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Relationships between freshwater sedimentary diatoms and environmental variables in Subarctic Icelandic lakes

Tammy L. Karst-Riddoch[1, *], **Hilmar J. Malmquist**[2] and **John P. Smol**[1]

Paleoecological Environmental Assessment and Research Laboratory (PEARL), Department of Biology, Queen's University, Canada

With 6 figures and 7 tables

Abstract: The distribution patterns of surface sediment diatom assemblages from 49 lakes were used to explore the relationship between limnological variables and diatom assemblages as well as to assess an ecological classification system as a tool for the management and conservation of Icelandic freshwaters. Lakes were limnologically diverse ranging from deep, oligotrophic, ionically dilute lakes, to shallow lakes with a wide range of nutrient and ionic contents. Physical conditions (depth, surface area, surface water temperature) and nutrient and ion concentrations differed significantly among ecological lake categories (i.e., plateau, spring-fed, direct-runoff, valley, glacial, and coastal lakes) (ANOVA, $p < 0.05$). Diatom assemblages were taxonomically diverse (329 taxa) with strong representation of planktonic, benthic and periphytic forms. Small benthic *Fragilaria sensu lato* (19 species and varieties) were the most abundant with combined abundances > 20 % in all but 4 of the lakes, most likely due to the generally cold lake water conditions in this subarctic region. Variation in diatom distributions was best explained by the combination of mean depth (influencing littoral versus planktonic habitats), surface water temperature, specific conductivity, alkalinity, total organic carbon, total nitrogen and SiO_2 in a canonical correspondence analysis (CCA). However, these variables did not explain distribution patterns amongst small benthic *Fragilaria* taxa, although some weak relationships between some taxa and these variables were evident. Distinct diatom assemblages and limnological properties among ecological lake categories support the classification of Icelandic freshwaters based on major topographic, geological and hydrological characteristics. More detailed inclusion of lake depth along with lake basin form, as well as more refined categories of lake water origin and topographical positioning to better approximate regional climatic conditions, may improve the ecological classification of Icelandic freshwaters for conservation and management practices.

Key words: diatom ecology, ecological lake classification, *Fragilaria,* Iceland, limnology, North Atlantic, paleolimnology, subarctic lakes.

Introduction

Lakes located in subarctic regions are sensitive ecosystems that represent ecologically and economically important freshwater resources. The physical and chemical properties of subarctic lakes, and hence their aquatic biota, are especially susceptible to both natural and human-induced environmental impacts (Schindler & Smol 2006). In Iceland, a subarctic island located in the North Atlantic Ocean (Fig. 1), a combination

Authors' addresses:

[1] Paleoecological Environmental Assessment and Research Laboratory (PEARL), Department of Biology, Queen's University, Kingston, Ontario, Canada, K7 L 3N6.

[2] Natural History Museum of Kópavogur, Hamraborg 6a, 200 Kópavogur, Iceland.

[*] Corresponding author; e-mail: Tammy.Karst@aecom.com

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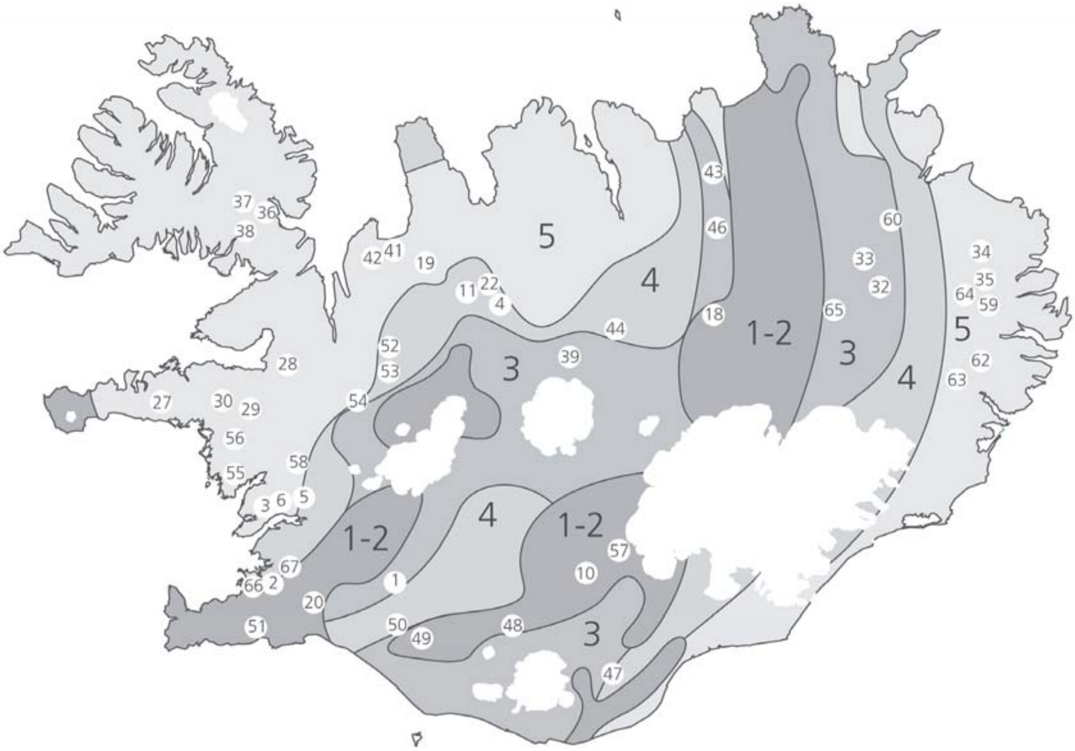

Fig. 1. Location of lakes analysed in this study (numbers refer to lake names provided in Table 1) and zonation of five major bedrock classes in Iceland (modified from Jóhannesson & Saemundsson 1998): 1–2) Historical (< 0.0011 Ma) and postglacial prehistoric (0.0011–0.01 Ma) basic and intermediate lavas; 3) Upper Pleistocene (0.01–0.8 Ma) basic and intermediate hyaloclastite pillow lava, interglacial and supraglacial lavas; 4) Upper Pliocene and Lower Pleistocene (0.8–3.3 Ma) basic and intermediate extrusive rocks; and 5) Upper Tertiary (> 3.3 Ma) basic and intermediate extrusive rocks.

of natural geomorphic, climatic and anthropogenic impacts has profoundly altered the terrestrial landscape over the course of the Holocene (Gerrard 1991, Maizels & Caseldine 1991). Such major environmental factors have undoubtedly influenced the limnology and biology of lakes in the region. However, as with other islands of the northern north Atlantic, contemporary and long-term limnological and paleolimnological data are limited (Anderson et al. 2004).

Large-scale and often catastrophic geomorphic events are common in Iceland because it is situated astride the geologically active Mid-Atlantic Ridge (MAR), a zone of plate divergence in the Atlantic Ocean. A 400-km long segment of the MAR is exposed and crosses Iceland from the southwest to the northeast, creating several volcanic zones with numerous active central volcanoes (Saemundsson 1986) and seismic epicentres (Einarsson 1986). Since deglaciation ca. 10 000 years ago, both land and lakes within the volcanic zones have been reshaped by processes related to postglacial volcanism and rifting (e.g., Saemundsson 1992), including the deposition of lava and ash over the landscape. Because of the volcanic origin of Icelandic soils, they are mainly andosols, which are easily weathered by streams, wind, ice, landslides and major meltwater flood events from subglacial thermal areas and volcanoes (Arnalds 1999). Areas flanking the active volcanic zones have undergone extensive soil erosion exposing underlying lava shields and contributing to high sediment deposition oceanward to the shelf around Iceland (Saemundsson 1986).

Postglacial climatic change has also influenced the Icelandic landscape. Several sedimentological studies of marine sediment cores off the coast of Iceland have documented significant climatic changes over the Holocene (e.g., Andrews et al. 2001a, b, Jennings et al. 2001, Andrews & Giraudeau 2003). Doner (2003) determined that erosion cycles over the last 1000 years in northwest Iceland are strongly linked to the North Atlantic Oscillation (NAO) from sedimentological and geochemical analysis of lake cores. In the same study, increased erosion rates during the Little Ice Age are inferred to have enhanced algal productivity via the influx of limiting nutrients (Doner 2003). In response to climate change, numerous glaciers throughout Iceland have undergone several advances and recessions during the Holocene (Martin et al. 1991, Gudmundsson 1997), reshaping the landscape through moraine deposits, glacial meltwater flow and sand development. In addition, cyclones are a common climatic disturbance, frequently reaching the southwest coast of Iceland, causing rapid, drastic changes in wind patterns and precipitation (Einarsson 1984).

Human impacts have been substantial on terrestrial and aquatic environments since European settlement of Iceland ca. AD 870. Agricultural practices, including deforestation, overgrazing and draining of wetlands, have been major, long lasting contributors to the extensive losses of soil (Thórarinsson 1962, Thorsteinsson & Arnalds 1992, Arnalds 1999, Ólafsdóttir & Gudmundsson 2002) and vegetative cover (Bjarnason 1978, Thorsteinsson & Arnalds 1992, Ólafsdóttir & Gudmundsson 2002) throughout Iceland. These factors along with hydroelectric development, road works and diatomite extraction are considered to constitute the main anthropological impacts on freshwater in Iceland (Malmquist 1998, Malmquist et al. 2001, WWF 2001, Ólafsson et al. 2002a, Einarsson et al. 2004). Other impacts on Icelandic freshwater ecosystems, resulting in changed faunal diversity and altered food web structures, include transplantations of salmonid fish to fishless areas and opening access of salmonids to upstream river sections (Malmquist 1998, Ólafsson et al. 2002a) and, most recently, climate warming (Malmquist et al., in press).

Future environmental changes on lakes and aquatic biota in Iceland are likely in light of geological (e.g., volcanism and rifting) and climatic events, and continued human influences. Recognizing the wide range of lake typology in Iceland, Garðarsson (1979) proposed an ecological classification system for Icelandic freshwater lakes to assist conservation efforts in consideration of these potential impacts. This 'lake type' classification is based on major geological, topographical and hydrological features that potentially have a large influence on the physical, chemical and biological conditions of Icelandic lakes (Garðarsson 1979). However, Garðarsson's (1979) classification system is qualitatively developed from the study of only a few freshwater systems with limited measured data, and this approach has not been formally tested for lakes. Recently, background water quality and aquatic biological community data on a landscape scale has become available to critically identify and monitor the effects of future environmental change on lakes, as well as to develop sound environmental impact assessments and conservation strategies. In 1992, the Ecological Survey of Icelandic Lakes (ESIL) was initiated to provide a standardized database of biological, limnological, hydrological and geological information on the main types of Icelandic lakes (Malmquist 1997, 1998, et al. 2000, 2001). Also, in 1995, an ecological survey of running waters in Iceland was started (Gíslason et al. 1998, Ólafsson et al. 2001, 2002b).

Studies of the modern distribution and community composition of diatom assemblages in relation to environmental conditions can provide important ecological information to assess past lake responses to environmental change in paleolimnological studies (Stoermer & Smol 1999) and to aid in the management of lakes (Smol 2008). Such studies exist for subarctic regions throughout North America (e.g., Pienitz & Smol 1993, Pienitz et al. 1995, Gregory-Eaves et al. 1999, Fallu et al. 2002, Rühland & Smol 2002, Wilson & Gajewski 2002, Rühland et al. 2003a, b) and Europe (e.g. Weckström et al. 1997, Bigler and Hall 2002). Various chapters in Pienitz et al. (2004) provide summaries for many of these regions. However, these studies may not be directly applicable for use in Iceland, which presents a unique subarctic environment with a very different climatic regime and geological structure. Several early taxonomic studies of the diatom flora of Iceland are reviewed in Foged (1974) and Hallgrímsson (2007), but few have investigated ecological preferences and/or distribution patterns of diatoms in Icelandic lakes. Notably, Foged (1974) published an extensive taxonomic treatise of mainly freshwater epipelic, epilithic and epiphytic diatom flora collected in 1954 from 170 localities in Iceland. More recently, Jónsson (1992) provided a detailed account of the community structure and metabolism of epilithic diatoms from Thingvallavatn, a large, oligotrophic lake in southwest Iceland.

This study explores the modern limnological characteristics and diatom assemblages from the surface sediments of 49 Icelandic lakes spanning a wide range of environmental conditions from samples collected between 1992 and 1998 as part of the Ecological Survey of Icelandic Lakes (ESIL) (Malmquist 1997, 1998, Malmquist et al. 2000). Observed distributional and ecological trends in the diatom assemblages are then used to assess the ecological classification system for Icelandic freshwaters of Garðarsson (1979), and its usefulness for effective conservation planning. Identified relationships between the composition of sedimentary diatom assemblages and limnological conditions provide an important framework for the use of diatoms as paleolimnological indicators to assess the response of Icelandic lakes to past natural- and human-induced environmental change. Importantly, this work provides baseline data for future monitoring, conservation planning and environmental assessment of Icelandic lakes.

Study area

The 49 lakes in this study span a wide geographic area to encompass the broad range of environmental conditions that characterize Iceland. Iceland is a large subarctic island (103,100 km^2) located between the latitudes of 63° 23′ and 66° 32′ N and longitudes of 13° 30′ and 24° 32′ W in the North Atlantic Ocean (Fig. 1). Glaciers cover approximately 11.5 % of the landscape, with the largest glacier, Vatnajökull, measuring about 8,400 km^2. Lowlands and river plains (< 200 m a.s.l.) occur mainly along the southern coastline, but approximately 75 % of the land is considered mountainous with elevations greater than 200 m a.s.l. (CBD, 2001). Plateaus dominate the interior of Iceland along a southwest to northeast transect of the exposed Mid-Atlantic Ridge (MAR).

