column and subsequent sedimentation (Stabel, 1986; Kalff, 2001).

At the sediment interface, undisturbed lakes had a higher content of organic nitrogen and carbon, arsenic, nickel, zinc, manganese, cobalt, and ignition loss values, while disturbed lakes had higher values of magnesium, calcium, and strontium. Similar results were observed for some variables in the PCA with nutrient data, specifically the delineation of differences in sediment chemistry according to sample location (Figure 3-3). Areas adjacent to the disturbance (*Da*) had a distinct chemistry content (*e.g.* higher Ca and Mg) from undisturbed lakes (*U*) and more similar to the areas opposite to the disturbance (*Do*).

This is likely the consequence of adjacent areas to the disturbance (*Da*) in *D* lakes being subjected to a heavier soil load and related different chemistry coming from the landscape

Mn is higher in undisturbed lake (*U*) sediment probably due to higher input of organic matter from undisturbed catchment, since most of this element and also P, N, Fe are known to be transported to aquatic systems adsorbed to organic and inorganic particles from the catchment (Kalff, 2001). Also, Cd, Zn, and Ni are mainly carried by Mn oxides (and Fe) to surface waters (Yigang, 1999), possibly explaining the higher levels of these elements in *U* lakes. Mn oxyhydroxides (and also Fe) aggregates can remove redox-sensitive trace metals and arsenic from the water column in non-acidic oxygenated waters (Kalff, 2001), which could be related to the higher arsenic levels encountered in *U* lakes sediment.

In *D* lakes, most of the differences in sediment chemistry were likely related to higher inputs of sulphate (SO_4^{-2}), magnesium, and calcium from runoff waters from disturbed slopes as found by Kokelj *et al.* (2005). Mg and Ca in high concentrations in *D* lakes sediment could be the direct resultant of enriched runoff input with the mentioned elements (Kokelj *et al.*, 2005) , not being completely taken up by biota or flushed from lakes. Higher concentrations of Sr in the sediment of *D* lakes could be somehow related to the enriched input of Ca and Mg or with the chemical behaviour of these elements. Sr and Ca have a similar geochemical behaviour, while Sr and Mg are known to be the most abundant minor chemical elements in calcium carbonates (Buchardt & Fritz, 1978; Probst et al., 2000).

In addition to the hypothesized smaller organic material input in *D* lakes, sulphate inputs could be highly correlated with the presence of low organic content in the sediment of *D* lakes. In anoxic environments, Fe oxide (FeOOH) and sulphate reduction takes place until depletion, followed by methane fermentation (Yigang, 1999). Normally, SO_4^{2-}

reduction is a dominant anoxic reduction process in marine sediment, but in freshwater systems with high organic carbon content, O_2 is rapidly consumed in the surface layer and low sulphate concentrations in freshwater lakes limit this process, leading to predominating methane fermentation of organic matter (Berner, 1985; Yigang, 1999). High inputs of SO_4^{2-} in the disturbed lakes could be leading to more degradation of organic matter via the microbial loop, with the utilization of SO_4^{2-} as an electron acceptor during anoxic periods.

Higher sulphate concentrations found in *D* lakes could also affect the release of phosphorus from the sediment and its availability to biota. Through microbial reduction, SO_4^{2-} is transformed to S^{2-} (sulphide) and adsorbs with iron, forming highly insoluble Fe monosulfides (FeS) and pyrite (FeS_2) (Yigang, 1999). This adsorption can remove enough iron from solution, allowing phosphorus to escape the same process (Kalff, 2001) and making it more directly available to the macrophytes.

Sulphate could also be involved in acidification processes in high-latitude lakes. Spring acid pulses have been observed in various arctic and sub-arctic lakes, and are related to the increased input of water with concentrated ions released during snowmelt periods, causing a drastic drop in pH (Forsstrom *et al.,* 2007). It can be caused by a variety of factors, including base-cation dilution that leaves the water more sensitive to acids (most common cause), release of mineral acids stored in the snow pack (sulphates and nitrates), and leaching of natural organic acids from soils in catchments in forested areas and wetlands (Forsstrom *et al.*, 2007). Upon acidification, DOM can increasingly coagulate due to aluminium released from sediment, as well as suffer photo- bleaching and oxidation leading to a more transparent water column (Kalff, 2001). This mechanism could be operating in *D* lakes as a result of high inputs of SO_4^{2-}, being essential for the establishment of macrophyte communities. This supposition needs to be tested with additional data beyond that collected in this study.

3.4.2 Macrophyte Biomass

Macrophyte biomass was higher in lakes with catchments disturbed by retrogressive permafrost thaw slumping. It is postulated that the difference between undisturbed and disturbed lakes is related to higher water transparency and changes in the availability of key nutrients in the sediment. Enriched nutrient runoff from disturbed catchments is postulated to alter nutrient availability in the sediment, making it more favourable for the growth and maintenance of the macrophyte community. Such conditions are likely to produce a structurally more complex benthic habitat due to macrophyte growth, and thus have a positive effect on the development of related benthic invertebrate communities.

Some studies suggest that macrophytes may use the sediment as a primary source of nitrogen, phosphorus, iron, manganese, and other micronutrients necessary for their metabolism (Barko *et al.*, 1991). However, contrary to results from temperate lakes, where macrophytes were correlated to N available at the sediment (Johnson & Ostrofsky 2004), the present study did not find macrophytes dominant in lakes with higher levels of organic N (*i.e.* *U* lakes). This could be a consequence of two possible mechanisms: 1) higher observed levels of organic matter in the sediment of *U* lakes could be interfering with nutrient uptake processes (Barko & Smart 1986) and/or, 2) related to the actual amount of organic nitrogen that is transformed to inorganic forms and available to macrophytes.

Based on the above, it is hypothesized that macrophytes in *D* lakes are more abundant than in *U* lakes for two primary reasons. First, higher levels of organic matter on the sediment of *U* lakes could exert a negative influence on nutrient uptake by macrophytes (Barko *et al.*, 1991). Second, underwater light availability (higher in *D* lakes) combined with changes in sediment nutrient availability due to enriched runoff, could favour macrophyte community development through an increase in potential photosynthetic activity. Despite the fact that *U* lakes had higher levels of certain micronutrients than *D* lakes, macrophyte communities would be limited by light availability and excess of organic matter at the sediment.

Perhaps more important than nutrient availability influencing macrophyte growth on the areas adjacent to the slump (*Da*), differences in littoral zones slopes between areas in disturbed lakes (*Do* and *Da*) might also have been responsible for the virtual absence of macrophytes in this area. Submerged macrophyte biomass is documented to be more related to underwater slope at depths where irradiance is not the primary limiting factor, with greatest density where slope is lower than 5%, and considered unable to grow where the slope is greater than 15-20% (Kalff, 2001). Slope affects sediment physical characteristics through its effect on sediment stability and deposition of fine nutrient-rich material, and it is related to the effect of waves at the littoral zone (Duarte & Kalff, 1986). Wave activity can bury macrophytes, remove plant biomass and prevent establishment of propagules (Riis & Hawes, 2003).

Based on preliminary bathymetric surveys and fieldwork observations, underwater slope near the physical disturbance seemed to be significantly steeper than the opposite areas on the same lake or *U* lakes. Based on the previous observations, it seems plausible that although *D* lakes have higher underwater light availability, slope-angle is also limiting macrophyte growth in the areas adjacent to the disturbance (*Da*). Moreover, depending on the level of ongoing physical disturbance in *Da* areas, it is also possible that macrophytes are being constantly buried by soil and vegetation from the lakeshore slump therefore not having the potential to fully colonize.

3.4.3 Macrophyte community structure

Light availability is a significant factor controlling community structure and biomass in the studied lakes, a pattern already documented for a variety of studies with freshwater macrophytes (*e.g*. Hough & Fornwal, 1988; Duarte & Kalff, 1990; Vestergaard & Sand Jensen, 2000; Squires *et al.*, 2002). In addition to their dependency on light availability, macrophytes can in turn influence water transparency through their effect on, for example, sediment stabilization, decrease of wave activity on sediment, and trapping of particles (Barko *et al.*, 1991; Havens, 2003).

Groups with higher biomass in the studied lakes were mosses, M*yriophyllum exalbescens*, *Potamogeton pectinatus*, and *Chara* spp. All the other taxa had mean biomass values of < 5 g/m^2 and are not discussed herein because of their low occurrences. Mosses were the group with the highest mean biomass, which agrees with the findings of Ramlal *et al.* (1994), who found that 90% of the submerged macrophyte biomass was composed of mosses in a lake in the nearby Tuktoyaktuk Peninsula. Mosses have also been found to be the only group encountered in some arctic lakes (Welch & Kalff, 1974).

Mosses are known to survive in environments with only 0.1-2% of surface irradiance, accumulating in the sediment due to their longevity, low decomposition rate (Sand-Jensen *et al.,* 1999), and presence at great depths (Welch & Kalff, 1974). Such an observation is congruent with the fact that bryophytes are considered stress tolerant, often being the predominant macro-vegetation where other plants are restricted by extreme environmental variables (Winton & Beever, 2004).

Chara was also found to be negatively correlated with light attenuation coefficient, being present only in the most transparent lakes (disturbed). In general, Characeae are known to be indicators of healthy aquatic ecosystems, and light reaching the lake bottom after germination is considered to be of extreme importance for their success (Kufel & Kufel, 2002; Rip *et al.*, 2007). This macrophyte group are known to be associated to waters with high concentration of calcium (Kufel & Kufel, 2002) which could be related to their higher abundance in disturbed lakes that were shown to be enriched in this element (Kokelj *et al*., 2005). Also, Characeae has been related to the resilience of clear-water phase in some shallow lakes (Ibelings *et al.*, 2007) and could be playing a role in the transparency of disturbed lakes.

Ramlal *et al.* (1994) documented the presence of *Potamogeton* spp. and *M. exalbescens* contributing to the macrophyte biomass on a lake near. Both taxa contributed to the greater macrophyte biomass in disturbed lakes and were more related to lower light availability as compared to moss and *Chara*. In general, the growth forms of aquatic plants are related to different capacities to adapt to various underwater light environments (Chambers & Kalff, 1987; Van den Berg *et al.*, 1998). *Potamogeton pectinatus* is one of the species that has the advantage of being able to reach the water surface and change its photosynthetic activity to compete more efficiently with other species in low light environments (Hootsmans, 1996; Van den Berg *et al.*, 1998). Furthermore, this species can out-compete some others through its early time of emergence and its tolerance to anoxic periods (Van den Berg *et al.*, 1998). *M. exalbescens* might have the same benefit to out-compete some other species that grow near the sediment due to its growth form towards the water surface being less dependent of higher water transparency for its success. However, depending on the presence of other species, this ability can be decreased. *P. pectinatus* can affect *M. exalbescens* success in low light environments, because its leaves can grow towards the water surface, consequentially spreading and shading *M. exalbescens* (Moen & Cohen, 1989).

Despite light attenuation being the primary variable correlated with observed community structure patterns in the studied lakes, a variety of other mechanisms could also be involved. For example, submerged macrophytes can be highly successful in acquiring nutrients from the sediment due to the contact of roots with anoxic sediment regions that have higher availability of elements released in a reducing environment (Jackson, 1998; Kalff, 2001). However, the relationship between sediment nutrient content and community structure can be masked by the different niche requirements of each species and by synergic effects with light availability, water chemical content, and inter-specific competition (Chambers & Kalff, 1987). Also, sediment bulk nutrient concentrations gives more of a general idea of chemical availability, while pore water content would give a more direct measure of nutrients readily available to uptake. Both of these values can be altered by changes at the root-sediment interface, where changes in redox potential and pH can alter the flux and availability of nutrients to aquatic plants (Yigang, 1999; Kalff, 2001).

Moreover, certain aquatic plants groups that are rooted can still be dependent on water nutrients. A similar dependence applies to mosses that are not attached to the sediment , as shown in Ramlal *et al.* (1994). *Myriophyllum* spp. were also documented as being flexible in relation to the nutrient source, taking up the nutrients in the path with least resistance (most concentrated source), with the sediment being more important in nutrient-poor waters (Kangasniemi, 1975). Internal recycling of nutrients in the macrophyte banks may also play a role (Carignan & Kalff, 1982; Carpenter & Lodge, 1986).

3.5 Conclusion

A variety of differences were observed between lakes undisturbed and disturbed by thaw slumping, and thus represent possible implications of permafrost thaw on arctic tundra lakes in a warming climate. In general, undisturbed lakes had lower water-column transparency, sediments enriched with organic material (C and N) and selected micronutrients (Zn, As, Mn, Co, Ni), and low biomass of submerged macrophytes. Disturbed lakes presented higher water-column transparency, sediments enriched with Ca, Mg and Sr, and the presence of a developed submerged macrophyte community.

Changes in runoff composition related to retrogressive permafrost thaw slumping with subsequent changes in water (as shown in Kokelj *et al.,* 2005) and sediment chemistry characteristics will likely lead to increased macrophyte production in a warming climate. Ion rich runoff could be playing a major role in lake characteristics through possible effects on light attenuation and on sediment nutrient cycling. This would favour macrophyte colonization and benthic primary production, with subsequent increases in littoral heterogeneity and habitat structure that could also benefit other trophic levels, as well as alter other water quality characteristics.

The expected pattern to be caused by permafrost degradation is an increase in pelagic productivity and decreased transparency associated with nutrient enrichment (Wrona *et al.,* 2005), which would negatively influence submerged macrophyte production due to light limitation. However, disturbed lakes were observed to have high transparency and macrophyte biomass, suggesting the possibility that at earlier stages of degradation, macrophytes could dominate lake production due to the higher transparency of the water column.

At a later stage, increases in the area of shoreline slumping would decrease the quality of littoral zone for the establishment of macrophyte communities due to large inputs of landscape material causing subsequent burial and shading of aquatic plants. Also, taking into consideration the great amount of undecomposed macrophytes (mosses) found in some lakes, an internal loading of nutrients to the water-column could be expected due to higher decomposition rates in warmer temperatures. In this case, enhanced nutrient availability could cause a shift to a more turbid state dominated by pelagic production (Vadeboncoeur *et al.*, 2001, 2003; Scheffer & Carpenter, 2003).

In addition to the thawing of permafrost, other environmental changes, and also the rate and magnitude of these modifications, need to be taken into consideration when projecting the effects of a warmer climate on upland arctic lakes. Permafrost thaw slumping could act synergistically with higher temperatures, higher UV penetration in lakes, and changes in runoff input due to alterations of biogeochemical cycles at landscape level. This would ultimately produce different patterns than the ones observed in this study. The present results demonstrate that thaw slumping can alter significantly the composition and production of macrophyte communities of upland tundra lakes, which can be an indicative of the possible impacts of large scale permafrost thawing. However, additional controlled investigations should be performed to understand the effects of runoff with high ionic content on water transparency, sediment nutrient availability, and resulting macrophyte community assemblages.

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Chapter 4 : Benthic invertebrate communities of upland tundra lakes and their relationship with retrogressive permafrost thaw slumps

Abstract

The benthic environment is believed to be especially sensitive to permafrost-induced ecological change. Permafrost disturbances such as retrogressive thaw slumping can affect lake systems through the input of enriched runoff, soil, and terrestrial vegetation. Such inputs significantly alter the stability and production within littoral zones and further affect benthic secondary production. Five lakes affected and three lakes not affected by retrogressive permafrost thaw slumping were sampled during late summer of 2006 to assess the potential effects of slumping on benthic invertebrates abundance and community structure. Significant differences ($p < 0.05$) between disturbed and undisturbed lakes were found for total invertebrate abundance and differences in community structure were also observed. These differences are possibly related to variations in underwater light attenuation and sediment characteristics between undisturbed and disturbed lakes. The results suggest that retrogressive permafrost thaw slumping has a positive effect on the total abundance of benthic invertebrates. Changes in sediment chemistry, organic matter concentrations, littoral slope, in conjunction with variation in habitat complexity (bare substrate, macrophyte covered substrate and terrestrial vegetation covered substrate) altering food availability (macrophytes, detritus, periphyton and bacterial mats) are suggested to explain the observed differences in community patterns. Changes in underwater habitat complexity and benthic community structure can have further effects on freshwater benthic production and the linkages between benthic and pelagic food webs, altering water quality and upper level production in upland tundra lakes.