The climate of Iceland in the south and west is temperate rainy with cool, short summers, while a snow climate predominates in the north and central highland regions. The occurrence of these two distinct climatic regimes in Iceland, as well as weather, is largely influenced by both meteorological (e.g., oceanic and atmospheric circulation patterns) and geographical factors (e.g., topography, latitude, and sea ice extent) (Einarsson 1984, Hanna et al. 2004). The North Atlantic Drift and Irminger Current carry warm waters northward along the south, west and north coasts of Iceland meeting the cold East Greenland Current (East Iceland Current), which flows southward along the east coast. Similarly, warm temperate and cold polar front air masses meet near Iceland. The convergence of these major air masses often creates cyclones that can cause rapid, drastic changes in Icelandic weather (Einarsson 1984). Mean annual temperatures in the southern and northern coastal lowlands ranges from 4–5ºC and 3–4ºC, respectively, and are slightly cooler in inland and highland areas. The annual range of temperatures in Iceland is small, ranging from 9–11 ºC near the coasts, and 12–13 ºC in most inland regions (Einarsson 1984, Hanna et al. 2004). Mean annual precipitation is variable within short distances, but is generally highest (often greater than 4,000 mm) in the southeast falling ahead of cyclones that typically arrive from the southwest of Iceland. Lowest annual precipitation (less than 600 mm) occurs in the north and northeast.

Lava formations that are rich in easily weathered basalts dominate the bedrock of Iceland. The five major bedrock classes (modified from Jóhannesson & Saemundsson 1998) include: 1) Historical (< 0.0011 Ma) basic and intermediate lavas; 2) Postglacial prehistoric (0.0011–0.01 Ma) basic and intermediate lavas; 3) Upper Pleistocene (0.01–0.8 Ma) basic and intermediate hyaloclastite pillow lava, interglacial and supraglacial lavas; 4) Upper Pliocene and Lower Pleistocene (0.8–3.3 Ma) basic and intermediate extrusive rocks; and 5) Upper Tertiary (> 3.3 Ma) basic and intermediate extrusive rocks (Fig. 1).

Soils are of volcanic origin formed by the rapid weathering of volcanic glass and crystalline parent materials, and are mainly basaltic in composition (Arnalds 1999). They exhibit typical andic properties with generally high concentrations of carbon, low bulk density, and lack cohesion because of low concentrations of clay minerals (Wada 1985). Icelandic soils are highly unstable and are strongly influenced by volcanic activity, cryogenic processes and active erosion (Arnalds 1999). Erosion is extreme in many areas of Iceland, creating approximately 40 000 km^2 of barren landscapes with infertile desert soils (Arnalds 1999). Recent studies suggest that erosion and related inwash events into lakes has been a major problem since the early Holocene (e.g., Caseldine et al. 2006, Wooller et al. 2008).

The 49 lakes in this study span a wide range of physical settings with differing bedrock geology and hydrology, as described by the ecological lake type categories proposed by Garðarsson (1979) and modified by the Ecological Survey of Icelandic Lakes (ESIL) working group (Malmquist 1997, 1998, Malmquist et al. 2000). The lake type categories include: 1) spring-fed lakes; 2) plateau lakes; 3) direct-runoff lakes; 4) valley lakes; 5) glacial lakes; and 6) coastal lakes. 'Spring-fed' lakes are found mostly in catchments dominated by postglacial and younger palagonite bedrock formations and are fed by cold-water spring-inlets that are characterized by annually stable temperatures and nutrients. 'Spring-fed' lakes display a wide range of depths and sizes, but are generally rich in dissolved nutrients and minerals. 'Plateau' lakes are mostly situated on vegetated heaths in the unpopulated highlands (~200–400 m a.s.l.) in catchments primarily of lower Pleistocene and Tertiary bedrock origin. The lakes are typically shallow, with moderate to high specific conductance, and are often buffered by direct runoff in vegetated wetland systems. 'Direct-runoff' lakes are similar to 'plateau' lakes in that they are generally shallow but, by contrast, they are situated in poorly vegetated and mostly barren highlands at higher elevations (> 400 m a.s.l.) and have relatively lower conductivities. 'Val-

Table 1. Geographic location and bedrock conditions of 49 calibration lakes classified by lake TYPE categories ('plateau', 'direct-runoff', 'spring-fed', 'valley', 'glacial' and 'coastal') modified from Garðarsson (1979). See also text in chapter on Study area and Fig. 1.

Lake Type	Lake Name	Lake No.	Latitude UTM (N)	Longitude UTM (W)	Location Code[2]	Bedrock Class[1]
Plateau:						
	Mjóavatn	11	6515	1948	NW	4
	Svartárvatn	18	6520	1714	NE	2
	V.-Friðmundarvatn	22	6518	1441	NW	4
	Oddastaðavatn	30	6454	2213	W	5
	Ánavatn	32	6513	1531	NE	4
	Sænautavatn	33	6516	1531	NE	4
	Eiðavatn	34	6524	1421	NE	5
	Urriðavatn	35	6517	1951	NE	5
	Vesturhópsvatn	42	6528	2039	NW	5
	Langavatn Þing.	43	6549	1717	NE	4
	Reyðarvatn Hofs.	44	6506	1832	SW	4
	Másvatn	46	6538	1714	NE	3
	Eystra-Gíslholtsvatn	49	6357	2029	S	3
	Hólmavatn/Tungukollur	52	6502	2033	NW	4
	Arnarvatn Stóra	53	6457	2019	NW	4
	Úlfsvatn	54	6453	2035	W	4
	Hólsvatn	55	6431	2208	W	5
	Sauravatn	56	6440	2207	W	5
	Sandvatn	64	6518	1441	NE	5
	Vífilsstaðavatn	66	6404	2152	SW	3
	Hafravatn	67	6407	2144	SW	3
Direct runoff:						
	Högnavatn	37	6548	2210	Wf	5
	Ónefntvatn	38	6542	2206	Wf	5
	Þuríðarvatn	60	6536	1510	NE	5
	Ódáðavatn	63	6450	1444	E	5
Spring-fed:						
	Apavatn	1	6410	2038	S	3
	Elliðavatn	2	6405	2148	W	1
	Langavatn	10	6407	1849	S	1
	Úlfljótsvatn	20	6406	2102	S	2
	Ásbjarnarvatn S.	39	6503	1848	NW	3
	Fljótsbotn	47	6352	1854	S	1
	Frostastaðavatn	48	6401	1903	S	2
	Langisjór	57	6410	1817	SW	3
Valley:						
	Eyraravatn	3	6425	2136	W	5
	Galtaból	4	6515	1943	NW	4
	Geitabergsvatn	5	6427	2131	W	5
	Glammastaðavatn	6	6426	2135	W	5
	Svínavatn	19	6532	2006	NW	5
	Baulárvallavatn	27	6455	2255	W	3
	Haukadalsvatn	28	6535	2137	W	5
	Hítarvatn	29	6453	2155	W	5
	Þiðriksvallavatn	36	6541	2146	Wf	5
	Hestvatn	50	6401	2042	S	4
	Skorradalsvatn	58	6427	2109	W	5
	Skriðuvatn	62	6457	1438	E	5
	Þríhyrningsvatn	65	6510	1546	NE	3
Glacial:						
	Lagarfljót	59	6510	1438	NE	5
Coastal:						
	Hópið	41	6531	2030	NW	5
	Hlíðarvatn	51	6352	2143	SW	2

[1] modified from Jóhannesson & Saemundsson (1998), 1 (Historical), 2 (Postglacial), 3 (Upper Pleistocene), 4 (Upper Pliocene and Lower Pleistocene), 5 (Upper Tertiary);
[2] E (east), NE (northeast), NW (northwest), W (west), Wf (west fjords), S (south), SW (southwest)

Table 2. Recently used synonyms for common diatom taxa found in the 49 Icelandic study lakes.

Taxon and authority	Synonym
Achnanthes clevei Grun.	*Karayevia clevei* (Grun. in Cleve & Grun.) Bukht. & Round
Achnanthes marginulata Grun.	*Psammothidium marginulatum* (Grun.) Bukht. & Round
Achnanthes minutissima Kütz.	*Achnanthidium minutissimum* (Kütz.) Czarn.
Achnanthes peragalli Brun & Hérib.	*Planothidium perigallii* (Brun & Hérib. in Hérib.) Bukht. & Round
Anomoeneis vitrea (Grun.) Ross	*Brachysira vitrea* (Grun.) Ross in Hartley
Cymbella minuta Hilse (ex. Rabenh.)	*Encyonema minutum* (Hilse ex Rabenh.) D. G.Mann in Round, Crawford & Mann
Cymbella silesiaca Bleish (in Rabenh.)	*Encyonema silesiacum* (Bleisch ex Rabenh.) D. G.Mann in Round, Crawford & Mann)
Fragilaria arcus (Ehrenb.) Cleve	*Hannaea arcus* (Ehrenb.) R. M.Patrick
Fragilaria brevistriata Grun. (in Van Heurck)	*Pseudostaurosira brevistriata* (Grun. in VanHeurck) D. M.Williams & Round
Fragilaria brevistriata var. *inflata* (Pantocsek) Hust.	*Pseudostaruosira brevistriata* var. *inflata* (Pant.) M. B.Edlund
Fragilaria construens var. *binodis* (Ehrenb.) Grun.	*Staurosira construens* var. *binodis* (Ehrenb.) Hamilton in Hamilton, Poulin, Prévost, Angell & Edlund
Fragilaria construens var. *venter* (Ehrenb.) Hust.	*Staurosira construens* var. *venter* (Ehrenb.) Hamilton
Fragilaria lapponica Grun.	*Staurosirella lapponica* (Grun. in VanHeurck) D. M.Williams & Round
Fragilaria parasitica (W. Smith) Lange-Bert.	*Synedra parasitica* (W. Sm.) Hust.
Fragilaria pinnata Ehrenb.	*Staurosirella pinnata* (Ehrenb.) D. M.Williams & Round
Fragilaria pinnata var. *intercedens* (Grun. in Van Heurck) Hust.	*Staurosirella pinnata* var. intercedens (Grun. in VanHeurck) Hamilton in Hamilton, Poulin, Prévost, Angell & Edlund
Navicula capitata Ehrenb.	*Hippodonta capitata* (Ehrenb.) Lange-Bert., Metzeltin & Witkowski
Navicula cocconeiformis Gregory	*Cavinula cocconeiformis* (Greg. ex Grev.) D. G.Mann & Stickle in Round, Crawford & Mann
Navicula elginensis (Gregory) Ralfs	*Placoneis elginensis* (Greg.) E. J.Cox
Navicula pseudoscutiformis Hust.	*Cavinula pseudoscutiformis* (Hust.) D. G.Mann & Stickle in Round, Crawford & Mann
Navicula seminulum Grun.	*Sellaphora seminulum* (Grun.) D. G.Mann
Rhizosolenia longiseta Zach.	*Urosolenia longiseta* (Zach.) M. B.Edlund & Stoermer

ley' lakes are large, deep, dilute lakes mostly situated in narrow valleys. Bedrock conditions and source of water origins are variable, but valley lakes are usually fed by direct runoff on poorly vegetated catchments of lower Pleistocene and Tertiary bedrock. 'Glacial' lakes are fed by glacial meltwater and are highly silted and turbid. Finally, 'coastal' lakes are low elevation lakes (0–10 m a.s.l.) that are proximal to coastal areas, and are saline due to marine inputs.

Methods

Sample collection

Limnological measurements were done and surficial sediments were collected from the deepest part of 49 lakes in Iceland in late-July to mid-September 1992–1998 by the Ecological Survey of Icelandic Lakes (ESIL) working group. The lakes were selected primarily according to lake size and depth, type of bedrock in the catchment and elevation to provide a representative set of lakes that span major physical gradients in Iceland. In each lake, a single sediment sample was collected with a Kajak corer, and the topmost 1–2 cm sediment layer retained and kept unfixed in a brown glass bottle in darkness until later analyses. Temperature, pH and conductivity were measured at the coring sites at 40–150 cm below surface. A water sample (1 L) was taken from each lake at the coring site at 20–40 cm below surface and the samples kept frozen for later analyses of chemical variables. Chemical analyses were conducted on unfiltered water samples at the Norwegian Institute of Water Research in Oslo. The environmental data set included 10 physical variables [latitude (LAT), longitude (LONG), altitude (ALT), mean depth (MD), maximum depth (Z_{max}), volume (VOL), surface area (SA), discharge (DISCH), drainage area (DRAIN), surface water temperature (TEMP)], 19 chemical variables [specific conductivity (COND), alkalinity (ALK), pH, total organic carbon (TOC), total phosphorus (TP), total nitrogen (TN), PO_4-P, NH_4-N, NO_3-N, SiO_2, Mg, Na, Ca, K, Cl, F, Al, Fe, SO_4], and 3 categorical variables [location (LOC), bedrock (BED), ecological lake type (TYPE)] (Table 1). Location (LOC) refers to the general geographical position (north, northeast, west, southwest, west fjords, east) of the sample lakes. Bedrock classes are modified from Jóhannesson & Saemundsson (1998) and lakes have been assigned to one of 6 ecological lakes type (TYPE) classes from the classification scheme for Icelandic freshwaters proposed by Garðarsson (1979) and modified by Malmquist et al. (2000). TYPE classes include: 1) plateau lakes; 2) direct-runoff lakes; 3) spring-fed lakes; 4) valley lakes; 5) glacial lakes, and 6) coastal lakes. Few of the lakes could be classified into a mixture of two categories. Notable examples are Lake Svartárvatn and Vífilsstaðavatn, both classified as plateau lakes in Table 1, but these are also quite strongly influenced by spring-fed inlets. Lake Apavatn could also be classified as a mixture of spring-fed and direct-runoff. Lake Másvatn could also be classified as a mixture plateau, direct run-off and valley.