Keywords: Tundra lakes; Benthic invertebrates; Macrophytes; Sediment chemistry; Retrogressive permafrost thaw slumping

4.1 Introduction

Benthic invertebrates are an important component of secondary production in lake systems, and are involved in the transfer of energy to upper trophic levels (Stoffels *et al*., 2005). Consumption of a variety of food resources by invertebrates ultimately results in energy transfer from benthic and pelagic habitats to pelagic food webs (Stoffels *et al*., 2005). In addition, macroinvertebrates are considered an index of potential fish productivity in lake systems (Rasmussen, 1988). Macroinvertebrates perform important ecosystem and community functions in lakes, but their effects are typically mediated through the influence of fish on invertebrates (Diehl & Kornijów, 1998). They are an important source of food to fish at different ontogenetic stages, thus having an influence on the structure of fish communities (Diehl & Kornijów, 1998; Kalff, 2001).

Various factors are related to the composition and abundance of zoobenthic communities, including biotic relationships, and spatial and physico-chemical factors that are influenced by the presence of submerged macrophytes (*e.g*. Diehl & Kornijów, 1998; Tolonen *et al.,* 2003; Rennie & Jackson, 2005; McAbendroth *et al*., 2005). The observed effects of submerged macrophytes on zoobenthos often differ with some studies indicating higher invertebrate abundance in areas with macrophytes, while others report the opposite. However, this could be somewhat related to some studies focusing on truly benthic forms (benthic invertebrates) only, while others consider epiphytic plus benthic lifeforms collectively (Ságová-Marecková, 2002; Michaletz *et al.*, 2005).

The relationship between macrophytes and macroinvertebrates has been mainly established for lakes and ponds that contain fish (Diehl & Kornijów, 1998). Rennie & Jackson (2005) found that lakes with fish had increased zoobenthic abundance accompanying increased macrophyte habitat complexity, while lakes without fish did not show the same pattern. Submerged macrophytes improve habitat complexity, thereby enhancing the number of niches and available area for the growth of periphytic algae. This has a positive effect on the amount of food for the invertebrates and subsequently on their abundance when compared to areas without macrophytes (Diehl & Kornijów, 1998; Tolonen *et al*., 2003).

In general, benthic invertebrates feed on particulate organic matter that grows or settles in the sediment such as algae, bacteria and detritus, which all can be altered by the presence of submerged macrophyte beds (Rasmussen, 1988; Beaty *et al*., 2006). Since secondary production is primarily limited by the amount of available food created by the pelagic and benthic primary producers, benthic invertebrate biomass and production have been correlated with variables that are related to trophic status, such as chlorophyll concentration in water, total phosphorus concentration (the main nutrient limiting algae growth in most lakes), and water transparency **(**Rasmussen & Kalff, 1987; Plane & Downing, 1989).

Littoral zone topography, exposure, and inputs of riparian material may also affect patterns of community spatial structure at coarser scales, while composition of substrate, particularly macrophytes and inorganic sediment can be important at finer ones (Stoffels *et al*., 2005). Littoral slope and fetch affect zoobenthos by influencing sediment size and retention of inorganic and organic material (Rasmussen & Kalff, 1987; Stoffels *et al*., 2005). Steep slopes have reduced ability to retain fine nutrient-rich sediments that are more beneficial to zoobenthos, and also affect invertebrates by slumping and side movement of the sediment (Duarte & Kalff, 1986; Rasmussen & Kalff, 1987; Rasmussen, 1988).

Considering that benthic production can be an important part of the overall primary and secondary production in arctic lakes (Sierszen *et al.*, 2003; Rautio & Vincent, 2007), a more comprehensive understanding of the possible effects of global warming on the benthos is needed. The arctic region has been predicted to be especially sensitive to the impacts of global warming and it is forecasted that warming will cause significant thawing of the permafrost that dominate much of the arctic landscape (ACIA, 2005).

Permafrost terrain in non-bedrock areas commonly has an ice rich-zone at the top of the permafrost table that is formed from downward moisture movement from the active layer at the end of summers and upward moisture movement from permafrost during winter. The seasonal leaching from thawed soils and ionic movement resultant from thermal-induced moisture migration contribute to the solute enrichment encountered at the near-surface permafrost (Kokelj & Burn 2003; Kokelj *et al.,* 2005).

Deepening of the active layer in a warmer climate can lead to the release of these solutes from near-surface permafrost increasing nutrient input to freshwater bodies, which in conjunction with a rise in solute rich runoff from the landscape, has been hypothesized to affect primary production (Hobbie *et al.*, 1999; Wrona *et al.*, 2005; Anisimov *et al.*, 2007). Some studies have already documented differences in lake water chemistry, macrophyte communities, and sediment chemistry related to retrogressive permafrost thaw slumps in a number of lakes in the area between Inuvik and Richards Island (N.W.T., Canada) (*e.g.* Kokelj *et al.*, 2005; Mesquita *et al.*, *in prep.*; Thompson *et al.*, *in prep.*), but the role of such landscape-related slumping on the benthic invertebrate communities and its relationship with submerged macrophyte biomass remains unknown. The presence of thaw slumps can be used as a surrogate to help understand the possible impacts of large scale permafrost thawing on aquatic nutrient cycling and community structure and composition of biota in arctic freshwater systems.

The current study investigated whether benthic invertebrate abundance and community composition differed between a subset of lakes undisturbed and disturbed by retrogressive permafrost thaw slumping, and examined whether observed differences were related to the presence of macrophyte communities and related sediment chemistry variables. Sediment nutrient content was included in the analysis as a potential surrogate to epipelic (algae at sediment) and bacterial production, which can be important food sources for invertebrates (Rasmussen, 1988; Beaty *et al.,* 2006). Epipelic algae have been found to utilize nutrients from the sediment (O'Brien *et al*., 1996; Goldsborough *et al*., 2005), while benthic bacterial production is related to the amount of organic content at the sediment (Beaty *et al.*, 2006).

4.2 Lakes Selection and Sampling Methods

A subset of 3 lakes not affected by retrogressive permafrost thaw slump (undisturbed or *U* lakes) and 5 lakes affected (disturbed or *D* lakes) were selected for detailed study between the area of Inuvik and Richards Island (N.W.T), based on lake and catchment characteristics, water quality data (Thompson *et al.*, *in prep.*) and field logistical constraints (Figure 4-1, Table 4-1). Although *D* lakes had mean lake area (La) higher than *U* lakes, these groups are considered comparable due to similar mean values of catchment area: lake area ratio (Ca:La) (Table 4-1).

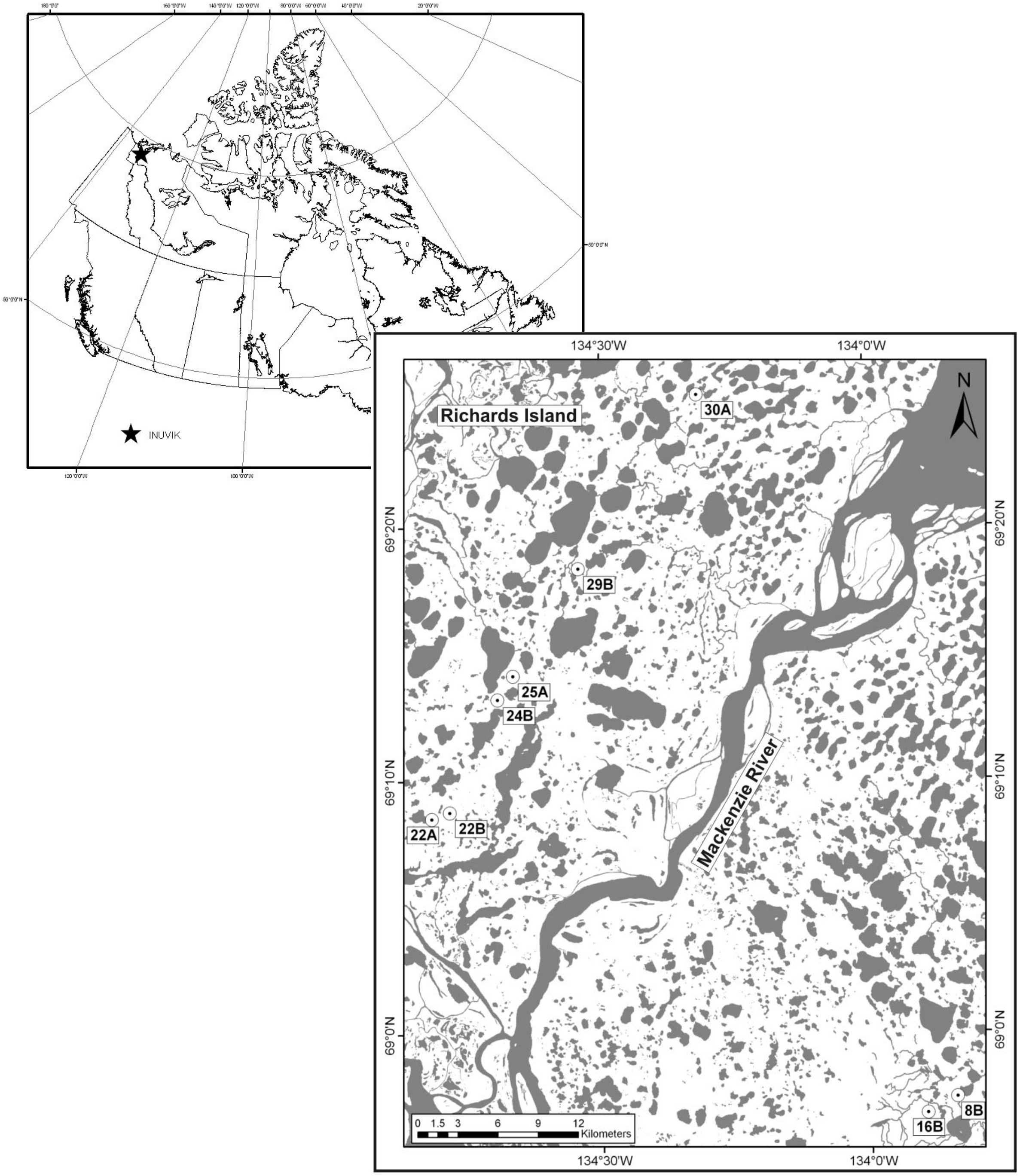

Figure 4-1: Geographic location of studied lakes. Source: Natural Resources Canada/CanVec (www.geogratis.gc.ca)

Table 4-1: Summary of lake attributes for undisturbed (*U*) and disturbed (*D*) lakes. Lake area (La), catchment area: lake area (Ca: La) ratio, catchment area: lake volume (Ca: Lv) ratio, maximum depth (Z_{max}), mean depth (Z_{mean}), number of lakes (N), mean, standard deviation (S.D), minimum and maximum values (Min and Max).

Lakes		La (m^2)	Ca:La	Ca:Lv	Z_{max} (m)	Z_{mean} (m)
U lakes	Mean	40,100	4.78	1.77	7.30	2.88
N= 3	S.D	19,419	0.44	0.14	2.88	0.92
	Min.	18,700	4.28	1.61	4.20	1.92
	Max.	56,600	5.11	1.88	9.90	3.76
D lakes	Mean	76,380	3.99	1.15	9.54	3.48
N= 5	S.D	40,514	1.18	0.63	4.33	0.80
	Min.	35,500	2.41	0.66	5.30	2.44
	Max.	142,900	5.04	2.01	16.80	4.52

Radial transects starting from the shoreline towards the center of the lake were used as the main sampling unit (replicate), and were distributed to encompass the different areas of each lake. Taking into consideration the focus on the littoral zone, sampling points were randomly placed in the vicinity of 1, 2 and 3-metre depths along the transects, yielding a maximum of 9 sample points (3 depths x 3 transects) in undisturbed lakes, and 9 in each of the two areas of disturbed lakes (maximum of 18 sample points in *D* lakes). Disturbed lakes were sampled in one area located at the opposite side (*Do*) of the physical disturbance caused by the slump, and another one in an area adjacent (*Da*) to the slump and thus directly affected by the disturbance (Figure 4-2). However, due to field logistical constraints, in some circumstances not all variables could be sampled at all depths in all lakes. These situations are discussed later when appropriate.

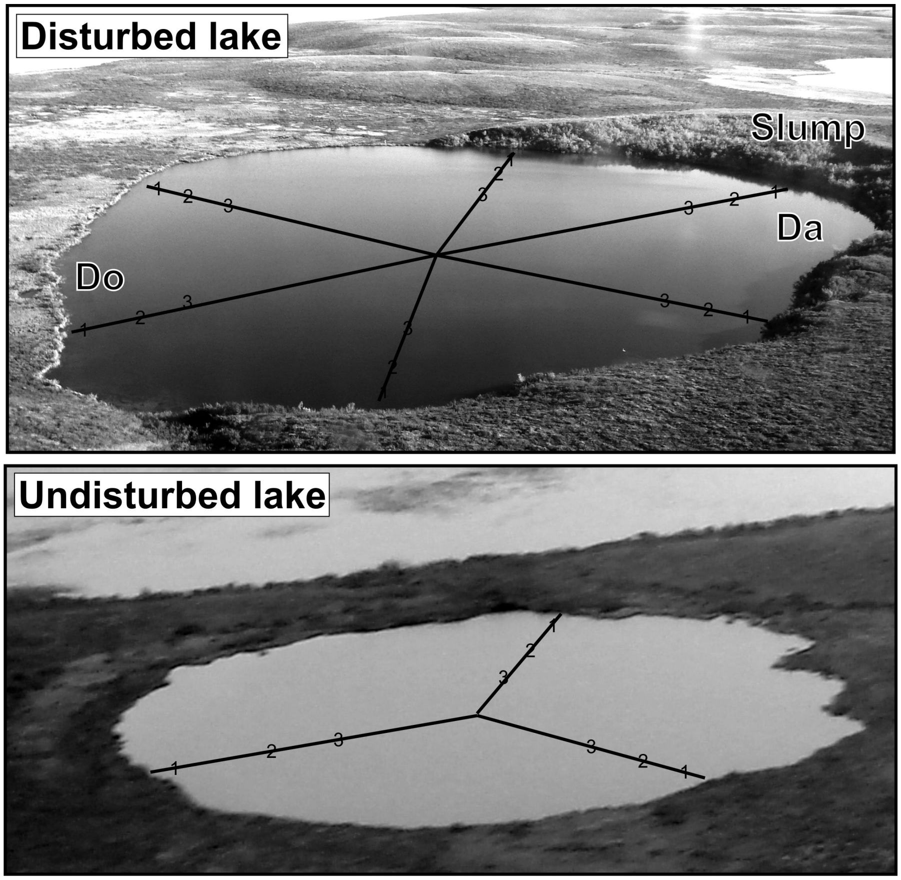

Figure 4-2: Schematic location of transects and sample points (1 to 3 m depth) in undisturbed lakes (*U*), disturbed lakes (*D*), and sample location in *D* lakes (*Do* - opposite to the disturbance, *Da* – adjacent to the disturbance).

Between 26 August 2006 and 5 September 2006, samples of sediment, submerged macrophytes, and benthic invertebrates were collected at the selected lakes. Additional information on macrophyte community structure, water-column and sediment characteristics are provided in Mesquita *et al*. *(in prep.)*. Submerged macrophytes were collected at 1, 2 and 3-metre depths with a telescopic macrophyte sampler (Marshal & Lee, 1994) that covered an area of 0.164 m^2. In the laboratory, the above-ground plant portions were washed and oven-dried to constant weight at 60ºC for dry-weight determination. When present, mosses were separated into live and dead parts, and only the live portion was utilized. Results were extrapolated to represent total dry biomass per m^2.

Sediment samples were collected with a sediment corer at 1 and 3-metre depths (internal diameters of 5cm and 6.6cm; Universal gravity corer – Aquatic Research Instrument; punch core – manufactured at Environment Canada, Instrument Technology Shop, Saskatoon, Canada). Samples from the top 15 cm were transported to the laboratory, homogenized and separated into two fractions. One fraction was frozen, freeze-dried and sent for analysis of nutrients at the Environment Canada National Laboratory for Environmental Testing (NLET), Burlington, Canada. The remaining fraction was oven-dried and burned for calculations of loss of ignition content (as a measure of organic matter content) in accordance with Hakanson & Jansson (1983). Sediment samples for estimation of invertebrate abundance and community structure were collected at 1, 2 and 3-metre depths. Samples from the top 5 cm were washed through a 250 μm sieve, and invertebrates were subsequently sorted, identified, counted and extrapolated to 1 m^2. Identification of invertebrates was performed using Smith (2001) and Thorp & Covich (2001).