Diatom sample preparation and enumeration

Samples for diatom analysis were prepared by acid digestion using standard methods (Wilson et al. 1996). Following acid digestion, many of the diatom samples contained long chains (often more than 20 valves) of small, benthic diatoms of the genera *Fragilaria, Staurosira, Staurosirella* and *Pseudostaurosira* (see Table 2 for taxonomic synonyms; formerly of the genus *Fragilaria* and herein collectively referred to as *Fragilaria sensu lato*). Long chains of these taxa caused difficulties in taxonomic identification of morphologically similar valves, an uneven distribution of valves across the coverslip, and the potential over-representation of *Fragilaria sensu lato* in the diatom counts. Therefore, problematic samples were sonicated prior to counting to disperse the *Fragilaria sensu lato* valves, resulting in a more even distribution of diatoms across the coverslip and greater numbers of valves positioned in valve view on the slide. Diatom valves were then identified and counted (~500 per sample) across transects of the coverslip at 1000× magnification using a Leitz DMRB light microscope fitted with differential interference optics (numerical aperture = 1.30). Primary taxonomic references for diatom identification included Foged (1974, 1981) and Krammer & Lange-Bertalot (1986–1991). Although diatom nomenclature continues to change, and new names continue to be debated, we have primarily used the taxonomic systems cited above to be consistent with the many Arctic and Subarctic diatom calibration sets published by our lab (and others). For some of the common taxa, we also supply synonyms of more recently used designations in Table 2.

Numerical analyses

Chemical variables with missing values or values below detection limits in more than 10 % of the lakes were eliminated from the environmental data set (i.e., DISCH, DRAIN, PO_4-P, NH_4-N, NO_3-N, F, Al). Otherwise, variables with missing values [pH (1 lake), ALK (3 lakes)] were replaced by the mean for that variable (and so would not influence our statistical analyses) and values below detection limits were set to the detection limit value. To correct for skewed distributions, log transformations were applied to MD, Z_{max}, COND, Mg, TOC, TN, Na, Fe, K, Cl, and SO_4, and SiO_2 was square-root transformed. Transformation of LAT, LONG, ALT, VOL, AREA, and TP did not correct the strongly skewed distributions of these variables, and they were eliminated from the data set.

Diatom taxa were expressed as relative abundances. Only those taxa with a relative abundance of at least 1 % in one lake and present in a minimum of 3 lakes were retained for further analyses. The relative abundances of all diatom taxa were square root transformed to stabilize variances and optimize the signal to noise ratio in the data following Brooks & Birks (2000) in all statistical analyses.

Three lakes were removed from statistical analyses (ANOVA, multivariate ordinations) reducing the original 49-lake data set to 46 lakes. These included the only two 'coastal' lakes, Hópið (41) and Hlíðarvatn (51), which were saline due to strong marine influence (Table 3), and had extreme environmental influence on COND (> 20 times influence) in a preliminary canonical correspondence analysis (CCA) of the diatom and environmental data. Also removed from statistical analyses was the deepest lake (maximum depth = 111.5 m), Lagarfljót (59), the only proglacial lake, which was an outlier on the first axes in a preliminary principle components analysis (PCA) of the environmental variables, and displayed > 10 times influence on MD and Fe in a preliminary CCA.

Pearson correlation with Bonferroni-adjusted probabilities was used to determine significant relationships ($p \leq 0.05$)

Table 3. Measured physical and chemical characteristics of the 49 calibration lakes classified by TYPE categories (modified from Garðarsson 1979)[1]. Information on ALT, AREA, MD and Zmax is partly based on Aðalsteinsson et al. (1989).

Lake type	Lake no.	Lake name	Year sampled	ALT m	AREA km^2	MD m	Zmax m	VOL Gl	TEMP °C	TP $\mu g\ l^{-1}$	TN $\mu g\ l^{-1}$	TOC $mg\ l^{-1}$	SiO_2 $mg\ l^{-1}$	COND $\mu S\ cm^{-1}$	pH	ALK $meq\ l^{-1}$	Cl $mg\ l^{-1}$	SO_4 $mg\ l^{-1}$	Ca $mg\ l^{-1}$	Fe $\mu g\ l^{-1}$	K $mg\ l^{-1}$	Mg $mg\ l^{-1}$	Na $mg\ l^{-1}$
All lakes:																							
		Mean:		**269**	**5.1**	**7.4**	**18.7**	**93.0**	**10.8**	**16**	**167**	**1.19**	**5.8**	**105**	**7.08**	**0.41**	**9.8**	**2.5**	**4.81**	**179**	**0.50**	**2.41**	**8.24**
		Maximum:		**770**	**53.0**	**51.0**	**111.5**	**2703.0**	**14.8**	**74**	**790**	**6.00**	**16.7**	**1131**	**11.1**	**0.82**	**127.0**	**16.3**	**10.30**	**2010**	**2.30**	**8.62**	**63.00**
		Minimum:		**1**	**0.2**	**0.2**	**0.4**	**0.1**	**7.0**	**3**	**17**	**0.21**	**0.1**	**25**	**6.4**	**0.08**	**0.3**	**0.0**	**1.01**	**3**	**0.08**	**0.66**	**2.25**
Plateau:																							
	11	Mjóavatn	1992	448	2.9	0.8	1.1	2.1	8.7	56	750	3.50	0.6	87	7.5	0.37	4.2	0.5	5.70	1080	0.63	2.09	4.36
	18	Svartárvatn	1993	395	1.9	1.0	2.0	2.0	8.0	72	345	1.10	13.7	95	8.5	0.63	1.6	7.0	4.81	580	0.75	2.59	12.70
	22	V.-Friðmundarvatn	1992	441	6.0	1.2	2.3	7.0	9.0	58	720	3.10	0.2	136	7.4	0.40	5.2	0.6	4.62	266	0.60	2.10	5.01
	30	Oddastaðavatn	1994	65	3.0	5.4	15.0	16.0	14.2	3	69	0.52	5.0	71	7.1	0.14	6.3	1.3	3.83	32	0.22	2.24	5.29
	32	Ánavatn	1994	521	4.9	6.0	24.0	29.0	11.2	8	87	0.79	9.6	62	11.1	0.60	1.8	1.1	7.40	76	0.42	2.49	7.32
	33	Sænautavatn	1994	524	2.3	7.6	23.0	18.0	9.8	8	93	0.89	8.6	86	9.4	0.80	1.9	1.0	9.83	190	0.38	3.61	7.19
	34	Eiðavatn	1994	32	1.2	4.0	10.0	5.0	13.8	6	117	1.50	7.2	64	6.7	0.48	6.5	1.3	5.34	54	0.21	2.81	5.32
	35	Urriðavatn	1994	38	1.0	4.4	10.5	4.5	14.6	7	175	2.10	6.0	98	9.8	0.68	10.7	3.1	8.58	70	0.55	4.28	7.43
	42	Vesturhópsvatn	1996	19	10.3	7.1	28.0	73.0	11.4	8	144	1.80	5.8	143	7.7	0.60	14.7	3.7	7.80	66	0.58	3.63	9.38
	43	Langavatn Þing.	1996	158	0.6	3.7	7.5	2.2	11.8	15	175	1.00	12.9	82	7.6	0.54	6.1	1.3	5.23	143	0.99	1.85	8.63
	44	Reyðarvatn Hofs.	1996	730	0.6	0.5	0.7	0.3	9.1	74	290	0.91	0.3	62	7.4	0.32	4.1	0.5	6.76	519	0.53	3.63	7.01
	46	Másvatn	1996	276	4.0	6.0	17.2	23.8	9.8	5	125	1.50	4.5	80	7.8	0.62	4.2	0.9	6.92	25	0.52	3.09	5.41
	49	Eystra-Gíslholtsvatn	1997	65	1.6	2.6	8.5	4.2	8.2	6	144	1.50	2.6	110	8.2	0.60	12.5	1.5	6.57	51	0.82	3.87	9.25
	52	Hólmavatn/Tungukollur	1997	470	0.2	0.5	1.0	0.1	11.7	7	170	2.00	1.5	49	7.4	0.30	5.0	0.4	2.17	140	0.23	2.28	3.06
	53	Arnarvatn Stóra	1997	540	3.9	1.0	2.5	3.9	7.6	16	220	1.50	0.4	64	7.4	0.52	5.6	0.8	3.03	73	0.61	1.73	5.39
	54	Úlfsvatn	1997	434	3.8	1.0	2.0	3.8	12.6	16	225	1.70	0.6	79	7.2	0.46	6.7	0.9	4.22	154	0.62	2.46	5.36
	55	Hólsvatn	1997	14	1.4	0.8	1.5	1.1	10.0	39	790	6.00	0.1	111	7.7	0.41	18.8	2.6	2.91	282	0.53	3.70	11.20
	56	Sauravatn	1997	35	0.8	0.2	0.4	0.2	10.2	21	415	5.10	0.9	127	7,5	0.41	15.5	2.4	3.99	680	0.44	4.62	12.90
	64	Sandvatn	1998	569	2.8	2.0	3.8	5.6	10.8	5	74	0.59	5.2	50	7.2	0.38	2.0	0.6	4.07	32	0.26	1.92	2.89
	66	Vífilsstaðavatn	1998	38	0.3	0.5	1.3	0.1	13.4	22	320	1.70	2.0	129	8.3	0.62	17.0	2.0	7.15	95	0.38	1.06	18.80
	67	Hafravatn	1998	76	1.0	8.0	28.0	8.2	13.0	5	81	1.00	7.5	79	6.6	0.38	13.7	2.4	5.17	52	0.39	2.06	10.80
		Mean:		**280**	**2.6**	**3.1**	**9.1**	**10.0**	**10.9**	**22**	**263**	**1.90**	**4.5**	**89**	**7.9**	**0.49**	**7.8**	**1.7**	**5.53**	**222**	**0.51**	**2.77**	**7.84**
		Maximum:		**730**	**10.3**	**8.0**	**28.0**	**73.0**	**14.6**	**74**	**790**	**6.00**	**13.7**	**143**	**11.1**	**0.80**	**18.8**	**7.0**	**9.83**	**1080**	**0.99**	**4.62**	**18.80**
		Minimum:		**14**	**0.2**	**0.2**	**0.4**	**0.1**	**7.6**	**3**	**69**	**0.52**	**0.1**	**49**	**6.6**	**0.14**	**1.6**	**0.4**	**2.17**	**25**	**0.21**	**1.06**	**2.89**
Direct runoff:																							
	37	Högnavatn	1995	410	0.3	2.5	3.5	1.0	7.4	10	120	0.66	0.8	40	7.9	0.41	6.9	1.7	1.22	31	0.18	0.71	4.61
	38	Ónefntvatn	1995	470	0.3	3.0	3.5	1.0	8.5	4	50	0.33	0.6	40	7.6	0.08	7.9	1.4	1.01	3	0.25	0.66	4.50
	60	Þuríðarvatn	1998	416	1.2	3.5	11.0	4.2	11.1	3	44	0.54	6.6	54	6.9	0.34	3.4	0.6	4.73	26	0.28	2.31	3.36
	63	Ódáðavatn	1998	615	2.5	4.0	7.0	10.0	9.7	4	120	0.53	2.0	25	6.8	0.21	1.7	0.7	1.72	27	0.08	0.75	2.25
		Mean:		**478**	**1.1**	**3.3**	**6.3**	**4.1**	**9.2**	**5**	**84**	**0.52**	**2.5**	**40**	**7.3**	**0.26**	**5.0**	**1.1**	**2.17**	**22**	**0.20**	**1.11**	**3.68**
		Maximum:		**615**	**2.5**	**4.0**	**11.0**	**10.0**	**11.1**	**10**	**120**	**0.66**	**6.6**	**54**	**7.9**	**0.41**	**7.9**	**1.7**	**4.73**	**31**	**0.28**	**2.31**	**4.61**
		Minimum:		**410**	**0.3**	**2.5**	**3.5**	**1.0**	**7.4**	**3**	**44**	**0.33**	**0.6**	**25**	**6.8**	**0.08**	**1.7**	**0.6**	**1.01**	**3**	**0.08**	**0.66**	**2.25**

Table 3. Continued.

Lake type	Lake no.	Lake name	Year sampled	ALT m	AREA km^2	MD m	Zmax m	VOL Gl	TEMP °C	TP µg l^{-1}	TN µg l^{-1}	TOC mg l^{-1}	SiO_2 mg l^{-1}	COND µS cm^{-1}	pH	ALK meq l^{-1}	Cl mg l^{-1}	SO_4 mg l^{-1}	Ca mg l^{-1}	Fe µg l^{-1}	K mg l^{-1}	Mg mg l^{-1}	Na mg l^{-1}
Spring-fed:																							
	1	Apavatn	1993	59	13.6	1.5	2.5	20.0	11.2	10	138	0.62	8.0	83	7.5	0.46	6.1	1.6	5.37	202	0.43	1.94	7.67
	2	Elliðavatn	1993	73	1.8	1.0	2.0	2.0	10.9	6	89	0.45	7.9	91	8.8	0.25	10.5	2.0	4.57	116	0.35	1.15	10.30
	10	Langavatn	1993	565	0.4	7.2	19.0	2.8	7.0	15	175	1.00	12.9	109	8.2	0.54	6.1	1.3	5.23	143	0.99	1.85	8.63
	20	Úlfljótsvatn	1993	79	3.6	4.7	34.5	17.0	9.0	17	108	0.49	10.5	80	8.8	0.41	6.6	2.2	4.11	41	0.59	1.40	8.15
	39	Ásbjarnarvatn S.	1996	770	0.5	0.7	2.0	0.3	8.7	34	185	0.63	7.5	79	8.2	0.32	2.3	1.4	4.27	89	0.78	3.70	7.91
	47	Fljótsbotn	1997	35	0.5	6.0	13.0	3.0	8.8	38	185	0.48	16.7	96	7.3	0.48	5.2	14.8	7.92	95	0.54	3.25	7.45
	48	Frostastaðavatn	1997	570	2.6	5.0	11.0	13.0	10.6	8	89	0.39	3.4	70	6.8	0.32	6.1	7.2	4.35	23	0.73	1.85	6.31
	57	Langisjór	1998	663	25.7	18.5	73.5	475.5	8.8	9	17	0.21	4.0	49	6.6	0.24	3.2	3.1	3.16	17	0.21	1.58	4.58
		Mean:		**352**	**6.1**	**5.6**	**19.7**	**66.7**	**9.4**	**17**	**123**	**0.53**	**8.9**	**82**	**7.8**	**0.38**	**5.8**	**4.2**	**4.87**	**91**	**0.58**	**2.09**	**7.63**
		Maximum:		**770**	**25.7**	**18.5**	**73.5**	**475.5**	**11.2**	**38**	**185**	**1.00**	**16.7**	**109**	**8.8**	**0.54**	**10.5**	**14.8**	**7.92**	**202**	**0.99**	**3.70**	**10.30**
		Minimum:		**35**	**0.4**	**0.7**	**2.0**	**0.3**	**7.0**	**6**	**17**	**0.21**	**3.4**	**49**	**6.6**	**0.24**	**2.3**	**1.3**	**3.16**	**17**	**0.21**	**1.15**	**4.58**
Valley:																							
	3	Eyraravatn	1992	75	0.8	3.4	12.5	2.8	12.2	9	95	0.67	7.2	56	7.8	0.34	6.5	2.0	3.15	42	0.22	1.31	5.23
	4	Galtaból	1992	450	1.2	4.1	10.0	5.0	9.9	7	141	1.30	0.4	48	8.0	0.34	5.9	0.8	3.76	16	0.50	1.80	4.36
	5	Geitabergsvatn	1992	79	0.9	9.4	21.0	8.2	11.5	6	75	0.66	8.6	51	7.5	0.22	0.3	0.0	2.84	41	0.36	1.39	5.30
	6	Glammastaðavatn	1992	77	1.4	6.6	24.0	9.0	11.6	6	75	0.64	8.0	64	7.7	0.34	1.4	0.4	3.31	33	0.23	1.37	5.13
	19	Svínavatn	1993	123	11.8	12.5	38.5	147.0	10.7	7	141	1.70	12.9	99	7.6	0.58	9.4	8.0	9.28	340	0.81	4.28	8.04
	27	Baulárvallavatn	1994	193	1.6	17.7	47.0	28.0	12.8	4	41	0.28	4.1	53	7.0	0.08	6.5	1.4	1.35	30	0.36	1.14	4.53
	28	Haukadalsvatn	1994	37	3.2	23.4	41.5	78.0	14.8	5	128	0.67	7.3	56	7.3	0.55	5.9	1.4	4.31	19	0.31	1.65	4.73
	29	Hítarvatn	1994	147	7.6	8.8	24.0	67.0	12.4	5	51	0.28	4.9	56	6.4	0.16	5.6	1.1	3.53	69	0.19	1.73	4.33
	36	Þiðriksvallavatn	1995	73	1.5	35.0	47.0	45.0	9.3	4	44	0.38	3.7	84	8.0	0.21	15.2	2.5	3.74	37	0.27	1.36	7.87
	50	Hestvatn	1997	495	6.8	23.7	60.0	161.2	12.9	3	74	1.00	5.4	82	7.8	0.40	10.8	2.1	4.02	41	0.66	2.77	7.40
	58	Skorradalsvatn	1998	57	14.7	22.5	48.0	331.0	12.9	3	56	0.50	6.8	47	7.2	0.20	11.3	2.1	2.95	22	0.31	1.76	7.54
	62	Skriðuvatn	1998	155	1.0	3.0	10.0	3.0	9.5	4	42	0.39	9.9	37	6.9	0.22	2.0	0.9	2.45	62	0.16	1.12	2.95
	65	Þríhyrningsvatn	1998	570	3.6	10.0	33.0	36.0	11.4	5	45	0.40	7.6	66	7.9	0.82	1.5	1.6	3.70	19	0.25	0.86	8.20
		Mean:		**195**	**4.3**	**13.9**	**32.0**	**70.9**	**11.7**	**5**	**78**	**0.68**	**6.7**	**61**	**7.5**	**0.34**	**6.3**	**1.9**	**3.72**	**59**	**0.36**	**1.73**	**5.82**
		Maximum:		**570**	**14.7**	**35.0**	**60.0**	**331.0**	**14.8**	**9**	**141**	**1.70**	**12.9**	**99**	**8.0**	**0.82**	**15.2**	**8.0**	**9.28**	**340**	**0.81**	**4.28**	**8.20**
		Minimum:		**37**	**0.8**	**3.0**	**10.0**	**2.8**	**9.3**	**3**	**41**	**0.28**	**0.4**	**37**	**6.4**	**0.08**	**0.3**	**0.0**	**1.35**	**16**	**0.16**	**0.86**	**2.95**
Glacial:																							
	59	Lagarfljót	1998	20	53.0	51.0	111.5	2703.0	12.3	67	59	0.33	7.9	48	6.4	0.40	1.9	2.1	5.75	2010	0.21	1.89	2.92
Coastal:																							
	41	Hópið	1996	1	29.8	5.5	8.5	163.0	13.1	29	165	1.60	10.4	1131	7.8	0.58	37.5	7.6	7.64	520	1.29	6.00	21.60
	51	Hlíðarvatn	1997	1	3.3	2.9	5.0	9.6	11.5	14	125	1.20	5.1	507	8.3	0.40	127.0	16.3	10.30	19	2.30	8.62	63.00
		Mean:		**1**	**16.6**	**4.2**	**6.8**	**86.3**	**12.3**	**22**	**145**	**1.40**	**7.8**	**819**	**8.0**	**0.49**	**82.3**	**12.0**	**8.97**	**270**	**1.80**	**7.31**	**42.30**
		Maximum:		**1**	**29.8**	**5.5**	**8.5**	**163.0**	**13.1**	**29**	**165**	**1.60**	**10.4**	**1131**	**8.3**	**0.58**	**127.0**	**16.3**	**10.30**	**520**	**2.30**	**8.62**	**63.00**
		Minimum:		**1**	**3.3**	**2.9**	**5.0**	**9.6**	**11.5**	**14**	**125**	**1.20**	**5.1**	**507**	**7.8**	**0.40**	**37.5**	**7.6**	**7.64**	**19**	**1.29**	**6.00**	**21.60**

[1] Abbreviations for the physical and chemical variables are ALT (altitude), AREA (surface area), MD (mean depth), Zmax (maximum depth), VOL (volume), TEMP (surface water temperature), TP (total phosphorus), TN (total nitrogen), TOC (total organic carbon), COND (conductivity), ALK (alkalinity).

between measured environmental variables. Limnological differences between TYPE categories of Icelandic lakes (i.e., ‘plateau’, ‘direct-runoff’, ‘spring-fed’, and ‘valley’) were assessed using Analysis of Variance (ANOVA). ANOVA analyses included *post hoc* tests ($p \leq 0.05$) based on Bonferroni test statistics. Pearson correlations and ANOVA analyses were performed using the computer program SPSS version 11.0. Principal components analysis (PCA), an indirect gradient, multivariate ordination technique, was used to further explore the relationships between environmental variables and assess the main direction of variation in limnological conditions between Icelandic lakes.

Detrended correspondence analysis (DCA, Hill & Gauch 1980) with detrending by linear segments and non-linear rescaling of axes was used to explore the main distributional patterns of diatom taxa among the training-set lakes and to assess the compositional gradient lengths of the ordination axes. The gradient length of the first DCA axis was 3.0 suggesting unimodal responses of the species data. Therefore, canonical correspondence analysis (CCA, Jongman et al. 1995), a multivariate direct gradient ordination technique, was used to assess contemporary relationships between the diatoms and the measured physical and chemical environmental conditions of the training-set lakes. The minimum set of environmental variables that significantly explained the variation in diatom distributions used in the CCA were determined using the methods suggested by Birks et al. (1990) and Hall & Smol (1992). Briefly, the environmental data set was reduced by: 1) eliminating significantly correlated variables determined using Pearson correlation with Bonferroni-adjusted probabilities ($p < 0.05$) that did not explain a significant additional amount of variation in the diatom assemblages in a series of partial CCAs (i.e., one variable was chosen as the sole explanatory variable and each correlated variable was used as the sole covariable); 2) only including variables that explained a significant and independent amount of the variation in the data set determined by a series of ordinations constrained to a single environmental variable; and 3) using a forward selection procedure to identify variables that account for additional, significant amounts of variation in the diatom data. In the final CCA, rare taxa were downweighted and species scores were scaled to be weighted averages of the sample scores. Significance testing was based on Monte Carlo permutation tests (999 permutations).

All multivariate ordinations (PCA, DCA, CCA) were performed using the computer program CANOCO, version 4.0 (ter Braak & Šmilauer 1998), and lakes were coded *a priori* in the ordination biplots into TYPE (i.e., plateau, direct-runoff, spring-fed, valley, coastal, and glacial lakes) categories following Garðarsson’s (1979) ecological classification scheme for Icelandic freshwaters. The two ‘coastal’ lakes [Hópið (41) and Hlíðarvatn (51)] and one ‘glacial’ lake [Lagarfljót (59)] were included as passive samples in the PCA and CCA ordinations.

Analysis of similarities (ANOSIM) was used to determine whether the diatom assemblages differ significantly among groups of lakes with different TYPE categories. ANOSIM is a non-parametric test analogous to multivariate one-factor analysis of variance (ANOVA) (Clarke & Warwick 1994). In the procedure, within- and across-group rank dissimilarities (based on Bray and Curtis similarities) are computed and compared to the initial rank dissimilarity, and reported as the R-statistic (Clarke & Warwick 1994). An R-statistic significantly greater than zero ($p < 0.05$) based on permutation tests (5000 permutations) indicates that differences between pairs of groups are greater than differences within each group. The contribution of individual diatom taxa to the average dissimilarity (Bray and Curtis similarities) between TYPE categories of lakes was then calculated using Bray and Curtis similarities. The above analyses were performed using the statistical package PRIMER version 4.0 beta (Clarke & Warwick 1994).

Results

Physical and chemical characteristics

The study lakes spanned a wide range of sizes, from 0.2 to 53.0 km^2. Similarly, the variation in lake depth

Table 4. Pearson correlation matrix of selected transformed environmental variables for the 49 Icelandic lakes set. Bolded values are significant ($p \leq 0.05$) based on Bonferroni-adjusted probabilities.

	MD	Zmax	TEMP	TN	TOC	SiO_2	PH	ALK	COND	Cl	SO_4	Ca	Fe	K	Mg	Na
MD	**1.00**															
Zmax	**0.96**	**1.00**														
TEMP	0.29	0.29	**1.00**													
TN	**–0.67**	**–0.70**	–0.21	**1.00**												
TOC	**–0.51**	**–0.51**	–0.04	**0.82**	**1.00**											
SiO_2	0.43	**0.52**	0.18	–0.37	–0.47	**1.00**										
PH	–0.08	–0.01	–0.10	0.17	0.12	0.21	**1.00**									
ALK	–0.09	–0.01	–0.02	0.35	0.35	0.25	**0.51**	**1.00**								
COND	–0.20	–0.16	–0.02	**0.56**	**0.57**	0.08	0.32	**0.53**	**1.00**							
Cl	–0.01	–0.06	0.19	0.23	0.39	–0.28	–0.04	–0.01	0.48	**1.00**						
SO_4	0.19	0.19	–0.06	0.04	–0.03	0.37	0.05	0.22	0.39	0.38	**1.00**					
Ca	0.00	0.07	0.08	0.29	0.26	0.34	0.46	**0.70**	**0.63**	0.12	0.34	**1.00**				
Fe	**–0.53**	**–0.53**	–0.19	**0.74**	**0.63**	–0.05	0.17	0.31	**0.58**	0.09	0.10	0.42	**1.00**			
K	–0.17	–0.14	–0.28	**0.53**	0.38	0.12	0.27	0.43	**0.66**	0.22	0.31	0.47	0.47	**1.00**		
Mg	–0.17	–0.13	0.03	0.44	**0.56**	0.05	0.20	0.42	**0.59**	0.23	0.27	**0.67**	**0.54**	**0.53**	**1.00**	
Na	–0.11	–0.09	0.02	0.36	0.32	0.19	0.40	0.46	**0.77**	0.49	0.49	0.46	0.40	**0.51**	0.35	**1.00**