4.2.1 Statistical Analyses

Figure 4-3 summarizes the logic-model and steps used to analyze the data. Initially, all the variables were tested for normality using a Kolmogorov-Smirnov (K-S) test ($p < 0.05$) (Figure 4-3; step 1) and, if necessary, $\log_{10}$ transformed to fit the assumptions of parametric testing. General Linear Model (GLM) regressions were performed to test for differences in invertebrate abundance (total and by taxa) between undisturbed (*U*) and disturbed (*D*) lakes, with depth as covariate (Figure 4-3; steps 2a, 2b). In cases where a significant difference between *U* and *D* lakes was found ($p < 0.05$), a second GLM with “a Bonferroni” simultaneous test between *U*, *Do* (opposite to disturbance), *Da* (adjacent to disturbance), and depth was performed (Figure 4-3; step 3a). These analyses were used to ascertain whether the differences were related to in-lake processes (*Do* vs. *Da*) versus between-lake (*U* vs. *Da*, *U* vs. *Do*) processes and physical proximity to the disturbance. All analyses were performed with MINITAB 13.1 (Minitab Inc., 2000).

The taxa that presented a significant difference ($p < 0.05$) between the previous analyses were log (x +1) transformed and analyzed by DCA (Detrended Correspondence Analysis) by segment, to determine if a unimodal (CA – canonical analysis) or linear ordination analysis (PCA – principal component analysis) was most suitable (Figure 4-3; step 3b). Detrending by segment assesses the heterogeneity in the “taxa data” through evaluation of the length of the community composition gradient (Lepš & Šmilauer, 2003). Since preliminary analysis found the largest value for the gradient < 2 (Figure 4-3; step 4b), the linear type of ordination (PCA) was employed in subsequent analysis (Figure 4-3; step 5b) (Lepš & Šmilauer, 2003). Only the sampled points that had data for invertebrate, sediment chemistry (samples obtained at 1 and 3 m), and macrophyte biomass data were utilized during the PCA.

PCA ordination of invertebrate taxa data had the objective of examining the distribution of sample points based on the most predominant taxon encountered in the studied lakes. Invertebrate abundance per taxa was added as “taxon data”. The scaling focus was on inter-sample correlation (scaling type 1), and taxon scores were chosen to be normalized by standard deviation so the variables with large variance would not dominate the diagram (ter Braak & Šmilauer, 2002). Macrophyte total biomass and sediment nutrient variables that were hypothesized as important for the distribution of the invertebrate community (organic nitrogen and carbon, ignition loss, and calcium) were included as “environment variables” (log (x+1)) to compare their direction with the ordination axes produced by the unconstrained ordination of invertebrate data. Macrophyte and sediment data had no influence on eigenvalue calculation, given that environment variables are added post-hoc on the ordination space in indirect gradient analysis (ter Braak & Šmilauer, 2002). In general, the taxon- environment correlations can be inferred from the biplot observing the cosine of the angle between the arrow of taxon and the arrows of environment variables. The relationship can be assumed to be positive (negative) if the arrows of one determined taxon and environmental variable are pointing in the same (opposite) direction (Jongman *et al*., 1995).

Broken-stick model calculations (following Legendre & Legendre, 1998) were used to evaluate if the variability explained by individual axes were non-random, interpretable variations in “taxon data” (Lepš & Šmilauer, 2003). The null model for this calculation gives relative length values for the same number of pieces into which a stick with a unit length would separate when selecting the breaking points randomly (Lepš & Šmilauer, 2003), and should be compared with the eigenvalues from the PCA. Axes with eigenvalues higher than the values predicted by the null model are considered interpretable non-random variation in the data (Lepš & Šmilauer, 2003). Other approaches, such as calculating the threshold values based on the total variability divided by the number of axes, are known to overestimate the number of interpretable ordination axes (Lepš & Šmilauer, 2003) and therefore are not used here.

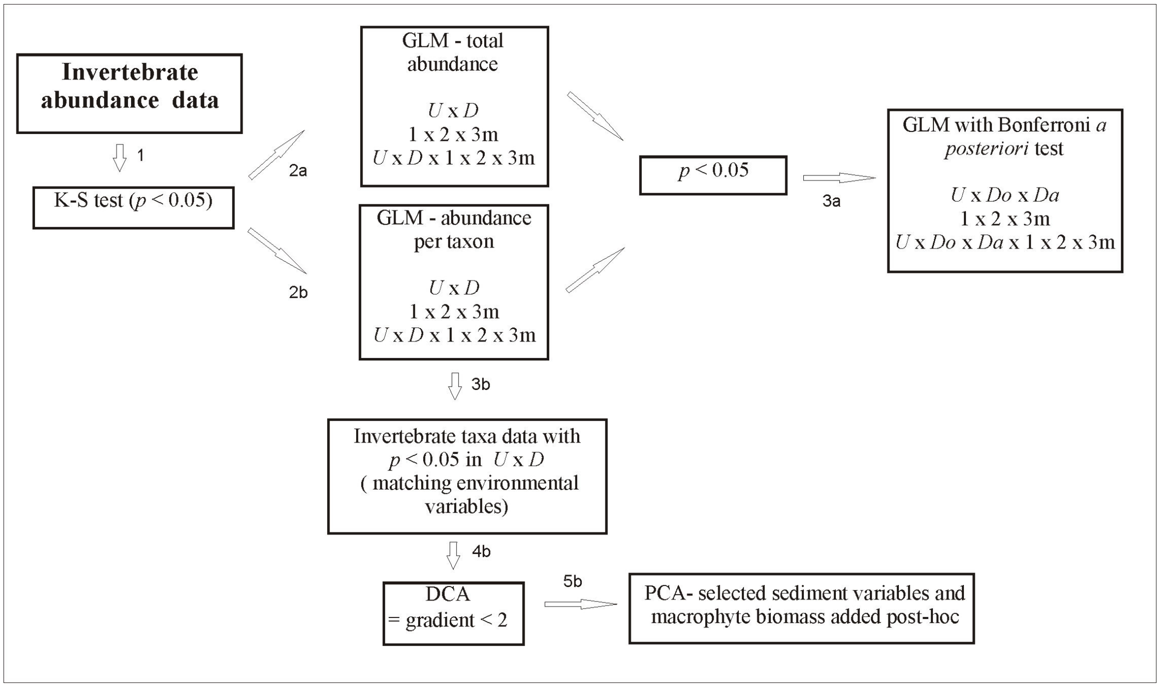

Figure 4-3: Schematic diagram representing the statistical steps followed with invertebrate abundance data. General linear model (GLM), Kolmogorov- Smirnov normality test (K-S), detrending correspondence analysis (DCA), principal component analysis (PCA), undisturbed (*U)* and disturbed (*D)* lakes, and opposite (*Do*) and adjacent (*Da*) areas to the disturbance in *D* lakes.

4.3 Results

Overall invertebrate abundance between undisturbed (*U*) and disturbed (*D*) lakes were found to be significantly different ($p < 0.01$), with higher mean values in *D* lakes (28,630 individuals (ind.) / m^2 in *D* versus 13,232 ind. /m^2 in *U* lakes). Differences between opposite (*Do*) and adjacent (*Da*) areas to the disturbance in D lakes were also significant, with mean values in *Da* (35,631 ind. /m^2) being significantly higher than the mean in *U* lakes, and than *Do* (22,247 ind. /m^2) ($p < 0.01$) (Table 4-2, 4-3). Interaction between *U*, *D*/*Do*/*Da*, and depth was significant ($p < 0.05$), indicating a covariation between these two variables (Table 4-3).

Table 4-2: Invertebrates abundance (ind. / m^2) summary table for undisturbed (*U)* and disturbed (*D)* lakes, and opposite (*Do*) and adjacent (*Da*) areas to the disturbance in *D* lakes. Number of samples (N), minimum and maximum abundance (Min. and Max.), mean and standard deviation (S.D).

Lake/ lake area		N	Min.	Max.	Mean	S.D.
Lake *U*		26	3,215	39,460	13,232	8,786
Lake *D*		68	2,037	119,549	28,630	24,482
	Do	35	2,037	97,334	22,247	22,818
	Da	32	4,584	119,549	35,631	25,055

Table 4-3: General linear model (GLM) results from analyses with invertebrate total abundance data in undisturbed (*U*) and disturbed (*D*) lakes, and opposite (Do) and adjacent areas (*Da*) to the disturbance in D lakes with depth as co-variate. F-statistics, *p*- values, and DF (degrees of freedom) displayed. * indicates significant at $p < 0.05$.

Comparisons	*U* x *D*	1m x 2m x 3m	*U* x *D* x 1m x 2m x 3m
p- value	0.003*	0.150	0.019*
F-statistics (DF)	9.07 (1)	1.94 (2)	4.13 (2)

Comparisons	*U* x *Do* x *Da*	1m x 2m x 3m	*U* x *Do* x *Da* x 1m x 2m x 3m
p- value	0.000*	0.496	0.015*
F-statistics (DF)	12.08 (2)	0.71 (2)	3.26 (4)

The taxa collected in samples were **Ostracoda** (order Podocopida), Arachnida (suborder **Hydracarina**), **Gastropoda** (families Valvatidae and Lymnaeidae), Branchiopoda (order **Cladocera** (mostly Chydoridae)), Maxillopoda (sub-class **Copepoda** (mostly Harpacticoida)), Insecta (order Diptera (family **Chironomidae**) and few Trichoptera), **Bivalvia** (family Sphaeriidae and other), Malacostraca (genera ***Gammarus***), Clitellata (mostly sub-class **Oligochaeta** and few Hirudinea), and the phylum **Nematoda**. These taxa represent the major groups found in the studied lakes and this level of categorization is deemed appropriate to assess food web - geochemistry relationships in these systems.

Ostracoda had the highest mean abundance (21,633 ind. /m^2 in *Da)* when comparing abundance per taxa data in all lakes, and also when analyzing only areas inside *D* lakes (Figure 4-3). This group was followed by Nematoda (3,303 ind. /m^2), Oligochaeta (2,684 ind/m^2), and Chironomidae (2,621 ind. /m^2), all being the most numerically predominant groups in *D* lakes. In *U* lakes, Chironomidae was the numerically predominant group (4,340 ind. /m^2), followed by Ostracoda (3,832 ind. /m^2), and Oligochaeta (2,019 ind. /m^2) (Figure 4-4, Table 4-4). No significant differences were found between lake types in all of the remaining taxa given their low mean abundance values, and they were therefore not considered in further analyses (Figure 4-4).

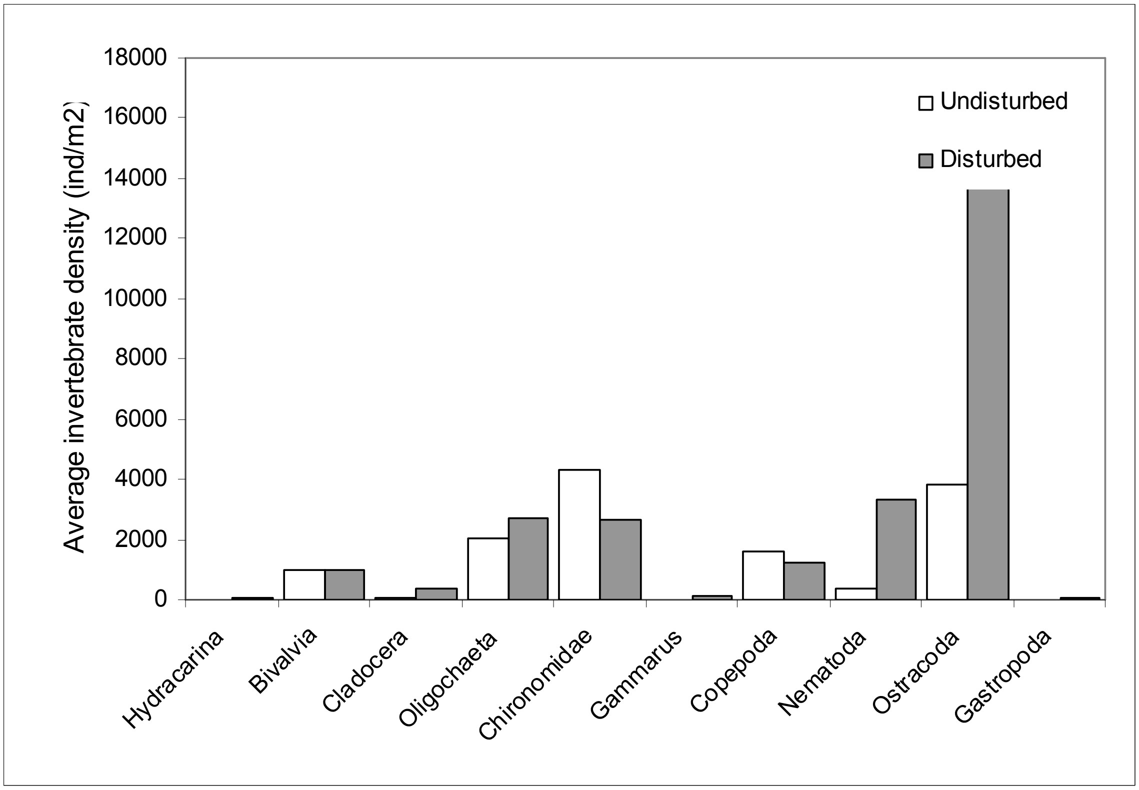

Figure 4-4: Average invertebrate abundance in undisturbed (*U*) and disturbed (*D*) lakes.

Table 4-4: Summary table of invertebrate abundance per taxa (ind. / m^2) for undisturbed (*U)* and disturbed (*D)* lakes, and areas opposite (*Do*) and adjacent (*Da*) to the disturbance in *D* lakes. Number of samples (N), minimum and maximum abundance (Min. and Max.), mean and standard deviation (S.D).

Taxon	Lake	N	Mean	S.D	Min.	Max.	Area in *D*	N	Mean	S.D	Min.	Max.
Oligochaeta	*U*	26	2,019	1,868	0	6,112						
	D	68	2,684	3,074	0	15,281	*Do*	36	1,959	1,963	0	7,641
							Da	32	3,499	3,845	0	15,281
Chironomidae	*U*	*26*	*4,340*	*4,364*	*0*	*20,461*						
	D	68	2,621	3,273	0	14,262	*Do*	36	1,824	1,706	0	6,138
							Da	32	3,517	4,277	0	14,262
Nematoda	*U*	26	350	725	0	3,566						
	D	*68*	*3,303*	*7,213*	*0*	*40,337*	*Do*	36	3,642	7,901	0	40,337
							Da	32	2,921	6,455	0	33,109
Ostracoda	*U*	26	3,832	2,975	0	11,716						
	D	*68*	*17,131*	*18,761*	*0*	*97,334*	*Do*	36	13,129	14,510	0	63,428
							Da	32	21,633	21,989	1019	97,334

Comparisons of invertebrate abundance per taxa between *U* and *D* lakes found that only Chironomidae abundance in *U* lakes was significantly higher than in *D* lakes ($p < 0.05$), while Ostracoda and Nematoda abundance were significantly higher in *D* lakes ($p < 0.05$) (Table 4-5). Nematoda had mean values 10 times higher in *D* lakes compared to *U* lakes, while Ostracoda had values 7 times higher in *D* lakes (Table 4-4). While Oligochaeta total mean abundance was not significantly different between *U* and *D* lakes (Table 4-5), mean abundance values of Oligochaeta and Chironomidae were found to be significantly affected by lake depth, but had no significant interaction with lake type (*U* vs. *D* lakes).

Table 4-5: General linear model (GLM) results from analyses of invertebrate separated by taxa data between undisturbed (*U*) and disturbed (*D*) lakes, and opposite (Do) and adjacent areas (*Da*) to the disturbance in *D* lakes, and depth. F-statistics, *p*- values, and degrees of freedom (in parenthesis) displayed. * indicates significant at $p < 0.05$.

Comparisons	*U* x *D*		1m x 2m x 3m		*U* x *Do* x *Da*		1m x 2m x 3m	
	p	F(1)	*p*	F(2)	*p*	F(2)	*p*	F(2)
Invertebrate taxa								
Oligochaeta	0.416	0.67	0.012*	4.61	-	-	-	-
Chironomidae	0.017*	5.95	0.012*	4.68	0.012*	4.66	0.026*	3.83
Nematoda	0.048*	4.01	0.944	0.06	0.119	2.18	0.897	0.11
Ostracoda	0.000*	15.29	0.486	0.73	0.000*	12.27	0.086	2.52

For the groups that showed significant differences between *U* and *D* lakes, Chironomidae and Ostracoda were the only taxa that were significantly different ($p < 0.05$) between *U*, *Do*, and *Da* (Table 4-5). Chironomidae in *Do* (1,706 ind. /m^2) had significantly lower abundance mean values than *U* lakes (4,340 ind. /m^2) and *Da (*4,277 ind/m^2), while Ostracoda in *Da* (21,633 ind. /m^2) had significant higher values than *Do* (13,129 ind. /m^2) and *U* lakes (3,832 ind. /m^2) (Figure 4-5).

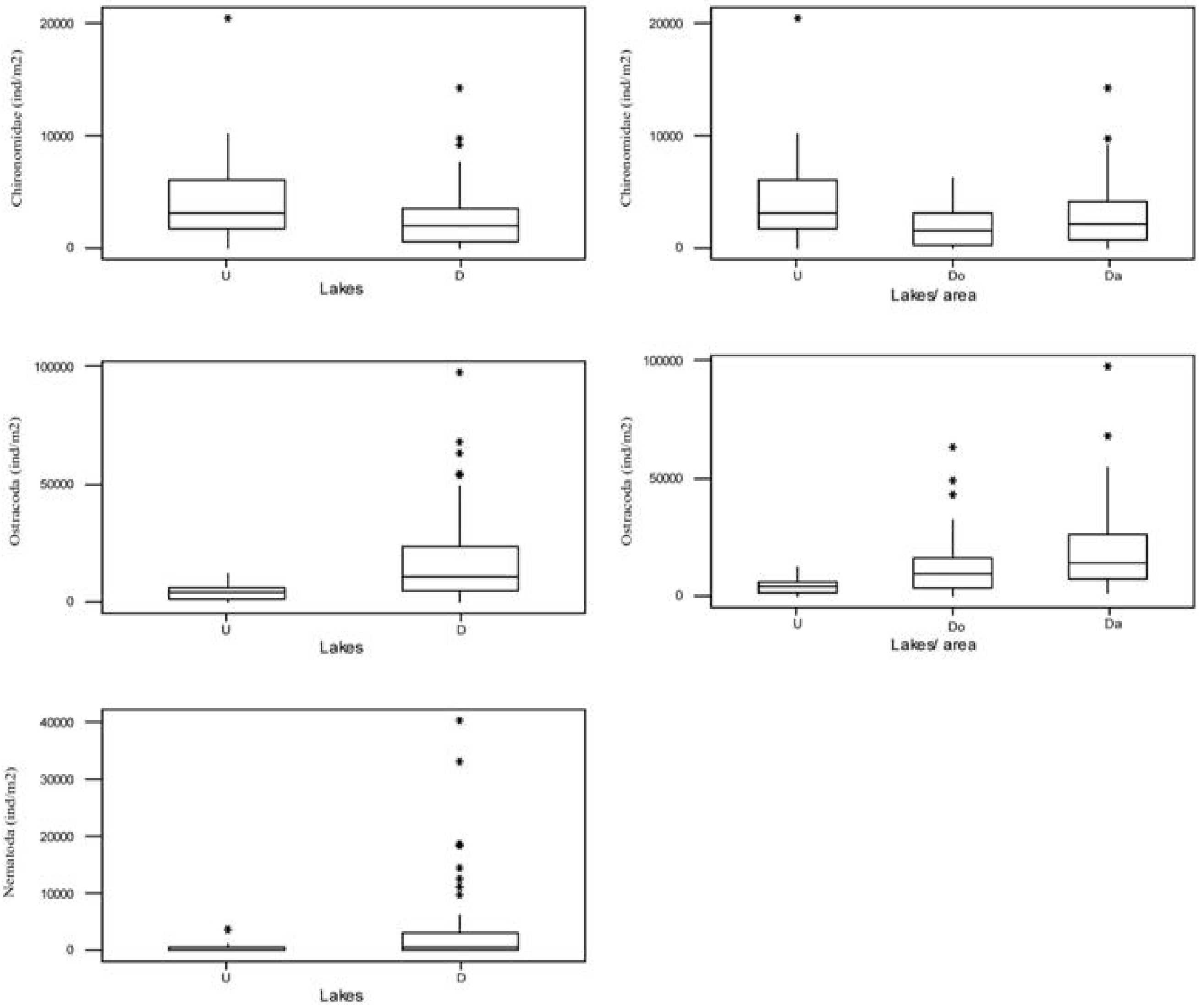

Figure 4-5: Box plot for invertebrate taxa that were significantly different between undisturbed (*U)* and disturbed (*D)* lakes, and between opposite (*Do*) and adjacent (*Da*) areas to the disturbance in *D* lakes. Line inside boxes indicates median values, horizontal upper and lower lines indicate Q_1 and Q_3 values, vertical lines indicate upper and lower limit of values, and * indicates outliers.

4.3.1 Ordination analysis

PCA analysis was performed on the taxa that displayed significant differences in mean abundance patterns between disturbed (*D*) and undisturbed (*U*) lakes. The PCA with Ostracoda, Nematoda, and Chironomidae produced eigenvalues of 0.631, 0.321, 0.047, which explains 100% of the variability in the invertebrate data. Eigenvalues give a measure of importance of the ordination axis, expressed as the total of variability in the "taxonomic data" explained by the corresponding axis (Jongman *et al.*, 1995; Lepš & Šmilauer, 2003). If the selected sediment chemistry variables (organic C and N, ignition loss, inorganic C and Ca) and macrophyte biomass data were used in a direct gradient analysis (*e.g.* Redundancy analysis) to explain the variability of invertebrate data, it would be able to explain only up to 18.8% (sum of all canonical eigenvalues) (Table 4-6). These sediment variables were selected for representing a pool of organic material (detritus, algae, bacteria) that can be utilized as food by the three most abundant invertebrate taxa. Calcium was included to represent a possible influence of this element on shell formation of Ostracoda as discussed later on this chapter.

Table 4-6: Summary results of PCA with invertebrate taxa.

Axes	1	2	3	4	Total variance
Eigenvalues	0.631	0.321	0.047	0.000	1
Taxon-environment correlations	0.421	0.445	0.520	0.000	
Cumulative percentage variance:					
a) of taxon data	63.1	95.3	100.0	0.0	
b) of taxon-environment relation	59.4	93.2	100.0	88.8	
Sum of all:					
a) eigenvalues					1
b) canonical eigenvalues					0.188

Broken–stick model calculations for this analysis with 3 invertebrate taxa and 47 samples produced eigenvalues of 0.611, 0.277, and 0.111 for the first three axes. Comparing these values with the eigenvalues obtained from the PCA, the first two axes describe non-random variation in the data, since their respective values exceeded the values predicted in the null model (Lepš & Šmilauer, 2003).

The first and the second axis of the PCA explained 95.2% (eigenvalues of 0.631 and 0.321 respectively) of the variability in the invertebrate data. The PCA biplot (Figure 4-6) shows that there is a grouping of samples distributed on the negative part of axis 2 (ordinate). Samples from undisturbed lakes (*U*) and adjacent areas to the disturbance (*Da*) are mainly located at the negative side (bottom) of axis 2. *U* lakes had 11 sample points located at the negative side of axis 2 and only 3 points at the positive side, while *Da* had 11 at the negative and 4 at the positive side. *Do* sample points were almost equally distributed between the positive and the negative sides of axis 2 (8 at the top, 9 at the bottom). Another observed pattern was that samples from *Da* and *Do* areas are mainly concentrated at the right side of the diagram (positive part of axis 1). *Da* had 10 samples on the positive side of axis 1 compared to 5 samples at the negative side, while *Do* had 10 samples on the positive side and 7 at the negative. *U* samples were equally distributed between positive and negative sides of axis 1 (7 samples in each side). Such patterns can somehow be explained by linkages to dominant environmental variables as discussed next.

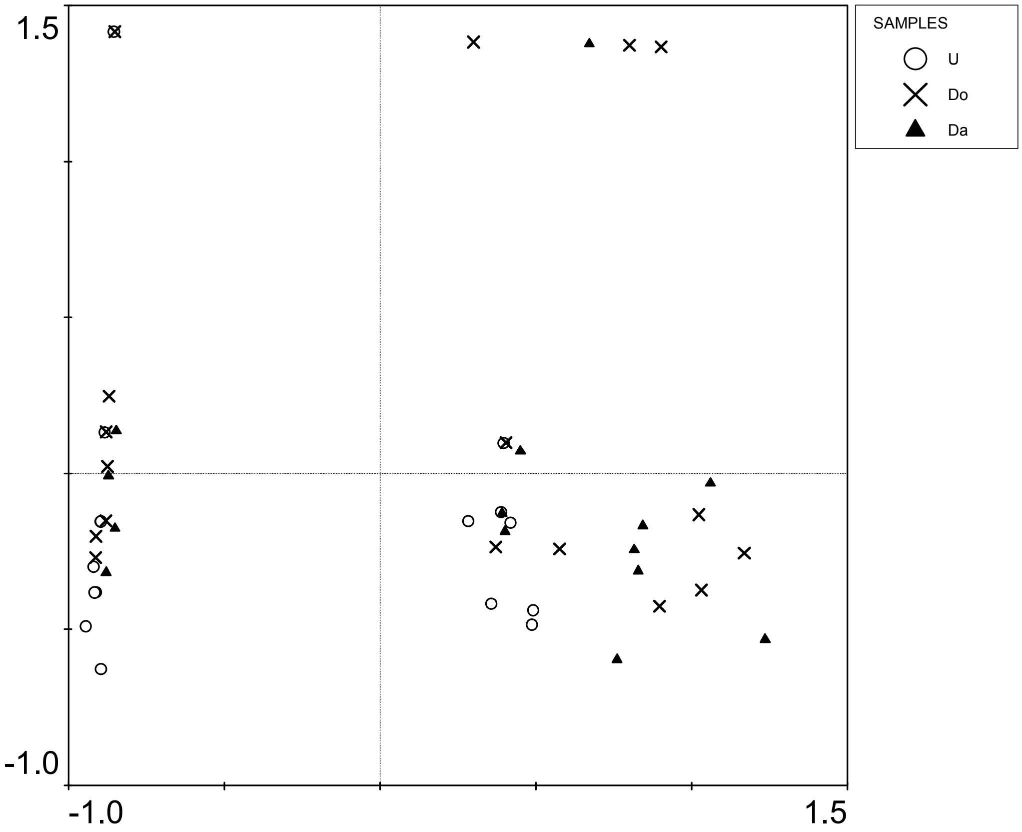

Figure 4-6: Sample scatter plot from results of PCA with invertebrate taxa. Undisturbed lakes (*U*), opposite areas to the disturbance (*Do*), and adjacent areas to the disturbance (*Da*) in disturbed lakes. Axis 1 located at abscissa, and axis 2 at the ordinate.

Nematoda and Ostracoda were the taxa most related with axis 1 (horizontal) (Table 4-8). Nematoda had a score of 0.99 on axis 1, while Ostracoda had a positive score of 0.31. Chironomidae had negative scores on axis 2 (-0.99) and is not strongly correlated with Ostracoda and Nematoda (Table 4-7) as can be observed by their perpendicular projection in the diagram. When analyzing the environmental variables that were added post-hoc to the ordination analysis (Figure 4-7), axis 1 is mainly dominated by variables related to organic sediments in the negative region of the ordination. Organic carbon and organic nitrogen had slightly higher correlation values on this axis compared to axis 2 (-0.28, -0.32 on axis 1 respectively) (Table 4-8). Axis 2 had higher positive correlation values for Ca (0.25), ignition loss (0.23), and macrophyte biomass (0.19). Inorganic carbon was equally correlated to axis 1 and 2 (-0.12) and is not considered on the interpretation of taxon-environmental relationships.

Based on the correlation values between the environmental data and the axes, axis 1 represents mainly an organic sediment gradient, while axis 2 represents a gradient composed of macrophyte biomass, organic content (ignition loss), and calcium. The main separation observed is the presence of two distinct groups of samples that are located at each of the sides of axis 1. Thus, the variables that had stronger correlation in this axis (organic C and N) are the primary explanatory environmental variables separating the sample points based on taxonomic composition. Also, few samples were positively correlated with macrophyte biomass, and calcium and ignition loss values (Figure 4-7).

An analysis of the direction of the arrows describing environmental variables in relation to the ones that describe taxonomic composition provides further insight into which environmental variables are influencing observed invertebrate community composition patterns. Ostracoda and Nematoda were negatively correlated with organic C and N, and to a certain extent positively correlated to Ca and macrophyte biomass (Figure 4-7). Chironomidae had a negative correlation with the variables positively correlated with axis 2 (Ca, macrophyte biomass, and ignition loss) and also had negative correlation with organic C and N (Figure 4-7).

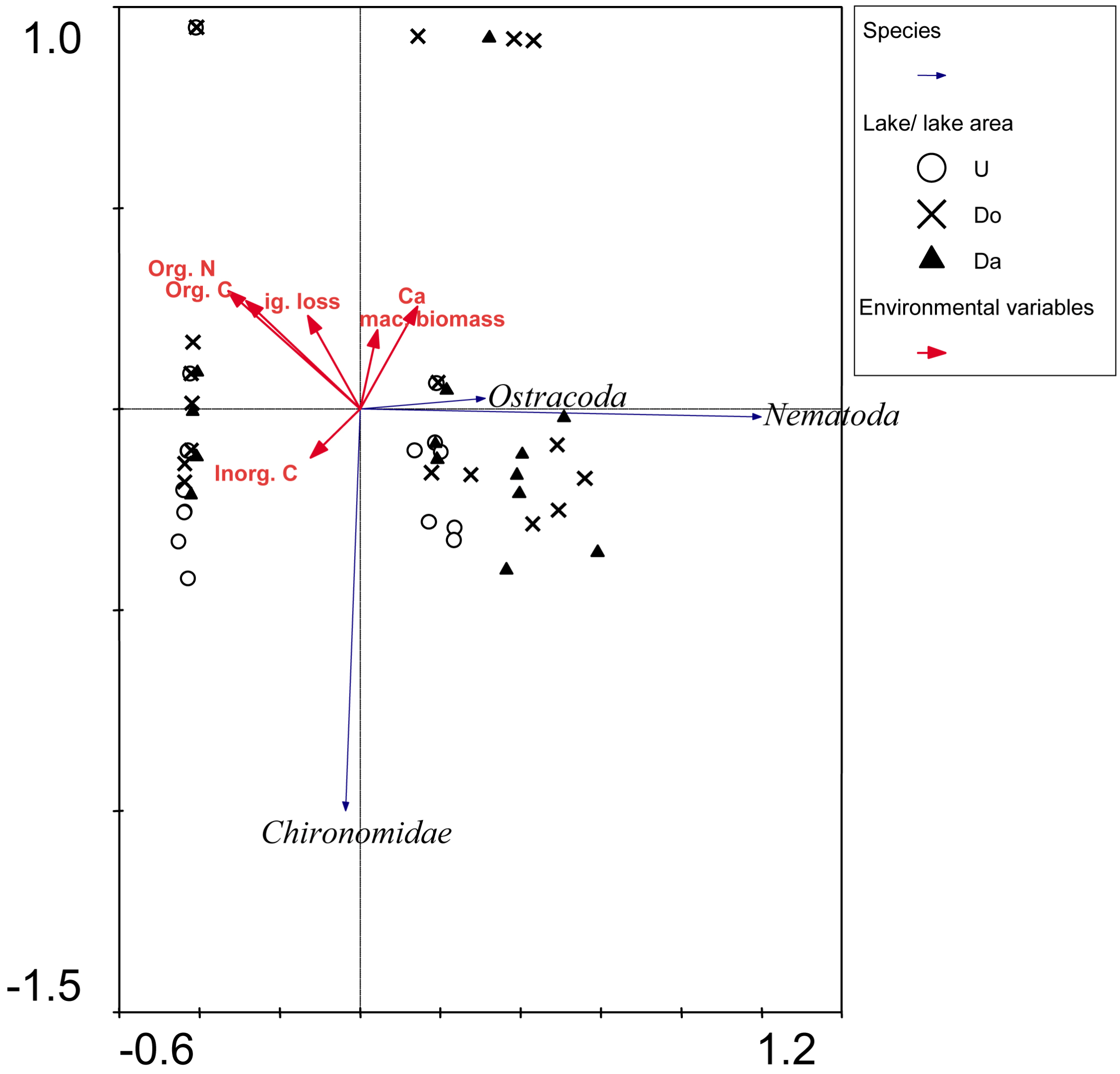

Figure 4-7: PCA triplot of invertebrate taxa with macrophyte biomass and sediment chemical variables added as post-hoc environmental variables. Undisturbed lakes (*U*), opposite areas to the disturbance (*Do*), and adjacent areas to the disturbance (*Da*) in disturbed lakes. Axis 1 located at abscissa, and axis 2 at the ordinate.