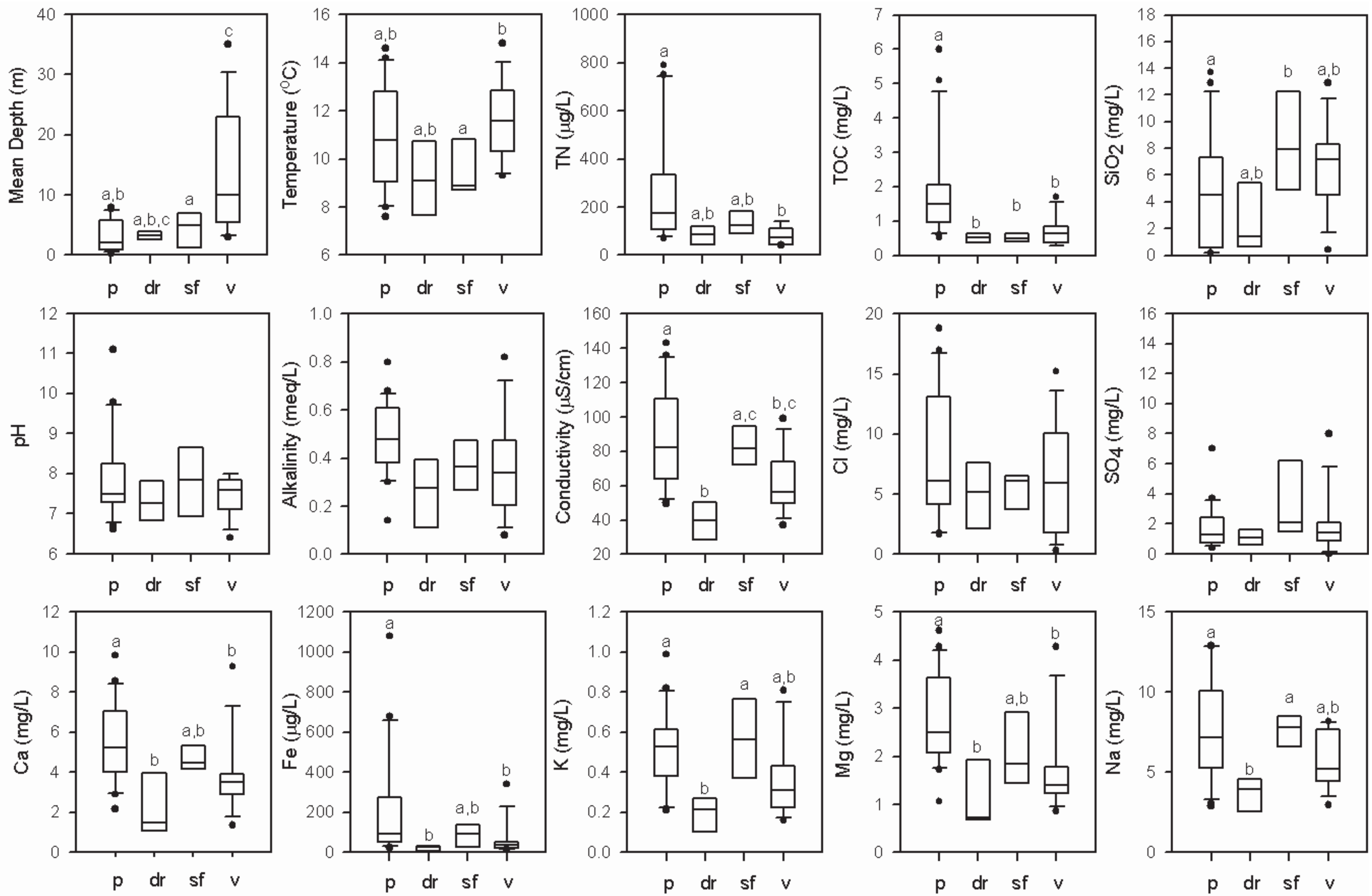

Fig. 2. Box plots of selected physical and chemical limnological variables comparing plateau (p; n = 21), direct-runoff (dr; n = 4), spring-fed (sf; n = 8) and valley (v; n = 13) lake TYPE classes as defined by Malmquist et al. (2000) (modified from Garðarsson 1979). Letters (a, b, c) denote significant differences ($p \leq 0.05$) between lake TYPE classes based on ANOVA and Bonferroni *post hoc* test statistics.

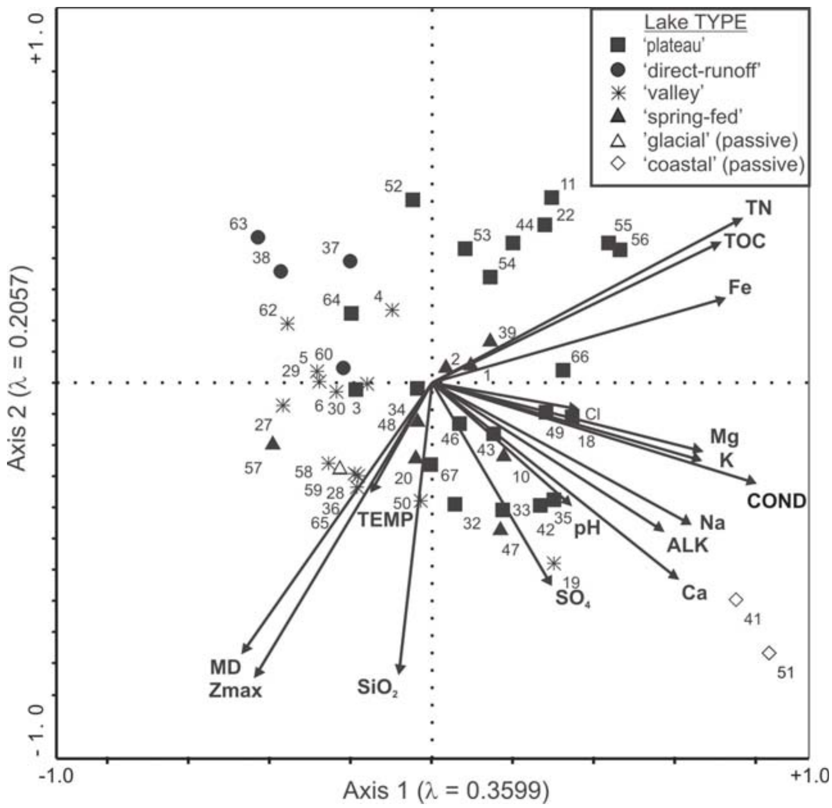

Fig. 3. PCA ordination biplot showing the relative position of Icelandic lakes (n = 49) with respect to 16 measured limnological variables. Lakes are coded *a priori* into ecological TYPE categories. 'Glacial' and 'coastal' lakes are plotted passively.

was also large ranging from 0.4 m to 111.5 m. However, nearly half of the lakes were relatively small (mean surface area < 2 km^2) and shallow with depths less than 5 m (Table 3). Maximum depth (Z_{max}) and mean depth (MD) were highly correlated (r = 0.96) and these measures of depth were negatively correlated with total nitrogen (TN), total organic carbon (TOC) and Fe (Table 4). ANOVA with Tukey *ad hoc* tests of TYPE lake categories revealed that the 'valley' lakes, which are mostly graben lakes located in southwest Iceland, are significantly deeper than 'plateau', 'direct-runoff' and 'spring-fed' lakes (Fig. 2). Lagarfljót (59), the only 'glacial' lake in the data set, was the deepest lake with a maximum depth of 111.5 m.

TP concentrations (Table 3) range from 3 to 74 µg l^{-1}; however, 65 % of the lakes can be classified as oligotrophic, with TP concentrations less than 10 µg l^{-1}. As with TP concentrations, TN and TOC concentrations are generally low in the study lakes with mean concentrations of 167 µg l^{-1} and 1.19 mg l^{-1}, respectively. TN and TOC are positively correlated (Table 4), and higher values of these variables (TN > 200 µg l^{-1}, TOC > 2 mg l^{-1}) occur only in a few of the shallow (< 2 m) 'plateau' lakes (i.e., lakes 11, 22, 35, 52, 55, and 56) (Table 3).

The study lakes are generally circumneutral to alkaline (mean pH = 7.7, range = 6.4 – 11.1), and have relatively high alkalinity (mean alkalinity = 0.41 meq l^{-1}, range = 0.08 – 0.82 meq l^{-1}) (Table 3).

Multivariate ordination of the measured limnological variables (n = 16 following data screening) by PCA revealed two main directions of variation in the Icelandic lakes' data set (Fig. 3). The first axis ($\lambda_1 = 0.36$) is defined primarily by gradients of ions and nutrients (COND, TN, Fe, TOC, K, Mg, Na, and Ca), while measures of lake depth (Z_{max}, MD), SO_4, and SiO_2 best account for the variation of lakes along the second axis ($\lambda_2 = 0.21$). Together, the first two PCA axes explain a relatively large portion (56.6 %) of the total variation in the data set. Eigenvalues of the third and fourth axes are relatively low ($\lambda_3 = 0.103$, $\lambda_4 = 0.073$) and explaining only 17.6 % of the variation in measured limnological variables, and are thus not discussed further.

Diatoms

The diatom flora identified in the surficial sediments of the 49 Icelandic lakes was taxonomically diverse and included a total of 329 taxa representing 14 genera (Appendix 4.2 in Karst-Riddoch 2004). Of these taxa, 139 were common in the data set with abundances of at least 1 % in one lake and present in 3 lakes (Table 5). Taxon identification numbers from Table 5 are provided in parentheses after the taxon names in the following discussion for reference. It should be noted that *Fragilaria construens* and *F. pseudoconstruens* were combined in the data set as *F. pseudoconstruens/construens* (84) due to taxonomic difficulties in differentiating these diatoms that occurred largely in girdle view on the slides. The final reduced data set of 139 diatom taxa accounts for a minimum of 83 % of the total diatom valves in the assemblages from the 49 Icelandic lakes.

Small benthic taxa of the genus *Fragilaria sensu lato* were the most common and abundant diatoms in the assemblages from Iceland, occurring in all of the 49 study lakes with combined relative abundances of over 20 %, with the exception of 4 deep 'valley' lakes ($Z_{max} > 25$ m) (Fig. 4a). Benthic diatoms of the genus *Fragilaria sensu lato* were highly diverse in the Icelandic lakes' set, including 19 different species and varieties. The most common small benthic *Fragilaria sensu lato* taxa were *F. brevistriata* (67), *F. construens* var. *venter* (75), *F. pinnata* (82), *F. pseudoconstruens/construens* (84), *F. parasitica* (81), *F. virescens* var. *exigua* (86), *F. lapponica* (79), and *F. construens* var. *binodis* (74), which most strongly dominated the assemblages from the shallowest lakes (< 5.0 m). High relative abundances (50 – 98 %) of these few *Fragilaria* spp. resulted in low species diversity indices (Hill's N2) of shallow lakes (< 5.0 m) in comparison to deeper lakes in the data set (Fig. 4a). Other benthic *Fragilaria* [i.e., *F. arcus* (66), *F. brevistriata* var. *inflata* (68), *F. capucina* and varieties (69–73), *F. elliptica* (78), *F. neoproducta* (80) and *F. pinnata* var. *intercedens* (83)] were also present in the diatom assemblages, but each of these occurred in less than 10 of the lakes and with generally low abundances (< 10 %).

Lakes with intermediate depths ranging from 5 to 25 m had the most taxonomically diverse diatom assemblages (Fig. 4a). In addition to small benthic *Fragilaria* diatoms that strongly dominated the shallow lakes, several other small benthic taxa, mostly from the genus *Achnanthes* [e.g., *A. minutissima* (18), *A. lacus-vulcani* (13), *A. pusilla* (25), *A. lanceolata* ssp. *frequentissima* (15), *A. suchlandtii* (28), *A. didyma* (8), *A. impexa* (11), *A. subatomoides* (27), and *A. gracillima* (9)], but also *Navicula minima* (105) and *Amphora pediculus* (32), were important components of the diatom assemblages from lakes with intermediate depths (Fig. 4b). Larger benthic and periphytic pennate diatoms [e.g., *Tabellaria flocculosa* (139), *Nitzschia acicularis* (115), *Cymbella silesiaca* (58), *N. dissipata* (117), *Rhopalodia gibba* (133), *Diatoma tenuis* (60), and *N. fonticola* (118)] commonly associated with littoral habitats occurred in many of the lakes with intermediate depths, but with comparatively low relative abundances of less than 10 % (Fig. 4b).

The dominant planktonic diatoms included *Cyclotella pseudostelligera* (51), *Asterionella formosa* (36), *Aulacoseira subarctica* (43), *Fragilaria* cf. *crotonensis* (76) and *C. comensis* (47) (Fig. 4b).

Relationships between diatoms and measured environmental variables

Of the 16 variables included in the final environmental data set (Z_{max}, MD, TEMP, COND, pH, ALK, TN, TOC, SiO_2, Fe, SO_4, Cl, K, Mg, Na, Ca), only pH and SO_4 did not explain a significant independent portion of variation in the diatom data in a series of constrained CCAs ($p < 0.05$), and were therefore removed from further analyses. Despite the large gradient in pH, surprisingly this variable did not explain more of the variation. Significant correlations ($p < 0.05$, with Bonferroni-adjusted probabilities) occurred between Fe and TN, as well as Ca and ALK. COND, K, Mg, and Na were also significantly correlated ($p < 0.05$). Following covariable analysis Fe, Ca, K, Mg, Na were also removed from the data set because they did not contribute significant explanatory power to the CCA in addition to that explained by their correlated counterparts. Forward selection of the remaining variables further reduced the environmental data set to include MD, COND, TOC, SiO_2, TN, ALK, and TEMP as the combination of variables that significantly explained independent and additional variation in the diatom assemblages of the Icelandic study lakes.