Table 4-7: Taxon-scores of PCA analysis with invertebrate abundance data, and macrophyte biomass and sediment chemical data added post hoc.

Variables	Loadings		
	Axis 1	Axis 2	Axis 3
Ostracoda	0.3110	0.0265	0.9501
Chironomidae	-0.0368	-0.9993	0.0050
Nematoda	0.9995	-0.0196	-0.0244

Table 4-8: Intra set correlation of environmental variables with the first two PCA axes of invertebrate abundance data

Environmental variables	Axis 1	Axis 2	Axis 3
Mac. biomass	0.0420	0.1972	0.1391
Ig. loss	-0.1303	0.2323	-0.3033
Inorg. C	-0.1234	-0.1206	-0.3165
Org. C	-0.2847	0.2695	-0.1444
Org. N	-0.3288	0.2943	-0.1736
Ca	0.1421	0.2545	0.3055

Figures 4-8 shows that Ostracoda and Nematoda were positively correlated, while Chironomidae had a negative correlation with both groups. Chironomidae and Nematoda were the main taxa dominating the distribution of samples points at the ordination plot since they were not encountered in all the samples. Ostracoda was present in most samples with abundance values in various degrees, and thus did not cause a clear separation on the projected samples (Figure 4-8). The main difference that can be observed is that most of samples at the left part of the ordination plot had Chironomidae and Ostracoda in their invertebrate community, while samples at the right section had the presence of Nematoda in addition (Figure 4-8).

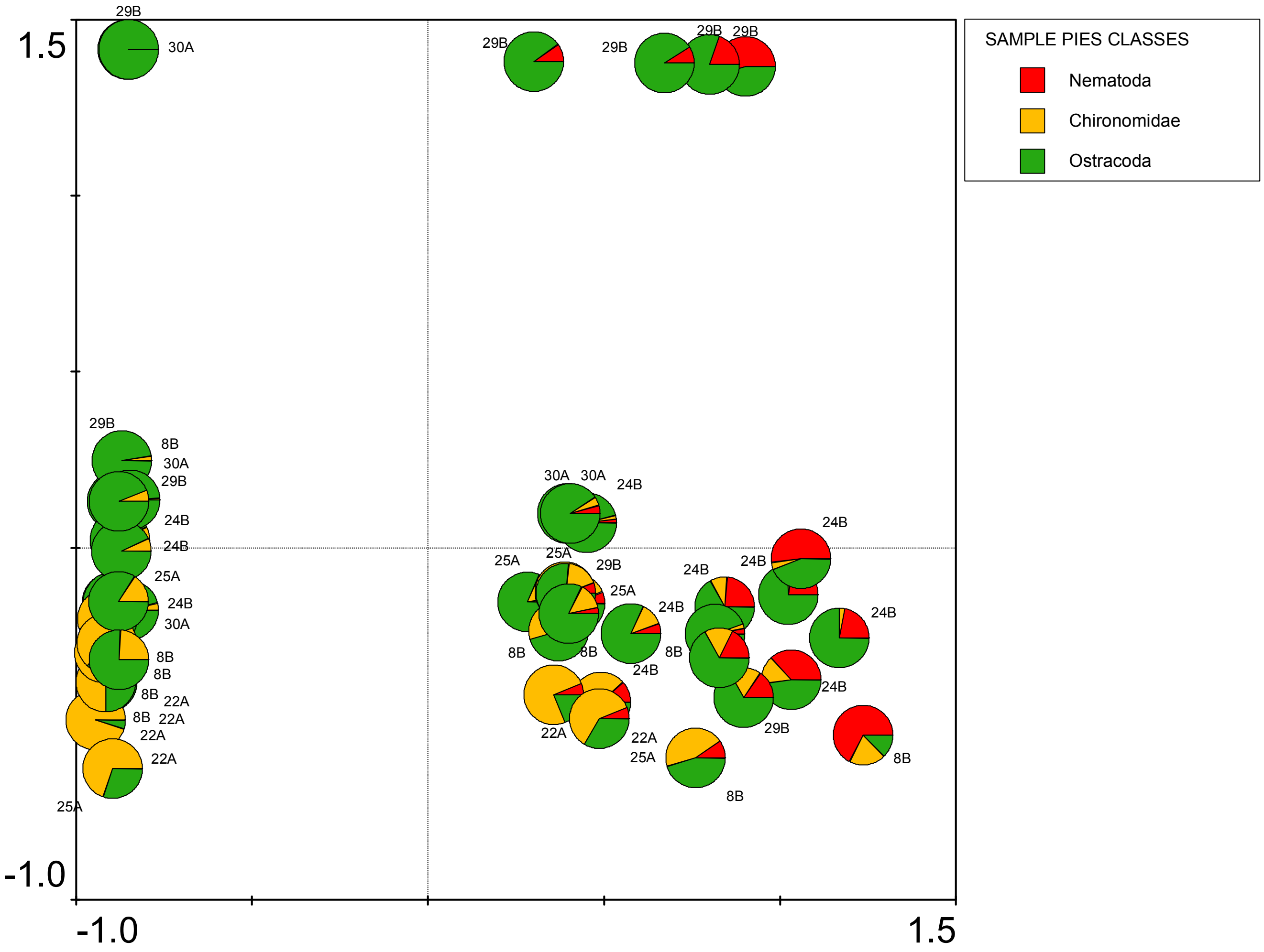

Figure 4-8: Pie-wedge sample scatter plots from PCA analysis with invertebrate taxa and environmental variables added post-hoc. Area occupied by sample class indicates the percentage composition of each invertebrate taxon. Numbers at the plot represent sample location: 30A, 25A, 22A- undisturbed lake, 8B, 24B and 29B - disturbed lakes. Axis 1 located at abscissa, and axis 2 at the ordinate.

4.4 Discussion

Littoral benthic invertebrate communities are an important component of secondary production of lake systems and are involved in energy transfer to higher trophic levels and energy distribution between benthic and pelagic food webs (Stoffels *et al*., 2005). Changes in the distribution of functional feeding groups ultimately leads to alteration in the way nutrient supplies are distributed within a system, with further impacts on food web structure and functioning of lake systems (Covich *et al*., 1999).

The larger mean abundance of total benthic invertebrates observed in disturbed lakes (*D*) (28,630 ind/m^2) was expected because these lakes had higher biomass of macrophytes when compared to undisturbed ones (*U*) (Mesquita *et al*., *in prep.*). However, when analyzing both areas of disturbed lakes (opposite to disturbance *–Do*, adjacent to disturbance- *Da*) in comparison to *U* lakes, it was observed that the highest mean total abundance of invertebrates was found in *Da* areas (35,631 ind. /m^2). This was contrary to the expectation that benthic invertebrates would be more abundant in the areas with highest macrophyte biomass. Mesquita *et al.* (*in prep*.) observed that in *D* lakes, *Do* areas were mostly covered with submerged macrophytes, while these were mainly absent in *Da* areas.

Although the presence of submerged macrophytes can have a positive impact on benthic invertebrate communities in shallow lakes (Diehl & Kornijów, 1998; Tolonen *et al*., 2003), it has been suggested that in areas with high macrophyte biomass, macroinvertebrates become more associated with the plants (epiphytic invertebrates) than directly with the sediment (Diehl & Kornijów, 1998; Kalff, 2001). This could be the case in the studied sites, however, more data collection is necessary to evaluate if this is a pattern encountered in tundra lakes.

The observed differences in total abundance of invertebrates and dominance per taxa between *U*, *D*, *Do* and *Da* could be a result of different habitat structure in each of these areas, favouring different functional feeding groups. Littoral zones of *U* lakes were observed to be most deprived of macrophyte communities, while *Do* areas (*D* lakes) were mostly covered by an abundant macrophyte community. In *D* lakes, *Da* areas were visually steeper than *Do* areas, and had the presence of terrestrial vegetation transported by the slumping, and very few macrophytes (Mesquita *et al.*, *in prep.*). For example, benthic collector-suspension feeders (*e.g.* Chironomidae larvae) can be affected by the presence of a high biomass of macrophytes that alter the settlement of particles under the plants and lead to a decreased amount of available food (Kornijów & Moss, 1998).

Chironomidae were the predominant insect group encountered in the studied lakes. This group was negatively correlated to macrophyte biomass in the ordination diagram, which agrees with the fact that they were more abundant in *U* lakes that in general are mostly absent of macrophytes. In general, Chironomidae are highly dominant in arctic lakes (Hershey & Lamberti, 2001; Wetzel, 2001) and in the arctic landscape (Oliver & Dillon, 1997). One of the factors that contribute to the success of Chironomidae in arctic lakes is their ability to live for limited periods in anoxic environments, as found for under-ice conditions in cold climates (Hershey & Lamberti, 2001). For example, members of the tribe Chironomini (*e.g. Chironomus* spp.) possess haemoglobin to store oxygen, thus being better prepared for anoxic periods than other benthic invertebrates (Hershey & Lamberti, 2001; Hilsenhoff, 2001).

Chironomidae have also been shown to grow faster on sediments containing high levels of organic matter that serve as substrate for the growth of bacterial communities utilized for ingestion (Beaty *et al.*, 2006).This could explain their significant higher abundance in *U* lakes that had organic carbon levels of 7.29% compared to 4.9% in *D* lakes (Mesquita *et al.*, *in prep.*). In *D* lakes, *Da* areas were covered in terrestrial vegetation from the thaw slumps and had significantly lower organic-carbon content (3.45%) in the sediment compared to *Do* areas (6.21%) and *U* lakes. However, Chironomidae abundance at *Da* areas was not significantly different from *U* lakes. The position of organic nutrients at the ordination diagram shows a negative relationship between Chironomidae and these sediment variables, indicating that other environmental factors could be related to abundance of this group in the studied lakes. Also, Chironomidae was observed to be positively associated with macrophyte presence, being 1.5 times more abundant on the plants than on bare sediment in an arctic lake (Hershey, 1985). Although benthic invertebrates associated directly with macrophyte standing crop were not collected in that study, it could be that the lower abundance of Chironomidae in *Do* areas of the studied lakes is an artifact of higher macrophyte biomass, and changes from a benthic-dominated to an epiphytic-dominant population could be occurring. High macrophyte biomass is believed to decrease the capture success in fishes that are visually guided to their prey (Rennie & Jackson, 2005), possibly creating an area where Chironomidae are more protected from the predation pressure. As epiphytic invertebrates were not sampled, it is not possible to evaluate whether macrophytes were related to high abundance of total macroinvertebrates.

In addition to having larger abundance of Chironomidae compared to *Do* areas, *Da* areas also had the largest abundance of Ostracoda compared to their abundance in *U* lakes and *Do* areas. These results raise the question: which habitat characteristics could be related to the observed greatest abundance of Ostracoda in *Da*, and to the similar abundance of Chironomidae encountered in *U* lakes and *Da*, but not in *Do?*

One hypothesis is that the terrestrial vegetation transported by the slump provides a larger surface for the growth of periphytic algae, which in conjunction with the bare sediment available for epipelic algae and bacterial community growth, have a positive effect on the Ostracoda and Chironomidae groups. Ostracoda are omnivorous and feed on bacteria, algae, detritus, and other microbiota by filtration (Brown, 2001). A second hypothesis for the Ostracoda higher abundance in *D* lakes is that higher Ca concentration in the water-column as observed for similar lakes located in the same geographical region (Kokelj *et al.*, 2005) could be favouring this invertebrate group. Ostracoda require Ca for the maintenance of their shells (Brown, 2001), and Ca dissolved in water was observed as the only source used for the calcification of the ostracod *Heterocypris* sp. (Turpen & Angel, 1971). Also, higher Ca concentrations at the sediment were observed in *D* lakes, without significant differences between *Do* and *Da* (Mesquita *et al., in prep.*). This could be a possible explanation for the differences in Ostracoda abundance between *U* and *D* lakes, but not for the observed differences between *Do* and the *Da* (higher abundance). These could in turn be more related to other factors, such as food availability, predation, and/or competition strategies. At the PCA analysis, sediment Ca and macrophyte biomass were found to be positively related to Ostracoda abundance, which supports the fact that all these variables had higher values in *D* lakes. In *D* lakes, macrophyte biomass was higher in *Do* areas, while Ca did not show a significant difference (Mesquita *et al.*, *in prep.*). Ostracoda was positively correlated with Nematoda in the ordination diagram, and both groups had high abundance values observed in *D* lakes suggesting that similar environmental variables may be controlling their populations.

As found with the Ostracoda group, Nematoda was also suggested to have a positive correlation with macrophyte biomass and Ca. Nematodes are known to reach high densities among the attached algae of dense emergent and submersed macrophytes (Wetzel, 2001). *D* lakes had the highest biomass of macrophytes at *Do* areas and presence of allochthonous terrestrial vegetation at *Da* areas (Mesquita *et al*., *in prep),* both of which can be colonized by epiphytic algae. The presence of higher concentration of some nutrients in sediment of *D* lakes, with the presence of macrophytes and terrestrial vegetation with the potential for algae growth, probably contributed to the one order of magnitude difference in mean abundance of Nematoda between *U* and *D* lakes and no differences between *Do* and *Da*.

4.5 Conclusion

In general, a higher abundance of invertebrates was found associated with areas adjacent to the shoreline disturbance. Differences in community structure between both types of lakes and areas of disturbed lakes were also observed, with the strongest trend being the low abundance of Chironomidae in sediments from areas where macrophytes were the most present (*Do*), high abundance of Ostracoda in the areas adjacent to the disturbance (*Da*), and high abundance of Nematoda in *D* lakes. These groups were the main determinants of the distribution of sampled points in the PCA ordination space. The presence of macrophytes did not appear to have a positive effect on the abundance of the benthic invertebrates, since higher abundances were located in areas without macrophytes and also the most predominant taxa were suggested to be negatively, or positively - but weakly, correlated with this variable at the PCA triplot.

Ostracoda was the most abundant taxonomic group in general, and reached its highest population numbers in the areas adjacent to the disturbance, thus potentially playing an important role in the transfer of energy through higher trophic levels and between benthic and pelagic food web. Some characteristics of areas adjacent to the disturbance can positively impact the Ostracoda population, and can involve the presence of altered communities due to a habitat mainly structured by the presence of deposited terrestrial vegetation. However, a more detailed study would be necessary to clarify the encountered patterns. Small fishes were observed in one undisturbed lake (25A) and in one disturbed (29B) lake during sampling campaigns. Thus, experiments controlling the fish population, habitat structure, and all the chemical and physical variables that are related to certain groups of invertebrates would give some insights about which or if any of the chemical variables are related to differences in community structure.

Many differences have been observed between undisturbed and disturbed lakes, such as submerged macrophyte biomass and community structure, water transparency, sediment chemistry (Mesquita *et al.*, *in prep.*), and water-column pH, conductivity and chemistry (Kokelj *et al.*, 2005). These results indicate that permafrost thaw slumps can cause changes in water-column and sediment physico-chemical characteristics that in turn affect lake biota production, energy flux, and diversity. The higher total abundance of invertebrates and dominance of Ostracoda and Nematoda in disturbed lakes opposed to the higher dominance of Chironomidae in undisturbed lakes shown by the present study suggests that retrogressive thaw slumping does affect the structure of benthic invertebrate communities in upland tundra lakes.

Changes in water-column and sediment chemistry characteristics due to enriched runoff (as observed by Kokelj *et al.*, 2005) can ultimately affect the amount and quality of food produced at the benthic and pelagic habitats that support benthic invertebrate production. Disturbance of the littoral zone due to permafrost thaw slumping has a considerable effect on the characteristics and habitat structure of the zone, which may also have an effect on the invertebrate communities. Disturbed areas appear to have steeper slopes when compared to areas opposite to the disturbance and undisturbed lakes, and also have a substantial amount of terrestrial material (vegetation, small rocks and soil), which seems to be especially beneficial to the Ostracoda population.

An increasing trend of higher temperatures with increased frequency of permafrost disturbance in the shoreline can progressively impact the structure of lake food webs, as suggested by the observed differences between disturbed and undisturbed lakes. Changes in habitat structure and possibly food supply, associated with physico-chemical modification in water-column and sediment, can cause a change from primarily Chironomidae-dominated communities as observed in undisturbed lakes, to Ostracoda/Nematoda-dominated communities as in disturbed lakes. Such differences in invertebrate communities can be propagated throughout the lake food web, affecting fish community composition, structure, and abundance, and thus other associated ecosystem parameters as pelagic productivity in these lakes.