The first four axes in the CCA constrained to the 7 forward-selected environmental variables captured a moderate amount of variation in the species data (23.8 %), and explained a large proportion of the variance in the diatom-environmental relationship (79.9 %). Eigenvalues of the first three CCA axes ($\lambda_1 = 0.267$, $\lambda_2 = 0.147$, $\lambda_3 = 0.081$) were significant when tested with Monte Carlo permutations (999 permutations, $p < 0.05$). However, to simplify the ordination diagram, only the first two CCA axes are presented (Fig. 5a,b). All of the environmental variables were significantly correlated to one of the first two CCA axes with the exception of TOC, which was also the only variable significantly correlated to the third axis. In order of interset correlation strength, gradients of MD, TN and TEMP are represented along the first

Table 5. Common diatom taxa and authorities in the 49 Icelandic lakes including their actual (#occ) and effective (Hill's N2) number of occurrences, and maximum relative abundances (%max). Recently used synonyms for some of the taxa are provided in Table 2.

No	Taxon and authority	# occ	Hill's N2	%max
1	*Achnanthes acares* Hohn & Hellermann	5	3.8	4.2
2	*A. calcar* Cleve	5	3.8	1.2
3	*A. carissima* Lange-Bert.	10	4.5	17.6
4	*A. chlidanos* Hohn & Hellermann	4	3.6	1.1
5	*A. clevei* Grun.	13	9.7	1.9
6	*A. curtissima* Carter	15	9.8	13.1
7	*A. daonnensis* Lange-Bert.	11	8.9	3.9
8	*A. didyma* Hust.	21	16.4	5.0
9	*A. gracillima* Hust.	15	11.9	6.1
10	*A. grana* Hohn & Hellermann	4	2.0	1.9
11	*A. impexa* Lange-Bert.	15	12.8	2.7
12	*A. kuelbsii* Lange-Bert.	3	2.7	2.9
13	*A. lacus-vucani* Lange-Bert. (in Lange-Bert. & Kram.)	33	23.2	10.6
14	*A. laevis* Oestrup	12	11.0	1.9
15	*A. lanceolata* ssp. *frequentissima* Lange-Bert.	28	21.7	4.0
16	*A. lanceolata* var. *rostrata* (Oestrup) Hust.	4	3.7	2.8
17	*A. marginulata* Grun.	14	11.8	1.9
18	*A. minutissima* Kütz.	40	28.8	12.3
19	*A. minutissima* var. *scotica* (Carter) Lange-Bert.	2	1.9	3.2
20	*A. nitidiformis* Lange-Bert.	14	11.7	2.0
21	*A. nodosa* Cleve	9	8.5	1.2
22	*A. oestrupi* (Cleve-Euler) Hust.	17	15.8	1.2
23	*A. peragalli* Brun & Hérib.	8	6.9	2.0
24	*A. petersenii* Hust.	3	2.4	2.9
25	*A. pusilla* (Grun.) De Toni	27	22.0	3.8
26	*A. saccula* Carter	9	8.6	1.4
27	*A. subatomoides* (Hust.) Lange-Bert. & Archibald	21	12.6	14.4
28	*A. suchlandtii* Hust.	20	17.4	2.6
29	*Amphipleura pellucida* Kütz.	14	11.4	1.9
30	*Amphora inariensis* Kram.	13	12.1	1.2
31	*A. lybica* Ehrenb.	12	10.2	1.2
32	*A. pediculus* (Kütz.) Grun.	17	13.8	3.3
33	*Anomoeneis brachyseira* (Bréb.) Grun.	3	3.0	1.2
34	*A. vitrea* (Grun.) Ross	16	15.0	2.1
35	*Asterionella formosa* Hass.	23	16.4	12.0
36	*Aulacoseira ambigua* (Grun.) Simonsen	15	13.1	2.2
37	*A. distans* (Ehrenb.) Simonsen	9	6.8	1.5
38	*A. alpigena* (Grun.) Kram.	11	8.8	5.5
39	*A. islandica* (O. Müll.) Simonsen	3	2.9	2.0
40	*A. italica* (Ehrenb.) Simonsen	3	2.6	1.5
41	*A. lirata* (Ehrenb.) Ross	7	4.6	3.4
42	*A. perglabra* (Oestrup) Haworth	5	3.8	3.9
43	*A. subarctica* (O. Müll.) Haworth	21	13.9	64.0
44	*Caloneis silicula* (Ehrenb.) Cleve	8	6.7	1.5
45	*Cocconeis neodiminuta* Kram.	7	6.2	1.3
46	*C. placentula* var. *euglypta* Ehrenb.	2	6.2	13.2
47	*Cyclotella comensis* Grun.	9	11.0	17.5
48	*C. distinguenda* Hust.	14	5.1	2.3
49	*C. distinguenda* var. *unipunctata* (Hust.) Håk. & Carter	6	1.6	3.7
50	*C. menenghiniana* Kütz.	3	2.5	2.1
51	*C. pseudostelligera* Hust.	28	22.1	26.9
52	*C. tripartita* Håk.	7	5.7	4.3
53	*Cymbella cistula* (Ehrenb.) Kirchn.	4	3.7	1.2
54	*C. cymbiformis* Agardh	5	4.7	1.2
55	*C. descripta* (Hust.) Kram. & Lange-Bert.	9	8.4	1.6
56	*C. microcephala* Grun. (in Van Heurck)	15	14.3	1.9
57	*C. minuta* Hilse (ex. Rabenh.)	8	5.3	1.2
58	*C. silesiaca* Bleish (in Rabenh.)	21	16.2	3.9
59	*Diatoma mesodon* (Ehrenb.) Kütz.	10	7.7	1.6
60	*D. tenuis* Agardh	16	12.7	7.4
61	*Diploneis elliptica* (Kütz.) Cleve	2	1.9	1.2
62	*D. ovalis* (Hilse) Cleve	4	3.7	1.5
63	*Epithemia adnata* (Kütz.) Brebisson	11	9.3	2.7
64	*Eunotia glacialis* Meister	8	7.6	1.2
65	*E. praerupta* Ehrenb.	5	4.4	1.4
66	*Fragilaria arcus* (Ehrenb.) Cleve	12	9.4	4.5
67	*F. brevistriata* Grun. (in Van Heurck)	46	34.9	49.2
68	*F. brevistriata* var. *inflata* (Pantocsek) Hust.	5	3.8	7.1
69	*F. capucina* Desm.	7	5.9	1.8
70	*F. capucina* var. *gracilis* (Oestrup) Hust.	13	9.0	4.1
71	*F. capucina* var. *mesolepta* (Rabenh.) Rabenh.	3	1.6	3.1
72	*F. capucina* var. *perminuta* (Grun.) Lange-Bert.	3	1.9	1.1

Table 5. Continued.

No	Taxon and authority	# occ	Hill's N2	%max
73	*F. capucina* var. *vaucheriae* (Kütz.) Lange-Bert.	34	24.7	9.5
74	*F. construens* var. *binodis* (Ehrenb.) Grun.	16	13.2	25.0
75	*F. construens* var. *venter* (Ehrenb.) Hust.	45	33.5	33.8
76	*F.* cf. *crotonensis* Kitton	17	12.1	7.3
77	*F. delicatissima* (W. Smith) Lange-Bert.	4	3.5	1.3
78	*F. elliptica* Schumann	7	5.8	15.7
79	*F. lapponica* Grun.	25	16.4	15.4
80	*F. neoproducta* Lange-Bert.	8	1.7	8.7
81	*F. parasitica* (W. Smith) Lange-Bert.	2	21.5	11.7
82	*F. pinnata* Ehrenb.	29	32.3	40.3
83	*F. pinnata* var. *intercedens* (Grun. in Van Heurck) Hust.	46	3.3	2.4
84	*F. pseudoconstruens* Marciniak	4	27.9	49.2
85	*F. tenera* (W. Smith) Lange-Bert.	40	20.3	5.1
86	*F. virescens* var. *exigua* Grun.	25	18.4	66.6
87	*F. nanana* Lange-Bertalto	30	6.4	1.7
88	*Frustulia rhomboides* (Ehrenb.) De Toni	2	1.8	1.8
89	*Gomphonema acuminatum* Ehrenb.	9	7.4	2.1
90	*G. angustatum* Kutz.	2	1.0	2.1
91	*G. angustum* Agardh	4	3.4	2.5
92	*G. parvulum* Kutz.	2	1.0	1.6
93	*Meloseira varians* Agardh	2	0.0	2.1
94	*Meridion circulare* (Greville) Agardh	14	8.7	5.4
95	*Navicula capitata* Ehrenb.	7	5.9	1.4
96	*N. cocconeiformis* Gregory	12	10.2	1.5
97	*N. cryptocephala* Kütz.	17	14.6	2.3
98	*N. cryptotenella* Lange-Bert.	7	6.5	1.5
99	*N. elginensis* (Gregory) Ralfs	3	2.7	1.1
100	*N. gregaria* Donkin	6	4.8	1.4
101	*N. ignota* var. *palustris* (Hust.) Lund	2	1.0	1.6
102	*N. jaernefeltii* Hust.	14	9.1	12.0
103	*N. vitiosa* Schimanski	3	2.5	6.0
104	*N. laevissima* Kütz.	5	4.6	1.1
105	*N. minima* Grun. (in Van Heurck)	27	21.8	2.6
106	*N. minuscula* Grun.	4	3.6	1.5
107	*N. pseudoscutiformis* Hust.	10	9.4	1.3
108	*N. pseudoventralis* Hust.	4	3.8	1.4
109	*N. pupula* Kütz.	14	12.8	2.3
110	*N. radiosa* Kütz.	16	15.0	1.5
111	*N. rhyncocephala* Kütz.	9	7.5	1.8
112	*N. seminulum* Grun.	10	8.1	2.0
113	*N. submuralis* Hust.	8	7.6	1.2
114	*N. subrotundata* Hust.	11	10.4	1.2
115	*Nitzschia acicularis* (Kütz.) W. Smith	25	17.8	4.8
116	*N. angustata* Grun.	6	5.0	2.3
117	*N. dissipata* (Kütz.) Grun.	19	15.8	3.1
118	*N. fonticola* Grun. (in Cleve & Moller)	15	12.0	3.4
119	*N. frustulum* (Kütz.) Grun.	12	9.8	1.7
120	*N. graciliformis* Lange-Bert. & Simonsen	4	3.8	1.5
121	*N. gracilis* Hantzsch	17	13.9	1.9
122	*N. inconspicua* Grun.	18	14.9	1.6
123	*N. linearis* (Agardh) W. Smith	5	3.9	1.0
124	*N. palea* (Kütz.) W. Smith	5	4.5	2.3
125	*N. perminuta* (Grun.) M. Peragallo	18	14.4	1.9
126	*N. pura* Hust.	13	10.9	2.3
127	*N. sigmoidea* (Nitzsch) W. Smith	3	1.0	2.3
128	*Pinnularia borealis* Ehrenb.	6	3.5	2.2
129	*P. interrupta* W. Smith	3	2.4	1.2
130	*P. viridis* (Nitzsch) Ehrenb.	7	5.8	2.7
131	*Rhizosolenia longiseta* Zach.	9	6.9	9.7
132	*Roicosphenia abbreviata* (Agardh) Lange-Bert.	4	2.9	1.6
133	*Rhopalodia gibba* (Ehrenb.) O. Müller	16	14.0	2.7
134	*Stephanodiscus minutulus* (Kutz.) Cleve & Möller	11	7.1	17.2
135	*S. parvus* Stoermer & Håk.	14	9.2	9.9
136	*Surirella bifrons* Ehrenb.	6	5.2	1.5
137	*Synedra biceps* Kütz.	9	6.4	2.9
138	*S. ulna* (Nitzsch) Ehrenb.	12	9.6	2.9
139	*T. flocculosa* (Roth) Kütz.	29	21.6	3.8