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Chapter 5 : Conclusion

Global warming is forecast to cause a variety of changes in the arctic environment (ACIA, 2005; Anisimov *et al.,* 2007), and modifications of permafrost terrain in non-bedrock areas, besides other landscape changes (e.g. vegetation changes, soil composition), will likely affect upland tundra lakes. The presence of retrogressive permafrost thaw slumps at shoreline areas of the studied tundra lakes were observed to be related to modifications of the sediment and water-column physico-chemical characteristics, and benthic macrophyte and invertebrate community structure.

Input of landscape material in areas adjacent to the disturbance, and the associated modifications in nutrient concentrations, are likely responsible for some of the dissimilarities observed between undisturbed and disturbed lakes. Sediment chemistry of disturbed lakes was found to be enriched in calcium, magnesium, and strontium, while undisturbed lakes had higher concentrations of organic carbon, organic nitrogen, nickel, cobalt, manganese, arsenic, and zinc. Based on other studies (Kokelj *et al.,* 2005), it can be hypothesized that calcium and magnesium have higher concentrations in disturbed lake sediment due to inputs from enriched runoff containing these elements. On the other hand, organic carbon and nitrogen are probably higher in undisturbed lakes because the runoff passes through the shallow organic soils that cover undisturbed catchments, transporting water enriched with organic material to these lakes (Carey, 2003). Without a significant uptake by the biota or flushing activity, these elements can accumulate in the sediment creating the observed differences. Variations in the other mentioned variables (*e.g.* nickel, arsenic) need to be further studied, since high levels of some metals can be toxic to the biota and might have affected the results.

The input of landscape soil near the disturbance is hypothesized to decrease the ability of macrophytes to establish in that area. Frequent burying, unstable sediment, and the presence of undecomposed terrestrial vegetation could be factors related to the major presence of submerged macrophytes only at the areas opposite to the disturbance. In undisturbed lakes, macrophytes also had lower biomass, but the factors attributed to this pattern were the presence of sediments with higher organic content and the lower transparency of the water column, when compared to the disturbed lakes. Higher water transparency in disturbed lakes could be related to smaller undisturbed catchment (organically covered) area bringing allochthonous organic matter, or even more related to chemical interactions of high ionic content runoff with water-column organic matter. Higher ionic concentrations supplied to the lakes from the enriched slump runoff as shown in Kokelj *et al.* (2005) could be adsorbing to organic compounds in the water column, causing increased precipitates and clearing of the water column. For example, calcite crystals are known to form aggregates that play a role in the removal of nutrients and organic matter from the water column and subsequent sedimentation (Stabel, 1986; Kalff, 2001). High sulphate concentrations in the water-column of disturbed lakes (Kokelj *et al.*, 2005) could also be related to elevated rates of anoxic degradation of organic matter and decreased organic compounds in the water and sediment.

Benthic invertebrate abundance also differed between undisturbed and disturbed lakes, with the highest mean abundances encountered in the latter. Within disturbed lakes, areas adjacent to the disturbance had higher invertebrate abundance values, contradicting general observations from previous studies that found higher invertebrate abundance mainly related to lakes with higher macrophyte biomass. The community composition of benthic invertebrates was also significantly different between undisturbed and disturbed lakes, with the greatest differences observed in the Ostracoda, Nematoda, and Chironomidae groups. In general, Ostracoda was the most abundant group, with the highest densities in disturbed lakes, particularly in areas adjacent to the disturbance. Nematoda was the second most abundant group in disturbed lakes, but did not show any difference in abundance patterns between areas opposite and adjacent to the disturbance. Chironomidae was the taxa more abundant in undisturbed lakes, and had abundance similar only to the areas adjacent to the disturbance in disturbed lakes. Dissimilarities in invertebrate community structure between the studied lakes are believed to be related to the differences in habitat structure and food availability, likely associated with the presence of submerged macrophytes, sediment composition (as measure by Mesquita *et al*., *in prep.*) and presence of terrestrial vegetation.

It is concluded that retrogressive permafrost thaw slumps, which are predicted to be more frequent in the Arctic in a warmer climate, have a direct effect on the benthic macrophytes and invertebrate communities, and also on sediment chemistry and water-column transparency of upland tundra lakes. Changes in biomass, abundance, and community structure of benthic macrophytes and invertebrates can have further effects on food web structure, primary and secondary production, and water quality of high latitude lakes.

Future research:

Further research is needed to evaluate how chemical differences in runoff between undisturbed and disturbed lakes affect sediment nutrient exchange, partitioning and availability, and also the interaction of nutrients with dissolved organic matter in the water column. An analysis of the presence/absence of different microorganisms on bacterial mats in the sediment at different times of the year could provide additional insight into the types of chemical transformations occurring in those lakes, as certain chemical reactions are occurring only in the presence of specific bacterial groups (Nealson, 1997). In addition, the effects of various physico-chemical factors such as pH, conductivity, redox potential, and temperature should be considered when analyzing the mentioned relationships, since small changes in these variables can affect the observed responses.

Experiments controlling the interactions between benthos, sediment chemistry, and food resources should be performed to understand how the community structure is affected by high dissolved organic matter (DOM) input (as in *U* lakes), by high submerged macrophytes cover (as in *Do*), and by disturbed littoral zone with presence of terrestrial vegetation (as in *Da*). The presence or absence of fish communities, with distinct biomass and structure, should also be assessed to fully understand the impacts of permafrost thaw slumping on the benthos. Fish communities can alter invertebrate community structure, composition, and even behavioural strategies influencing the prevalence of different taxa with diverse functional importance.

In conclusion, further research is still necessary to more fully understand the impacts of global warming through retrogressive permafrost thaw slumping on high latitude shallow lakes located in areas of ice-rich permafrost. A better understanding of these fragile systems is deemed important for the enhanced predictions of how the production and diversity of arctic lakes will be altered by global warming. Knowledge about these freshwater systems will also help to understand how water supply and food-availability can be altered and its possible impacts on consumers/users that depend on some resource from the lakes. Similar investigations can be used to investigate future impacts of development plans on water quality from that region.

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Appendix

Appendix A: Descriptive statistics of sediment chemical variables of undisturbed lakes (U) and disturbed lakes (D). Number of samples (N), minimum (Min.) and maximum (Max.) values, mean, and standard deviation (S.D). Values in mg/kg with the exception of C and N in %.

	Undisturbed lakes (*U*)					Disturbed lakes (*D*)				
Variables	N	Min.	Max.	Mean	S.D	N	Min.	Max.	Mean	S.D
As	17	11	36	20.12	8.05	40	8	23	15.45	3.78
Be	17	1.1	2.39	1.57	0.36	40	0.7	2.17	1.48	0.39
Bl	17	0.1	0.3	0.21	0.05	40	0.1	0.3	0.22	0.07
Cd	17	0.3	1.4	0.63	0.33	40	0.2	0.9	0.53	0.15
Ga	17	8.78	17.8	12.89	2.65	40	5.53	19.1	12.56	3.64
La	17	16.8	25.5	21.76	2.42	40	9.57	28.5	21.42	3.63
Li	17	30.8	64.8	44.62	9.85	40	18.3	70.9	45.77	13.63
Mo	17	1.5	6.1	3.68	1.44	40	1.1	7	2.93	1.35
Ni	17	30.2	102	51.64	20.71	40	25.9	58.2	41.5	8.89
Pb	17	10.8	18.6	14.48	2.3	40	6	21.5	14.71	3.56
Rb	17	49.8	105	73.3	17.21	40	30	105	68.57	22.7
Sb	17	0.2	0.7	0.44	0.15	40	0.2	0.7	0.43	0.14
Tl	17	0.39	0.81	0.58	0.13	40	0.26	0.81	0.55	0.16
U	17	1.51	2.81	2.18	0.44	40	1.12	3.95	2.29	0.66
Al	17	29200	62700	45023.5	9767.2	40	19100	69500	44975	14514
Ba	17	441	1020	659.59	149.28	40	342	918	633.38	142.48
Cr	17	45	87	64.47	12.14	40	26	89	62.18	17.56
Cu	17	21	47	31.24	7.8	40	16	44	30.38	7.63
Fe	17	22200	50500	37800	9738.5	40	17800	46300	33090	7896.86
P	17	526	1220	838.71	217.88	40	411	975	753.1	141.51
V	17	92	171	133.18	22.09	40	54	183	129.7	34.68
Zn	17	72	288	137.35	64.02	40	47	162	106.25	28.72
Ca	17	3440	6100	4856.47	848.18	40	4990	20500	9441.25	3772.13
Mg	17	4310	7720	5748.82	1000.1	40	4210	10800	7357	1641.47
Na	13	533	979	695.31	138.46	22	510	951	665.59	103.12
K	17	6800	15600	10274.7	2591.5	40	4500	15600	10164.5	3418.84
P_inorg	17	324	812	534.82	169.4	40	181	743	559.05	126.52
C-inorg	16	0.1	5.04	1.451	1.432	33	0.01	2.6	0.723	0.668
C-org	17	2.32	15.1	7.288	4.027	40	0.97	35.5	4.905	5.604
N-org	17	0.2	1.19	0.6065	0.3146	39	0.07	1.85	0.3431	0.301

Appendix B: Descriptive statistics of sediment variables not normally distributed. Number of samples (N), minimum (Min.), maximum (Max.), Median, and first and third quartiles (Q_1, Q_3). Mn, Co and Sr in mg/kg and Ignition loss in %.

	Undisturbed lakes (*U*)						Disturbed lakes (*D*)					
Variables	N	Min.	Max.	Median	Q_1	Q_3	N	Min.	Max.	Median	Q_1	Q_3
Mn	17	243	6330	830	670	1500	40	210	1750	422.5	364.3	644.8
Co	17	10.9	40.6	15.4	12.4	19	40	5.4	17	13.2	11.625	14.675
Sr	17	48	76	60	57	68.5	40	41	83	73.5	60.25	76.75
Ig. loss	26	6.14	51.98	13.26	8	26.02	67	3.27	62.95	9.67	6.76	12.31

Appendix C: Descriptive statistics of sediment variables significantly different between *Do* and *Da* areas. Number of samples (N), minimum and maximum values (Min.,Max.), mean, standard deviation (S.D). C, N, in %. Mg and Ca in mg/kg.

	Opposite to disturbance (Do)					Adjacent to disturbance (Da)				
Variables	N	Min.	Max.	Mean	S.D	N	Min.	Max.	Mean	S.D
C organic	21	1.69	35.5	6.21	7.24	19	0.97	8.3	3.464	2.357
N organic	20	0.07	1.85	0.444	0.374	19	0.07	0.55	0.237	0.142
Ca	21	4990	20500	8459.05	3441.02	19	5920	17400	10526.84	3912
Mg	21	4210	9610	7122.86	1883.96	19	4950	10800	7615.79	1326.51

Appendix D: Descriptive statistics of sediment variables (not normally distributed) significantly different between *Do* and *Da* areas. Number of samples (N), minimum and maximum values (Min.,Max.), median, and first and third quartiles (Q_1, Q_3). Ignition loss in %. Mn, Co, Sr in mg/kg.

Opposite to disturbance (Do)							Adjacent to disturbance (Da)					
Variables	N	Min.	Max.	Median	Q_1	Q_3	N	Min.	Max.	Median	Q_1	Q_3
Mn	21	210	1750	424	339	666	19	219	887	418	372	611
Co	21	5.4	17	13	10.7	15.65	19	8.7	15.7	13.4	11.7	14.1
Sr	21	41	80	74	55.5	76.5	19	45	83	69	61	78
Ig. Loss	34	3.27	62.95	9.93	8.36	12.12	33	3.44	38.95	8.71	5.69	14.33

Appendix E: Percent reduction of upcoming PAR as a measure of underwater vertical attenuation at the littoral zone of undisturbed (U) and disturbed (D) lakes. Number of samples (N), minimum (Min.) and maximum (Max.) values, median, and first and third quartiles (Q_1, Q_3). Kruskal-Wallis test results between K_d in undisturbed (U) and disturbed (D) lakes, and opposite (Do) and adjacent areas (Da) to the disturbance in D lakes. H-statistics, p- values, and DF (degrees of freedom) displayed. * indicates significant at $p < 0.05$.

		N	Min.	Max.	Median	Q_1	Q_3
U		20	40.63	72.36	56.78	52.14	67.35
D		47	25.27	67.39	45.68	41.46	52.31
	Do	21	31.98	67.39	48.03	43.02	52.92
	Da	26	25.27	65.44	44.95	41.25	52.02

Comparisons	*U* x *D*	*U* x *Do* x *Da*	*Do* x *Da*	*U* x *Do*	*U* x *Da*
p- value	0.000*	0.000*	0.487	0.002*	0.000*
H-statistics (DF)	16.34 (1)	16.77 (2)	0.48(1)	9.96 (1)	14.87 (1)

Appendix F: Underwater PAR measurements and attenuation coefficient from *U* and *D* lakes. Lake name, undisturbed or disturbed (*U/D*) lakes), undisturbed lake or opposite or adjacent areas to disturbance in D lakes (*U*/*Do*/*Da*).

Lake	U/D	U/Do/Da	Transect	Depth	Measurement depth		kd =ln(0.1)- ln(0.6)/ 0.6	Percentage reduction of surface PAR
					0.1	0.6		
30A	U	U	1	3	720.4	385.5	1.04	46.49
30A	U	U	1	2	793.6	376.8	1.24	52.52
30A	U	U	1	1	790.2	366.5	1.28	53.62
25A	U	U	1	1	232	105.5	1.31	54.53
25A	U	U	1	2	335.6	108.8	1.88	67.58
22A	U	U	1	1	64.19	20.33	1.92	68.33
25A	U	U	1	3	339.9	94.85	2.13	72.09
30A	U	U	2	2	642.8	381.6	0.87	40.63
30A	U	U	2	1	690	398.6	0.91	42.23
30A	U	U	2	3	690.8	328	1.24	52.52
22A	U	U	2	1	240.5	107.3	1.35	55.38
25A	U	U	2	3	361.3	134.9	1.64	62.66
25A	U	U	2	1	356.3	122.2	1.78	65.70
25A	U	U	2	2	362.9	100.3	2.14	72.36
30A	U	U	3	1	679.8	361.2	1.05	46.87
30A	U	U	3	3	668.9	321	1.22	52.01
25A	U	U	3	1	412.6	172.6	1.45	58.17
25A	U	U	3	3	528.2	193.8	1.67	63.31
30A	U	U	3	2	695.1	231.9	1.83	66.64
25A	U	U	3	2	499.7	151	1.99	69.78
29B	D	Do	1	1	366.6	242.3	0.69	33.91
24B	D	Do	1	3	768.6	485.5	0.77	36.83
24B	D	Do	1	2	813	463.4	0.94	43.00
8B	D	Do	1	1	207.3	118.1	0.94	43.03
24B	D	Do	1	1	848.3	475.6	0.96	43.93
29B	D	Do	1	2	397.9	213.9	1.03	46.24
8B	D	Do	1	2	181.8	94.18	1.10	48.20
8B	D	Do	1	3	156.7	75.98	1.21	51.51
29B	D	Do	1	3	305.8	123.6	1.51	59.58
29B	D	Do	2	1	166.3	93.6	0.96	43.72
8B	D	Do	2	1	185.1	101.3	1.00	45.27
29B	D	Do	2	3	249.9	119.1	1.24	52.34
29B	D	Do	2	2	265.8	123.6	1.28	53.50
8B	D	Do	2	2	265.1	86.44	1.87	67.39
8B	D	Do	3	2	222.3	151.2	0.64	31.98
24B	D	Do	3	1	727	480.2	0.69	33.95
29B	D	Do	3	1	281.1	146.1	1.09	48.03
29B	D	Do	3	3	221.8	111.4	1.15	49.77
24B	D	Do	3	3	732	352.5	1.22	51.84
29B	D	Do	3	2	192.5	87.95	1.31	54.31
24B	D	Do	3	2	695.9	271.3	1.57	61.01
22B	D	Da	4	1	154.8	97.4	0.77	37.08
8B	D	Da	4	3	189.9	111.6	0.89	41.23
8B	D	Da	4	2	178.2	104.7	0.89	41.25
24B	D	Da	4	2	226.7	127.1	0.96	43.93
8B	D	Da	4	1	189.2	105.6	0.97	44.19
29B	D	Da	4	3	426.3	207.8	1.20	51.25
29B	D	Da	4	2	320.9	154.3	1.22	51.92
24B	D	Da	4	3	274.3	130.8	1.23	52.31

24B	D	Da	4	1	382.7	161.5	1.44	57.80
29B	D	Da	4	1	308.2	106.5	1.77	65.44
24B	D	Da	5	2	637.7	423	0.68	33.67
8B	D	Da	5	1	173.2	105	0.83	39.38
8B	D	Da	5	3	244.1	142.9	0.89	41.46
24B	D	Da	5	3	638.6	370.4	0.91	42.00
24B	D	Da	5	1	600.6	334.9	0.97	44.24
29B	D	Da	5	2	214.4	117.8	1.00	45.06
29B	D	Da	5	3	333.1	174.4	1.08	47.64
29B	D	Da	5	1	325.7	137.4	1.44	57.81
8B	D	Da	6	3	222.4	166.2	0.49	25.27
29B	D	Da	6	3	176.4	125.6	0.57	28.80
8B	D	Da	6	1	234.1	129	0.99	44.90
24B	D	Da	6	1	634.4	344.6	1.02	45.68
24B	D	Da	6	2	712.6	364.7	1.12	48.82
29B	D	Da	6	2	225.4	111.3	1.18	50.62
24B	D	Da	6	3	744.6	354.1	1.24	52.44
29B	D	Da	6	1	216.9	100.7	1.28	53.57

Appendix G: Sediment chemistry data from *U* and *D* lakes. Lake name, undisturbed or disturbed (*U/D*) lakes, transect (T), undisturbed lake or opposite or adjacent areas to disturbance in D lakes (*U*/*Do*/*Da*), depth, and chemical elements. All data in mg/kg with the exception of and C and N in %. * indicates measurements smaller than detection limit.