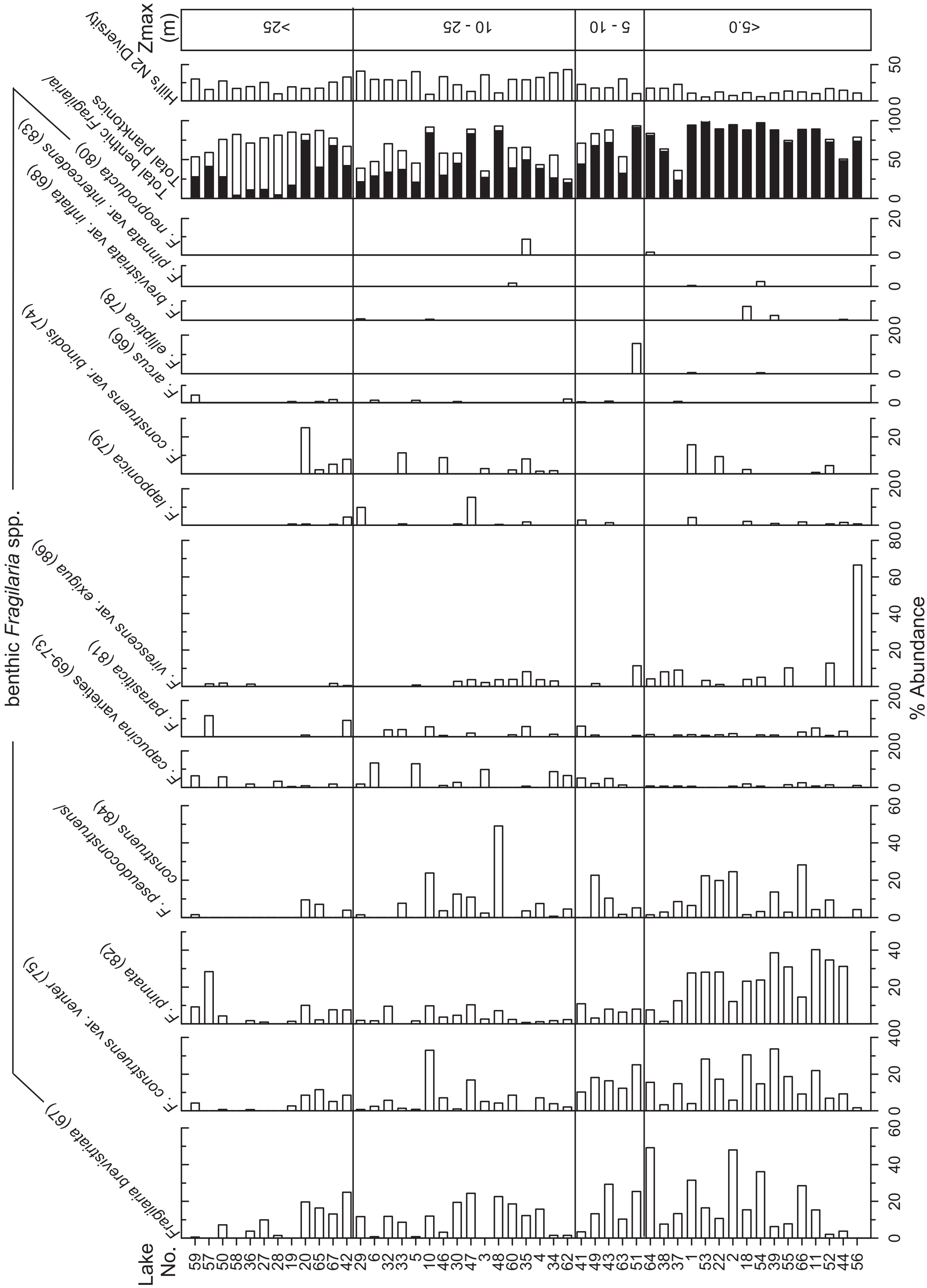

Fig. 4a. Relative abundance profiles of benthic *Fragilaria* spp., total benthic *Fragilaria* versus total planktonic taxa, and Hill's N2 diversity indices for 49 Icelandic lakes arranged by maximum lake depth (Z_{max}).

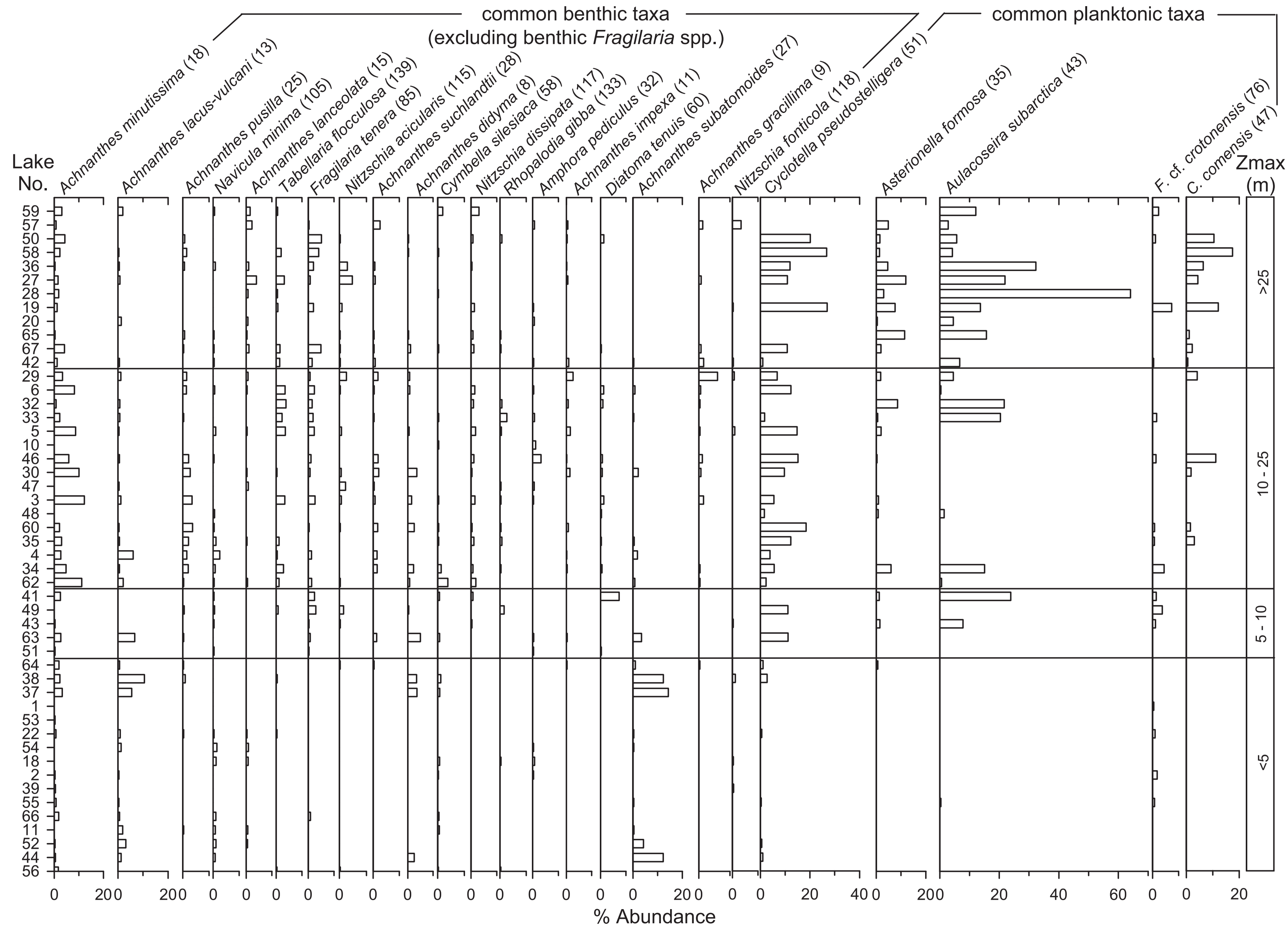

Fig. 4b. Relative abundance profiles of diatom taxa present in at least 3 lakes and with a relative abundance of more than 5 % in 1 lake (excluding benthic *Fragilaria* spp.) from 49 Icelandic lakes arranged by maximum lake depth (Z_{max}).

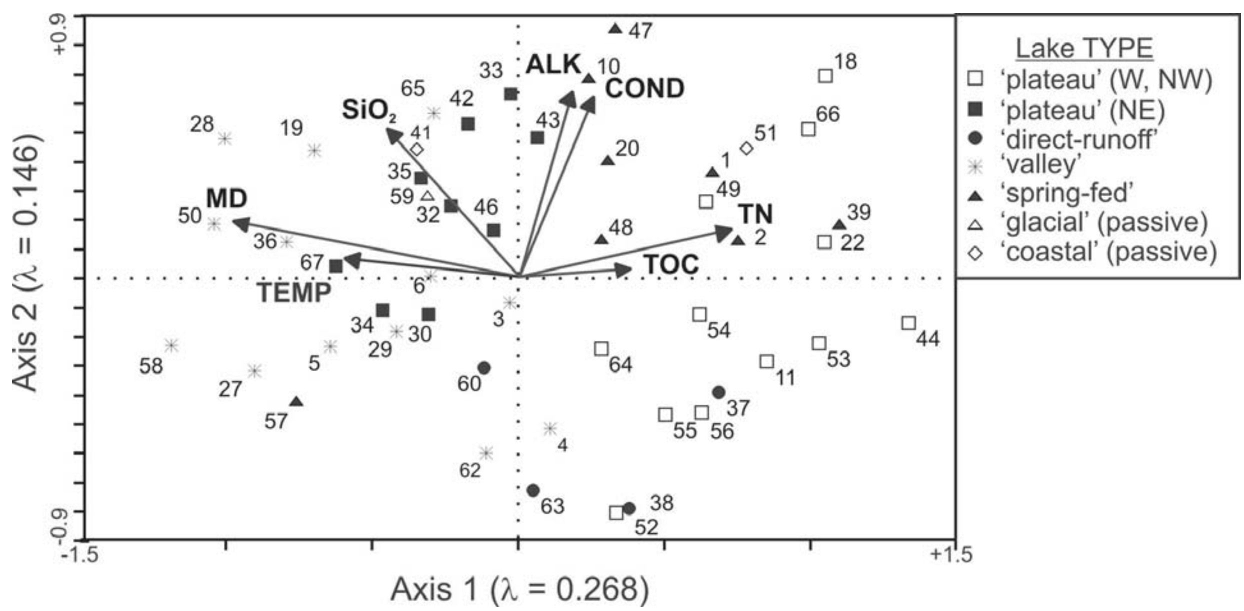

Fig. 5a. Distribution of 49 Icelandic lakes with respect to 7 environmental variables that best describe the variation in the diatom assemblages in a canonical correspondence analysis (CCA). Lakes are coded *a priori* by ecological TYPE categories. 'Glacial' and 'coastal' lakes are plotted passively in the ordination biplot. Lake numbers correspond to the names provided in Table 1.

CCA axis, whereas ALK, COND, and SiO_2 gradients are reflected along the second CCA axis.

Most of the small, benthic and periphytic diatoms of the genera *Achnanthes, Fragilaria sensu lato* and *Navicula* plot in the right quadrants of the CCA indicating that these taxa are most common in shallower, cooler lakes that are relatively more nutrient-rich (Fig. 5a,b). Separation of these small benthic and periphytic taxa along the second CCA axis reflects differences in the influence of ionic composition and silica concentrations on their distribution. Most small benthic *Fragilaria sensu lato* taxa including *F. brevistriata* (67), *F. brevistriata* var. *inflata* (68), *F. construens* var. *binodis* (74), *F. construens* var. *venter* (75), *F. elliptica* (78), *F. lapponica* (79), *F. parasitica* (81), *F. pinnata* (82), and *F. pseudoconstruens/construens* (84) have affinities for relatively higher lakewater alkalinity, conductivity and silica concentrations that best typify 'spring-fed' lakes in this data set.

In contrast to the small benthic *Fragilaria*, numerous lightly silicified, small, benthic *Achnanthes* [e.g., *A. acares* (1), *A. curtissima* (6), *A. kuelbsii* (12), *A. lacus-vulcani* (13), *A. nodosa* (21), *A. oestrupii* (22), *A. peragalli* (23), *A. saccula* (26), and *A.subatomoides* (27)] and *Navicula* [e.g., *N. jaernfeldtii* (106), *N. laevissima* (108), *N. pseudoscutiformis* (112) and *N. vitiosa* (107)] taxa display ecological preferences for more dilute, less alkaline lakewater conditions and lower concentrations of silica that characterize the shallow (< 5 m) 'plateau' lakes located in the west and northwest of Iceland.

A diversity of other relatively small benthic and periphytic taxa from several genera including *Achnanthes, Cymbella, Gomphonema, Navicula* and *Nitzschia* cluster near the centre and lower left quadrant of the CCA ordination (Fig. 5a,b) suggesting that these taxa have an affinity for intermediate depth, temperature and nutrient conditions relative to the ranges of these variables represented by the Icelandic lakes' set, but prefer somewhat lower alkalinity and conductivity. Distribution patterns of these diatoms are not strongly associated with a particular TYPE class, but are most abundant in the shallow, dilute 'direct-runoff' lakes.

Larger, more heavily-silicified pennate taxa such as *Amphora lybica* (31), *Diploneis ovalis* (62), *Epithemia adnata* (63), *Nitzschia sigmoidea* (127), *Pinnularia borealis* (128), *Rhoicosphenia abbreviata* (132), *Synedra biceps* (137), *S. ulna* (138) and *Tabellaria flocculosa* (139) are largely confined to the upper left quadrant of the CCA biplot indicating their preference for relatively deeper lakes with higher silica and ion concentrations.