Lake	U/D	T	U/Do/Da	Depth	As	Be	Bl	Cd	Co	Ga	La	Li	Mo	Ni	Pb	Rb	Sb	Tl	U
29B	D	1	Do	1	23	1.63	0.2	0.5	14.6	14.2	22.0	50.6	3.0	43.8	15.3	80.3	0.5	0.632	2.25
29B	D	1	Do	3	14	1.80	0.3	0.5	12.1	15.8	22.1	56.9	2.5	41.8	16.1	93.4	0.3	0.708	2.07
29B	D	2	Do	1	8	0.70	0.1	0.4	5.4	5.53	9.57	18.3	2.1	27.7	6.0	30.0	0.4	0.255	2.29
29B	D	2	Do	3	19	1.75	0.2	0.6	12.4	15.6	20.7	53.6	5.2	47.6	15.4	88.8	0.6	0.671	3.89
29B	D	3	Do	1	20	1.70	0.2	0.5	13.0	14.5	21.1	51.4	2.8	41.1	15.0	85.1	0.5	0.653	2.28
29B	D	3	Do	3	21	1.98	0.3	0.5	14.6	17.7	21.9	66.3	5.0	52.5	17.9	105.	0.6	0.812	2.79
8B	D	1	Do	1	10	1.10	0.2	0.3	11.4	9.09	22.0	29.4	1.2	36.4	11.6	44.8	0.4	0.376	1.47
8B	D	1	Do	3	15	1.98	0.3	0.7	14.7	16.2	24.5	56.0	2.6	50.5	18.2	89.2	0.4	0.703	2.77
8B	D	2	Do	1	17	1.98	0.3	0.7	15.9	17.3	26.3	58.0	1.9	52.8	19.4	96.6	0.3	0.750	2.71
8B	D	2	Do	3	18	2.12	0.3	0.7	16.5	18.7	27.5	63.4	2.3	57.0	20.5	103.	0.3	0.753	3.04
8B	D	3	Do	1	16	1.95	0.3	0.8	16.1	17.4	25.4	56.5	2.1	52.8	19.2	94.5	0.5	0.722	2.99
8B	D	3	Do	3	18	2.17	0.3	0.7	17.0	19.1	28.5	63.4	2.4	58.2	21.2	104.	0.3	0.788	3.06
22B	D	1	Do	1	11	1.20	0.2	0.2	9.9	9.60	17.9	36.2	1.7	28.6	12.0	48.6	0.4	0.397	1.53
22B	D	3	Do	1	12	1.18	0.1	0.4	11.7	9.35	19.3	34.0	1.7	36.0	11.4	46.4	0.4	0.391	1.64
22B	D	3	Do	3	11	1.13	0.2	0.3	9.3	9.64	17.0	34.9	2.1	30.3	11.2	50.0	0.5	0.407	2.12
24B	D	1	Do	1	17	1.85	0.3	0.5	15.4	16.3	26.1	63.3	3.5	48.3	18.3	93.6	0.3	0.738	2.70
24B	D	1	Do	3	16	1.78	0.3	0.5	14.2	15.0	20.0	60.6	5.8	47.5	17.4	87.9	0.5	0.712	2.66
24B	D	2	Do	1	16	1.10	0.2	0.4	9.5	8.70	15.3	33.7	3.3	30.9	11.0	46.8	0.4	0.432	1.88
24B	D	2	Do	3	23	1.95	0.3	0.6	16.9	16.5	24.3	70.9	7.0	56.6	21.5	92.6	0.5	0.772	3.06
24B	D	3	Do	1	10	0.92	0.1	0.4	9.0	7.26	18.2	27.9	1.8	27.2	10.5	35.6	0.4	0.329	1.35
24B	D	3	Do	3	16	1.81	0.3	0.5	12.8	15.7	21.3	61.9	3.3	42.6	17.6	93.7	0.2	0.732	2.16
29B	D	4	Da	1	12	0.91	0.1	0.3	9.4	7.53	18.0	24.9	1.8	28.0	9.5	38.4	0.3	0.308	1.12
29B	D	5	Da	1	17	1.35	0.2	0.5	14.0	11.1	22.0	41.1	3.4	40.7	14.5	57.4	0.6	0.497	2.62
29B	D	5	Da	3	17	1.43	0.2	0.6	12.6	12.2	21.5	46.4	2.8	40.1	14.3	66.0	0.6	0.541	1.94
29B	D	6	Da	1	18	1.51	0.2	0.5	15.5	11.7	22.7	43.2	3.8	44.2	15.0	61.8	0.6	0.536	2.66
8B	D	4	Da	1	12	1.18	0.2	0.5	11.6	9.93	23.0	34.0	1.7	36.2	12.5	49.1	0.4	0.410	1.78
8B	D	4	Da	3	13	1.20	0.2	0.5	11.7	9.88	22.6	33.6	1.6	35.7	12.3	48.8	0.3	0.399	1.80
8B	D	5	Da	1	9	0.78	0.1	0.3	8.8	6.50	19.2	22.0	1.2	25.9	8.6	31.2	0.3	0.260	1.38
8B	D	5	Da	3	8	0.85	0.1	0.4	8.7	7.09	19.4	24.0	1.1	27.2	9.0	33.5	0.3	0.282	1.42
8B	D	6	Da	1	17	1.84	0.2	0.7	15.7	15.7	27.3	58.3	2.2	51.9	17.5	87.4	0.3	0.661	2.33
8B	D	6	Da	3	13	1.60	0.2	0.5	13.7	13.4	25.8	47.9	1.8	42.9	15.1	72.7	0.2	0.568	2.15
22B	D	4	Da	1	14	1.43	0.2	0.5	12.8	10.9	20.0	44.3	2.0	39.2	14.2	55.9	0.5	0.447	1.76
22B	D	5	Da	1	17	1.61	0.3	0.5	14.0	13.8	21.3	54.0	2.9	46.2	15.6	74.8	0.3	0.605	2.06
22B	D	6	Da	1	15	1.46	0.2	0.7	14.1	12.4	17.5	46.7	2.3	42.6	13.4	71.3	0.3	0.562	2.66
24B	D	4	Da	1	16	1.48	0.2	0.7	14.4	12.0	23.0	43.6	4.1	44.1	15.6	61.0	0.4	0.556	3.95
24B	D	4	Da	3	17	1.64	0.3	0.9	13.4	14.1	23.2	51.2	4.7	45.7	17.2	76.7	0.7	0.650	3.32
24B	D	5	Da	1	19	1.30	0.2	0.6	15.7	10.8	19.9	40.0	4.5	42.1	14.2	58.8	0.5	0.536	2.07
24B	D	5	Da	3	19	1.19	0.2	0.6	12.8	9.64	19.1	35.6	3.9	40.5	13.4	50.0	0.7	0.449	2.11
24B	D	6	Da	1	15	1.24	0.2	0.5	12.2	10.4	18.8	37.7	4.2	35.8	14.0	56.1	0.7	0.501	2.01
24B	D	6	Da	3	19	1.61	0.2	0.5	13.5	14.3	21.7	54.9	3.7	40.6	15.8	81.8	0.5	0.662	1.88
30A	U	1	U	1	18	1.11	0.2	0.5	11.7	9.62	17.9	30.8	3.0	31.9	11.0	51.4	0.5	0.412	1.76
30A	U	1	U	3	36	1.89	0.3	0.8	18.3	16.0	23.2	55.6	6.1	67.0	18.2	100.	0.7	0.732	2.65
30A	U	2	U	3	13	1.14	0.1	0.5	14.8	8.78	16.8	31.9	1.8	38.6	10.8	49.8	0.4	0.393	1.51
30A	U	3	U	1	11	1.48	0.2	0.3	11.3	13.4	25.5	44.8	1.5	33.8	13.8	75.9	0.2	0.578	2.09
30A	U	3	U	3	31	1.65	0.2	0.7	13.0	14.7	20.7	49.2	5.5	51.7	16.1	87.6	0.4	0.685	2.43
25A	U	1	U	1	22	1.38	0.2	0.5	16.0	10.1	21.6	34.6	4.1	42.0	13.4	54.6	0.3	0.457	2.42
25A	U	1	U	3	20	1.55	0.2	0.7	19.7	12.6	20.6	44.6	4.9	55.9	14.3	71.9	0.4	0.594	2.81
25A	U	2	U	1	23	2.15	0.2	1.4	40.6	15.6	23.1	56.4	3.6	91.5	15.6	87.3	0.3	0.710	2.55
25A	U	2	U	3	26	2.39	0.3	1.3	33.9	17.8	24.9	64.8	5.0	102.	18.6	105.	0.2	0.814	2.79
25A	U	3	U	1	11	1.35	0.2	0.6	13.4	9.97	22.5	36.4	1.7	43.5	12.6	53.5	0.4	0.435	2.12
25A	U	3	U	3	36	1.95	0.2	1.0	27.3	14.8	23.3	53.5	5.1	73.4	16.4	82.9	0.5	0.659	2.67
22A	U	1	U	1	14	1.27	0.2	0.3	11.8	11.0	20.0	37.7	2.5	33.3	12.8	60.9	0.5	0.467	1.66
22A	U	1	U	3	19	1.64	0.2	0.5	17.4	14.7	21.7	48.9	4.8	48.5	15.9	83.3	0.6	0.657	2.20
22A	U	2	U	1	12	1.10	0.2	0.3	10.9	9.59	20.5	31.6	2.0	30.2	11.9	53.4	0.4	0.417	1.55
22A	U	2	U	3	18	1.59	0.3	0.5	14.5	14.4	22.1	49.9	3.8	48.6	16.4	81.0	0.7	0.641	2.10
22A	U	3	U	1	15	1.53	0.2	0.3	15.6	12.6	25.4	43.6	3.0	44.3	14.0	69.6	0.5	0.555	1.68
22A	U	3	U	3	17	1.50	0.2	0.5	15.4	13.4	20.1	44.2	4.1	41.6	14.4	78.0	0.5	0.610	2.00

Lake	U/ D	T	U/Do /Da	Depth	Al	Ba	Cr	Cu	Fe	Mn	P	Sr	V	Zn	Ca	Mg	Na	K	P_{inorg}	C_{inorg}	C_{org}	N_{org}
29B	D	1	Do	1	46600	718	66	32	33900	1750	768	76	140	109	12800	6610	630	11500	551	0.38	6.44	0.51
29B	D	1	Do	3	59700	709	83	34	37600	546	819	78	165	122	8610	8750	785	14700	571	0.62	4.75	0.48
29B	D	2	Do	1	19100	342	26	19	17800	534	551	74	54	47	20500	4210	*	4500	181	*	35.5	1.85
29B	D	2	Do	3	50600	678	71	35	33500	676	782	79	141	107	12100	7820	767	12400	453	*	14.5	0.87
29B	D	3	Do	1	50300	643	71	30	33000	718	639	74	144	106	11300	6720	747	11900	390	0.1	7.37	0.48
29B	D	3	Do	3	63900	763	89	39	44400	934	876	80	176	134	8030	9180	951	15600	616	0.44	3.83	0.44
8B	D	1	Do	1	27500	441	46	22	21900	343	564	47	88	68	6840	5000	*	5810	442	1.67	1.69	0.14
8B	D	1	Do	3	66100	870	87	37	43700	395	922	75	175	149	7770	9370	654	14400	683	0.12	3.17	0.41
8B	D	2	Do	1	66100	790	87	39	39300	421	804	74	171	154	7680	8450	686	14200	602	*	4.61	0.44
8B	D	2	Do	3	69500	918	89	40	45500	424	921	77	178	152	7650	9610	775	15100	692	0.36	3.38	0.28
8B	D	3	Do	1	68200	814	89	40	36900	416	750	75	177	162	6710	8140	712	14400	512	0.37	6.2	*
8B	D	3	Do	3	67800	895	89	41	46300	427	954	76	175	149	7630	9420	707	14700	727	0.13	3.27	0.07
22B	D	1	Do	1	37700	484	52	20	28900	302	472	50	107	78	7510	5040	*	7010	296	0.7	3.26	0.23
22B	D	3	Do	1	34900	552	49	21	27600	691	604	55	104	88	4990	4700	*	7190	459	0.39	2	0.12
22B	D	3	Do	3	31700	442	43	22	25000	244	411	50	96	70	9550	4530	*	6540	313	2.34	3.83	0.28
24B	D	1	Do	1	52600	625	70	36	29600	467	650	67	151	116	5670	6770	534	12100	505	1.41	4.39	0.39
24B	D	1	Do	3	60400	699	79	38	45400	279	812	75	176	137	6370	8580	603	14200	552	0.11	4.07	0.41
24B	D	2	Do	1	34000	494	46	24	30700	656	612	56	108	81	6900	4620	*	7360	457	*	7.75	0.47
24B	D	2	Do	3	51600	623	71	44	43800	335	893	71	159	136	6370	8170	*	11500	642	0.4	3.6	0.41
24B	D	3	Do	1	24200	419	36	21	21700	210	616	41	79	71	7110	5480	*	5050	544	1.32	3.25	0.23
24B	D	3	Do	3	65400	773	85	32	44000	365	941	79	183	137	5550	8410	684	15400	665	0.12	3.54	0.37
29B	D	4	Da	1	21800	405	35	16	19900	364	609	45	74	58	7530	4950	*	5490	503	1.05	1.29	0.1
29B	D	5	Da	1	39000	637	59	30	32900	692	778	76	126	97	7800	6990	700	8950	538	0.11	2.82	0.17
29B	D	5	Da	3	43400	673	65	32	34800	666	921	69	131	110	9240	8180	670	9930	687	*	5.05	0.33
29B	D	6	Da	1	36000	620	54	31	31400	611	830	66	118	97	6270	5790	585	8190	601	0.01	4.18	0.25
8B	D	4	Da	1	32800	526	51	23	25500	375	752	71	97	84	16900	8500	*	7270	524	0.93	0.98	0.11
8B	D	4	Da	3	32200	534	46	23	24900	372	624	68	95	80	17400	8560	*	7230	566	0.67	0.97	0.1
8B	D	5	Da	1	24900	453	39	17	21800	286	601	52	80	68	13800	7550	*	5370	483	1.34	1.3	0.07
8B	D	5	Da	3	24600	409	38	17	20800	219	632	45	80	70	12400	8160	*	5280	529	1.41	1.18	0.16
8B	D	6	Da	1	54700	735	72	38	36400	437	817	82	150	122	14100	10800	543	12200	650	0.33	2.74	0.15
8B	D	6	Da	3	47200	674	64	30	31700	410	760	73	129	106	13100	9320	*	10400	722	1.27	1.64	0.14
22B	D	4	Da	1	39200	587	55	27	30700	418	822	62	114	98	8800	7620	*	8170	621	0.63	2.38	0.17
22B	D	5	Da	1	51000	759	71	33	36500	548	791	83	143	116	5920	7910	645	12500	630	1.04	1.58	0.13
22B	D	6	Da	1	50300	644	66	31	39200	411	640	81	133	122	17400	7350	510	11400	414	0.08	8.3	0.55
24B	D	4	Da	1	35900	601	49	36	28700	387	736	61	107	100	8950	6760	*	7860	604	*	6.9	0.39
24B	D	4	Da	3	48900	702	63	39	34600	350	909	76	142	125	10200	8120	537	11300	625	1.21	8.29	0.55
24B	D	5	Da	1	40200	701	57	30	35900	887	916	82	126	106	8880	7520	585	9670	698	0.19	3.33	0.27
24B	D	5	Da	3	34100	578	49	31	33100	443	852	60	109	102	9090	7250	*	7770	715	*	4.32	0.27
24B	D	6	Da	1	38100	634	54	33	31200	436	798	63	124	96	5940	5570	*	8540	656	2.6	3.82	0.27
24B	D	6	Da	3	56800	771	76	32	43100	685	975	78	163	120	6290	7800	633	13500	743	0.01	4.74	0.32
30A	U	1	U	1	33200	564	49	22	35600	1920	823	56	105	86	5780	4540	537	7120	489	3.12	15.1	0.93
30A	U	1	U	3	55100	768	76	47	48900	1080	1020	70	162	169	5240	6730	798	12800	488	2.88	8.86	0.86
30A	U	2	U	3	34000	441	52	23	22200	347	526	49	115	124	3610	4670	*	8010	359	0.38	4	0.37
30A	U	3	U	1	46300	586	67	26	27500	744	611	60	137	96	3440	5740	636	10800	364	0.83	4.94	0.42
30A	U	3	U	3	53700	742	75	43	41000	947	785	69	156	149	6080	6560	811	12500	324	0.58	12.2	1.04
25A	U	1	U	1	34000	632	53	29	41000	1010	935	68	111	108	4430	5190	553	8580	686	1.05	2.32	0.2
25A	U	1	U	3	48600	620	72	35	38100	686	763	66	141	156	5100	6400	751	12200	573	*	7.15	0.57
25A	U	2	U	1	56300	1020	81	38	48400	6330	1020	73	155	288	4440	6950	839	13900	765	0.38	3.63	0.41
25A	U	2	U	3	62700	880	87	41	50500	2410	1140	76	171	281	4180	7720	979	15600	812	0.1	2.92	0.28
25A	U	3	U	1	29200	453	45	28	22200	243	685	48	92	99	4140	4330	*	6800	505	1.3	3.01	0.29
25A	U	3	U	3	48400	760	70	37	49000	4480	1080	63	138	190	4420	6270	722	11700	767	0.13	4.46	0.36
22A	U	1	U	1	39100	552	57	23	29600	653	586	59	120	84	5760	5130	533	8540	550	2.28	7.39	0.58
22A	U	1	U	3	50600	690	70	31	42700	801	899	63	144	120	6100	6220	710	10700	439	0.61	13	0.9
22A	U	2	U	1	33600	498	50	21	25700	522	565	51	108	72	4530	4310	*	7060	325	5.04	5.78	0.42
22A	U	2	U	3	50600	714	67	32	45100	810	1220	59	145	114	5530	6130	558	9900	755	0.71	11.1	1.19
22A	U	3	U	1	41600	637	59	27	31000	830	623	58	126	87	4200	4990	*	8060	337	3.23	6.14	0.46
22A	U	3	U	3	48400	656	66	28	44100	867	977	60	138	112	5580	5850	612	10400	554	0.59	11.9	1.03

Appendix H: Macrophyte community structure data from *U* and *D* lakes. Lake name, undisturbed or disturbed (*U*/*D*) lakes, transect (T), undisturbed lake or opposite or adjacent areas to disturbance in *D* lakes (*U*/*Do*/*Da*), depth (*D*), and macrophyte taxa. Dry biomass data expressed as g/m^2.

Lake	U/D	T	U/Do/Da	D	P. pectinatus	Moss	M. exalbescens	Chara	R. tricophyllus	C. hermaphroditica	Z. palustris	H vulgaris	H. vulgaris fluviatilis	P. filiformis
22A	U	1	U	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25A	U	1	U	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30A	U	1	U	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22A	U	1	U	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25A	U	1	U	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30A	U	1	U	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30A	U	1	U	3	0.00	24.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22A	U	1	U	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25A	U	1	U	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22A	U	2	U	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25A	U	2	U	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30A	U	2	U	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22A	U	2	U	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25A	U	2	U	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30A	U	2	U	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22A	U	2	U	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25A	U	2	U	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30A	U	2	U	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30A	U	3	U	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.00	0.00
22A	U	3	U	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25A	U	3	U	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30A	U	3	U	2	0.00	2.76	0.00	0.61	0.00	0.00	0.00	0.00	0.00	0.00
22A	U	3	U	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25A	U	3	U	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30A	U	3	U	3	0.00	0.00	0.00	0.00	0.00	0.00	6.71	0.00	0.00	0.00
22A	U	3	U	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25A	U	3	U	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16B	D	1	Do	1	12.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	1	Do	1	9.76	0.00	38.41	0.00	0.00	9.15	0.00	15.85	0.00	0.00
29B	D	1	Do	1	0.61	158.17	14.63	0.00	0.00	0.00	0.00	7.93	0.00	0.00
8B	D	1	Do	1	21.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	1	Do	2	0.61	0.00	70.12	0.00	0.00	1.22	0.00	0.00	0.00	0.00
8B	D	1	Do	2	0.00	700.00	5.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16B	D	1	Do	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	1	Do	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16B	D	1	Do	3	0.00	0.00	0.00	0.00	1.22	0.00	0.00	0.00	12.20	0.00
24B	D	1	Do	3	31.71	0.00	1.22	0.00	0.00	0.61	0.00	0.00	0.00	0.00
8B	D	1	Do	3	0.00	0.00	0.00	67.07	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	1	Do	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16B	D	2	Do	1	2.44	4.36	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.00
24B	D	2	Do	1	11.59	44.15	42.07	0.00	0.00	1.22	0.00	0.00	0.00	0.00
29B	D	2	Do	1	0.00	0.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	2	Do	1	15.24	266.83	4.88	0.00	3.05	0.00	0.00	0.00	0.00	0.00
24B	D	2	Do	2	0.00	0.00	95.73	0.00	0.00	13.41	0.00	0.00	0.00	0.00
8B	D	2	Do	2	133.54	47.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	2	Do	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	2	Do	3	0.00	36.54	0.00	103.66	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	2	Do	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

24B	D	3	Do	1	0.00	55.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	3	Do	1	0.00	0.00	69.51	0.00	0.00	0.61	0.00	0.61	0.00	0.00
8B	D	3	Do	1	26.83	0.00	0.00	0.00	0.61	0.61	0.00	0.00	0.00	0.00
16B	D	3	Do	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	3	Do	2	28.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	3	Do	2	0.00	363.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16B	D	3	Do	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	3	Do	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16B	D	3	Do	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.88
29B	D	3	Do	3	0.61	0.00	0.00	0.00	0.61	0.00	55.49	0.00	0.00	0.00
8B	D	3	Do	3	0.00	64.06	0.00	59.76	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	3	Do	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	4	Da	1	0.00	0.00	76.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	4	Da	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	4	Da	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16B	D	4	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	4	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	4	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	4	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	4	Da	3	17.07	0.00	0.61	0.00	0.00	0.00	0.00	0.61	0.00	0.00
16B	D	4	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	4	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	4	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	5	Da	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	5	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	5	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	5	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	5	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	5	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	5	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	6	Da	1	18.90	0.00	23.78	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16B	D	6	Da	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	6	Da	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	6	Da	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	6	Da	2	0.00	0.00	4.88	0.00	0.00	1.22	0.00	0.00	0.00	0.00
16B	D	6	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	6	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	6	Da	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16B	D	6	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24B	D	6	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29B	D	6	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8B	D	6	Da	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix I: Benthic invertebrate community structure data from *U* and *D* lakes. Lake, undisturbed or disturbed (*U*/*D*) lakes, transect (T), undisturbed lake or opposite or adjacent areas to disturbance in *D* lakes (*U*/*Do*/*Da*), depth, and invertebrate taxa. Data expressed as abundance/m2.

Lake	U/ D	T	U/Do /Da	D	Ostracoda	Nematoda	Chironomidae	Oligochaeta	Hydracarina	Gammarus	Gastropoda	Bivalvia	Cladocera	Copepoda
22B	D	1	Do	1	4584	0	3056	0	0	0	0	2037	0	0
22B	D	2	Do	1	9169	3566	509	1528	0	509	0	0	0	0
22B	D	3	Do	1	0	509	1019	0	0	0	0	509	0	0
22B	D	3	Do	3	4584	2037	3056	509	0	0	0	509	0	0
24B	D	1	Do	1	10815	0	877	6138	0	0	0	877	0	0
24B	D	1	Do	2	14030	292	292	2338	0	0	0	585	0	292
24B	D	1	Do	3	14322	11107	4677	1754	0	0	0	1754	0	0
24B	D	2	Do	1	16953	1169	2631	2631	0	877	0	0	877	1754
24B	D	2	Do	2	43260	292	2923	4092	0	0	0	585	0	2046
24B	D	3	Do	1	31860	9646	1461	877	0	0	0	2046	0	0
24B	D	3	Do	2	25137	18415	877	3800	0	0	0	1754	292	292
24B	D	3	Do	3	63428	18707	2631	1169	0	0	0	877	585	292
29B	D	1	Do	1	4384	5261	0	2631	292	292	0	0	0	0
29B	D	1	Do	2	3800	0	292	585	0	0	0	0	0	0
29B	D	1	Do	3	2631	292	0	292	0	0	0	0	0	0
29B	D	2	Do	1	5554	0	0	1169	0	877	0	877	0	292
29B	D	2	Do	2	1754	0	0	0	0	0	0	292	292	0
29B	D	3	Do	2	2923	2338	292	1461	0	0	0	0	292	0
29B	D	3	Do	3	11984	2923	0	877	0	0	0	0	292	292
8B	D	1	Do	1	2037	0	2547	0	0	0	0	1528	0	0
8B	D	1	Do	2	3056	0	1528	0	0	509	0	0	0	0
8B	D	1	Do	3	9678	509	509	1019	0	0	0	509	0	0
8B	D	2	Do	1	2037	0	3566	509	509	0	0	0	1019	1019
8B	D	2	Do	2	9169	0	0	2547	0	0	0	1019	0	0
8B	D	2	Do	3	10697	0	2037	3566	0	0	0	509	0	1528
8B	D	3	Do	1	2547	509	2547	1528	0	1019	0	0	509	1019
8B	D	3	Do	2	1528	0	3566	2037	0	0	0	1019	0	0
16B	D	1	Do	3	26487	509	5094	1528	0	0	0	3056	0	509
16B	D	2	Do	1	5603	0	2547	509	0	1019	0	0	0	0
16B	D	3	Do	1	2547	6112	0	3566	0	0	0	509	0	509
16B	D	3	Do	3	22922	509	3566	7641	0	0	0	509	0	0
22B	D	4	Da	1	11206	0	14262	1528	0	0	0	2037	0	0
22B	D	4	Da	2	20884	0	9169	2037	0	0	0	0	0	0
22B	D	4	Da	3	4075	509	2037	509	0	509	0	1528	0	0
22B	D	5	Da	1	3566	0	509	509	0	0	0	0	0	0
22B	D	6	Da	1	35147	0	7641	8659	0	0	0	2037	0	0
22B	D	6	Da	2	1019	509	1528	2547	0	0	0	1019	0	0
22B	D	6	Da	3	7641	0	4075	3056	0	509	0	1019	0	0
24B	D	4	Da	1	26891	585	585	292	0	0	0	292	292	1754
24B	D	4	Da	2	48813	2338	0	292	0	0	0	292	0	8184
24B	D	4	Da	3	53490	0	2338	585	0	0	0	1169	877	17538
24B	D	5	Da	1	7600	2923	292	9938	292	0	0	4677	0	1169
24B	D	5	Da	2	23676	5261	1169	2923	292	1461	0	5846	0	2923
24B	D	5	Da	3	12276	4384	1754	877	0	0	0	877	2631	7015
24B	D	6	Da	1	10523	12569	877	7892	0	0	0	2631	0	877
24B	D	6	Da	2	67812	14322	0	1169	0	292	0	877	585	2338
24B	D	6	Da	3	97334	3215	2631	2923	0	0	0	5846	877	6723
29B	D	4	Da	1	6622	509	1528	15281	0	509	0	1019	0	0
29B	D	4	Da	2	54503	509	2037	3566	0	0	0	509	0	0
29B	D	5	Da	1	15281	1528	0	8150	0	0	0	2037	509	509

29B	D	5	Da	2	16809	0	1528	11206	0	0	0	509	1019	509
29B	D	5	Da	3	43297	0	509	3056	509	0	0	0	3056	0
29B	D	6	Da	1	13753	0	1019	9169	509	0	0	1528	8659	0
8B	D	4	Da	1	14262	0	4584	509	0	0	0	0	0	1019
8B	D	4	Da	3	11716	509	2037	0	0	0	0	0	0	0
8B	D	5	Da	1	4075	1019	14262	2037	0	509	0	2547	0	4075
8B	D	5	Da	3	14262	3056	14262	1528	509	0	0	1528	0	2547
8B	D	6	Da	1	6112	33109	9678	4075	0	0	0	509	509	2547
8B	D	6	Da	3	15281	4075	3566	2037	0	0	0	509	0	1528
16B	D	4	Da	1	8150	0	4075	3056	0	0	0	0	0	0
16B	D	6	Da	1	5603	1528	0	509	509	0	0	509	0	0
16B	D	6	Da	3	6112	1019	2547	1528	509	0	0	0	0	0
24B	D	2	Do	3	49106	40337	2046	292	0	0	292	585	585	4092
29B	D	2	Do	3	10523	0	292	2923	0	0	292	1169	1754	0
29B	D	3	Do	1	23676	5554	6138	4384	292	0	292	585	1169	8769
8B	D	3	Do	3	7641	0	509	0	0	0	509	0	0	0
16B	D	4	Da	3	24450	0	2037	509	509	0	509	0	0	509
16B	D	1	Do	1	12225	509	4584	6622	0	0	1019	2037	0	1019
22A	U	1	U	1	2547	0	6112	5094	0	0	0	2037	0	5094
22A	U	1	U	2	1019	0	3566	3056	0	0	0	0	509	1019
22A	U	1	U	3	1019	1019	6622	2037	0	0	0	509	0	5603
22A	U	2	U	1	509	0	10187	3566	0	0	0	3566	0	509
22A	U	2	U	2	2037	3566	10187	6112	0	0	0	509	509	509
22A	U	2	U	3	2037	0	6112	1528	0	0	0	1019	509	0
22A	U	3	U	1	1528	509	6112	3566	0	0	0	2547	0	509
22A	U	3	U	2	0	0	2037	2547	0	0	0	509	0	509
22A	U	3	U	3	1528	0	4075	1019	0	0	0	0	0	2547
25A	U	1	U	1	9061	292	1754	2338	0	0	0	1169	0	292
25A	U	1	U	2	2338	292	3508	0	0	0	0	292	0	1169
25A	U	1	U	3	4092	0	2046	0	0	0	0	292	0	585
25A	U	2	U	1	4677	877	8477	0	0	0	0	4092	292	12569
25A	U	2	U	2	292	585	3215	292	0	292	0	0	0	0
25A	U	2	U	3	1169	585	1461	0	0	0	0	0	0	0
25A	U	3	U	1	8769	0	20461	4969	0	0	0	292	0	4969
25A	U	3	U	2	3215	292	2923	585	0	0	0	0	0	292
25A	U	3	U	3	6430	585	1754	0	0	0	0	292	0	292
30A	U	1	U	1	6112	509	509	5094	509	0	0	1019	0	1019
30A	U	1	U	2	6622	0	1528	1019	0	0	0	1528	0	0
30A	U	1	U	3	4584	0	0	1019	0	0	0	0	0	0
30A	U	2	U	2	4075	0	2547	509	0	0	0	1019	0	0
30A	U	2	U	3	4584	0	2037	1528	0	0	0	1528	0	0
30A	U	3	U	1	11716	0	4584	4075	0	0	0	2547	0	3056
30A	U	3	U	2	4075	0	509	1019	0	0	0	509	0	1019
30A	U	3	U	3	5603	0	509	1528	0	0	0	509	0	0