Most planktonic taxa [i.e., *Asterionella formosa* (35), *Aulacoseira islandica* (39), *A. italica* (40), *A. subarctica* (43), *Cyclotella comensis* (47), *C. distinguenda* (48), *C. distinguenda* var. *unipunctata* (49), *C. pseudostelligera* (51), *C. tripartita* (52), and *Rhizosolenia longiseta* (131)] occur in deep, oligotrophic 'valley'

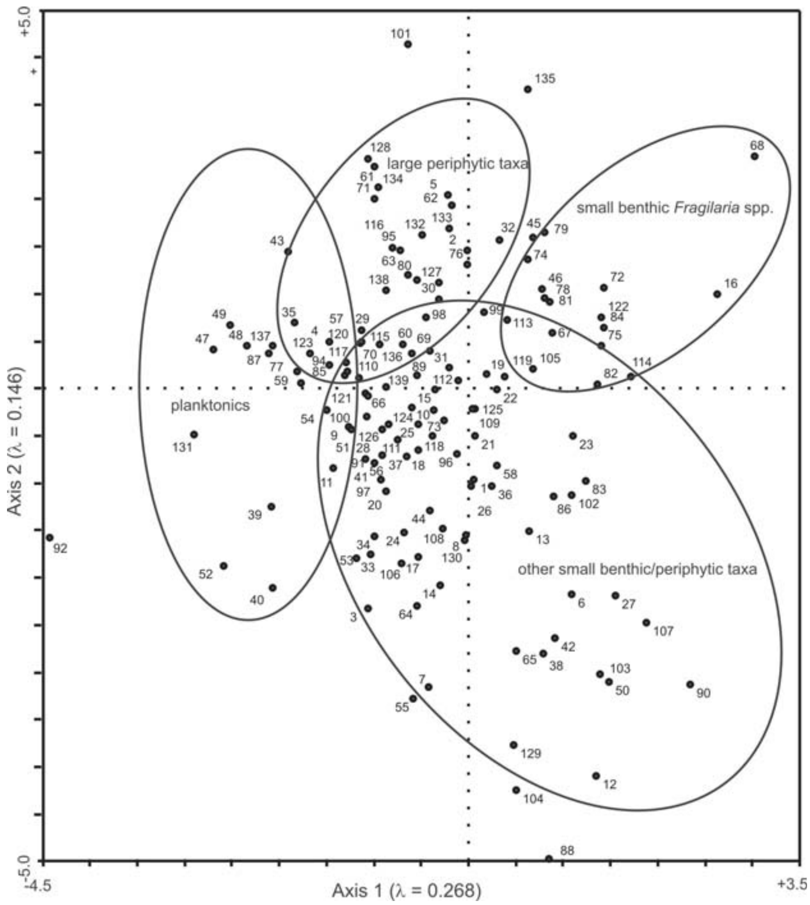

Fig. 5b. Distribution of common diatom taxa (n = 126) in Icelandic lakes with respect to 7 environmental variables that best describe the variation in the diatom assemblages in a canonical correspondence analysis (CCA) as depicted in Fig. 5a. Ellipses broadly encompass the position of planktonic, large periphytic, small benthic *Fragilaria*, and other small benthic/periphytic diatoms in the biplot. Species numbers correspond to the names provided in Table 5.

Table 6. Analysis of similarities (ANOSIM) results indicating differences between TYPE categories of lakes ('plateau', 'direct-runoff', 'spring-fed' and 'valley') based on diatom assemblages. The sample statistic (Global R) = 0.348, p = 0.0.

Groups of TYPE lake categories	Sample statistic (R)	Significance level (p)
'spring-fed' vs. 'direct-runoff'	0.649	0.004 *
'spring-fed' vs. 'plateau'	0.196	0.027 *
'spring-fed' vs. 'valley'	0.733	0.000 *
'direct-runoff' vs. 'plateau'	0.125	0.176
'direct-runoff' vs. 'valley'	0.261	0.064
'plateau' vs. 'valley'	0.334	0.000 *

* statistical significance $p \leq 0.05$

lakes with low ion concentrations that predominate in the relatively warmer region of western Iceland, and plot in the left quadrants of the CCA (Fig. 5a,b) at the high end of the mean depth and temperature vectors. Exceptions are *Stephanodiscus minutulus* (134) and *S. parvus* (135), which are common indicators of productive lakewater conditions. Not surprisingly, these taxa plot further to the right in the CCA ordination relative to other planktonic taxa indicating that they prefer higher nutrient concentrations.

Supporting the patterns in diatom distributions observed in the CCA, results from analysis of similarities (ANOSIM) indicate that the composition of sedimentary diatom assemblages differs significantly among ecological TYPE categories of Icelandic lakes (i.e., 'spring-fed', 'direct-runoff', 'plateau' and 'valley') (Global R-statistic = 0.348, $p < 0.05$) (Table 6). Diatom assemblages from 'spring-fed' are significantly different from those of both 'direct-runoff' and 'valley' lakes, while 'valley', and 'plateau' lakes have

Table 7. Contribution of *Achnanthes, Fragilaria*, *Cyclotella* and *Aulacoseira* spp. to the % dissimilarity of diatom assemblages between pairs of TYPE categories of lakes identified as having significantly different diatom assemblages (refer to Table 6).

Lake TYPE		*Achnanthes* spp.	*Fragilaria* spp.	*Cyclotella* spp.	*Aulacoseira* spp.
Direct-runoff	Average abundance	29.94	33.58	8.88	5.31
Spring-fed	Average abundance	4.36	80.84	0.24	2.30
	% of dissimilarity	35.74	18.14	5.75	10.39
Valley	Average abundance	12.49	17.41	19.05	13.05
Spring-fed	Average abundance	4.36	80.84	0.33	1.47
	% of dissimilarity	20.75	22.63	11.97	5.13
Valley	Average abundance	12.49	17.41	19.05	13.06
Plateau	Average abundance	7.59	58.46	5.29	3.59
	% of dissimilarity	21.59	21.3	11.56	5.25

significantly different assemblages. There are no significant differences between the diatom assemblages from 'plateau' and either 'spring-fed' or 'direct-runoff' lakes (Table 6). The relative amounts of small periphytic *Achnanthes* spp., small benthic *Fragilaria* spp., and planktonic *Cyclotella* spp. and *Aulacoseira* spp. account for most of the dissimilarity (> 60 %) between the diatom assemblages of TYPE categories of lakes with significantly different diatom assemblages (Table 7).

Discussion

General limnological conditions among Icelandic lakes

The 49 lakes in this study display a wide range of physical and chemical properties (Table 3), reflecting the diverse limnological conditions of subarctic lakes in Iceland. The chemical composition (nutrients and ions) of lakes from most other subarctic regions is strongly influenced by vegetation gradients across circumpolar or alpine treeline from forest to tundra ecozones. Ecotonal boundaries in these subarctic regions are largely controlled by strong latitudinal and/or altitudinal gradients in climate and the position of the Arctic Front. In Iceland, however, climatic conditions do not follow the typical strong latitudinal/altitudinal gradient observed in most other subarctic environments. Rather, climatic conditions in Iceland are more strongly influenced by maritime factors related to oceanic currents, which are modified to some extent by mountain topography (Einarsson 1984, Hanna et al. 2004). Therefore, unlike other subarctic regions that span circumpolar treeline, variations in limnological conditions among Icelandic lakes appear to be most strongly related to differences in climatic conditions related to maritime influence, bedrock geology, hydrology and lake morphometry. Importantly, significant limnological differences are apparent among TYPE categories of lakes following the ecological classification scheme for Icelandic freshwaters (modified from Gardarsson 1979).

Nutrients (TP, TN, TOC)

Higher TP concentrations indicative of mesotrophic to eutrophic conditions (> 20 µg l^{-1}) occur only in relatively shallow lakes (Z_{max} < 13 m and MD < 6.0 m), most of which are 'plateau' lakes and/or lakes located at low elevation. An exception is the deep (Z_{max} = 111.5 m) 'glacial' lake Lagarfljót (59), which has high concentration of TP (67 µg l^{-1}). The inverse relationship between TP and lake depth most probably reflects increasing effects of wind-induced resuspension of minerals from the bottom sediments as the lakes get shallower. TP in lake Lagarfljót is likely minerogenic originating from substantial glacial meltwater inputs, also creating highly turbid lakewater conditions. Despite elevated TP concentrations, Lagarfljót (59) is otherwise nutrient poor with low concentrations of TN (59 µg l^{-1}) and TOC (0.33 mg l^{-1}).

Significantly greater concentrations of TOC in the 'plateau' lakes in comparison to the 'direct-runoff', 'spring-fed' and 'valley' lakes are likely due in part to inputs from poorly-drained wetlands that characterize their catchments, and partly due to greater wind-induced resuspension of minerals from the bottom sediments of these generally shallow lakes. This is supported by the significantly higher concentrations of Fe in the more productive 'plateau' lakes, and the significant positive correlation of TOC and Fe in the data set (Fig. 2, Table 4). Fe can be mobilized under anoxic conditions that potentially develop in poorly drained wetland areas, forming complexes with DOC that likely enter the lakes with direct runoff, thereby contributing to the higher TOC and Fe in several of the 'plateau' lakes. Comparatively less allochthonous inputs of TOC to 'direct-runoff' and 'valley' lakes are expected due to the poor vegetation and lack of similar wetland systems in the catchments of these lakes.

pH and major ions

High pH and alkalinity and the lack of significant differences in these variables between TYPE categories of lakes can be attributed to the predominance of easily weathered volcanic bedrock and soils throughout Iceland that provide a rich source of alkalinity generating ions to the lakes. However, the concentrations of several major ions (i.e., Ca, K, Mg, Na, Fe), which are correlated to alkalinity and specific conductivity, vary significantly among TYPE categories of Icelandic lakes (Fig. 2). Not surprisingly, the two 'coastal' lakes that receive significant marine aerosols are the most ionically concentrated of the study lakes (Table 3).

'Plateau' and 'spring-fed' lakes generally have greater concentrations of ions than the 'valley' and 'direct-runoff' lakes. Differences in ionic composition between these TYPE categories of lakes appear to be related to several factors including lake morphometry, bedrock conditions, and hydrology. Evaporative concentration of ions is likely a chief mechanism resulting in the higher ionic content of the 'plateau' lakes, which are generally shallow and located in dry interior regions of Iceland. By contrast, more elevated ion concentrations in the 'spring-fed' lakes are most likely attributed to local bedrock conditions. 'Spring-fed' lakes in this study are generally situated on ion-rich, historical and postglacial basaltic bedrock formations in southern Iceland, unlike the older bedrock that underlies most of the other lakes in this study (Table 1). Gislason et al. (1996) determined that fluxes and mobility of elements from chemical weathering is greater in younger postglacial rocks than older rocks because they contain more soluble basaltic glass and generally have less vegetative cover. Therefore, chemical weathering of soluble postglacial bedrock likely contributes to greater inputs of ions to these lakes relative to the 'plateau', 'direct-runoff' and 'valley' lakes that are situated on older bedrock formations. Cool spring waters do not likely contribute to the high ionic concentrations in 'spring-fed' lakes, as they are relatively poor in dissolved inorganic carbon, calcium and magnesium (Gislason et al. 1996).

Positioning of lakes in the PCA ordination diagram clearly displays differences in the limnological conditions of lakes among TYPE categories (Fig. 3). 'Direct-runoff' lakes and 'valley' lakes cluster at the lower ends of the nutrient and ion gradients consistent with their relatively dilute lakewater conditions, but are separated along the second PCA axis due to differences in lake depth. As expected, the shallower 'direct-runoff' lakes plot toward the low end of the MD and Z_{max} gradients, while the deeper 'valley' lakes are positioned at the higher ends of these gradients. 'Spring-fed' lakes are placed to the right of the 'direct-runoff' and 'valley' lakes indicating their relatively higher nutrient and ion concentrations. An exception is Langisjór (57), which is an exceptionally large (area = 25.7 km^2) and deep (Z_{max} = 73.5 m) 'spring-fed' lake, and is more limnologically similar to the deeper 'valley' lakes. 'Plateau' lakes display the most scatter in the PCA ordination, and overlap with the spring-fed lakes indicating that they span a wider range of physical and chemical limnological conditions than the other TYPE categories of lakes. However, 'plateau' lakes are generally more nutrient rich and ionically concentrated than lakes in the other TYPE classes excluding the 'coastal' lakes. Clustering of 'plateau' lakes into two groups is evident in the PCA ordination and appears to be related to differences in their geographic position in Iceland, and hence prevailing climate condition. 'Plateau' lakes located in warmer, wetter regions of northwest and west Iceland tend to be shallower with higher nutrient and lower ion concentrations relative to 'plateau' lakes that are located in colder, drier regions in the south and NE of Iceland.

Patterns in diatom flora among Icelandic lakes

General floristic composition of diatom assemblages

Both benthic and planktonic forms were well represented in the diatom assemblages largely owing to the wide range of lake depths of the study lakes, and hence the availability of both littoral and open water habitats. Small benthic *Fragilaria* taxa (particularly *F. brevistriata, F. construens, F. construens* var. *venter, F. pinnata*, and *F. pseudoconstruens*) were predominant in the diatom assemblages, however, most likely reflecting the generally cold lake water conditions that characterize subarctic Icelandic lakes. The ability of these *Fragilaria* spp. to tolerate and proliferate in cold environmental conditions, often growing under ice cover or in shallow moats of partially frozen ponds, is well known (e.g. Smol 1988, Douglas & Smol 1999, Lotter & Bigler 2000).

Similar to other studies of shallow subarctic lakes, planktonic diatoms were rare or absent in lakes less than 5 m deep. Because some planktonic diatoms may require stratification of the water column to maintain their position in the photic zone, the lack of planktonic diatoms in smaller, shallower lakes (< 5 m) suggests that these lakes may not thermally stratify, or may only become weakly stratified during the open water season, or they are simply too shallow to support large planktonic diatom communities. By contrast, planktonic forms were important components of the diatom assemblages in most of the deeper lakes (> 5 m), attaining relative abundances of over 50 % in all of the deepest 'valley' lakes (> 25 m) (Fig. 4a). Lower abundance of planktonic diatoms in many lakes, including deeper lakes, may result from the influence of strong winds. Due to the lack of forest cover, the lakes are exposed to the effects of wind, which can prevent stratification or cause stratification to break down. For example, in Iceland´s largest lake, Lake Þingvallavatn, a relatively weak thermocline may in some years develop at 20–25 m depth for a month or two (July–August), but the lake is, in most years, more or less mixed from bottom up throughout the year due to wind mixing (Malmquist et al. 2008).

Although abundant in similarly deep lakes belonging to other ecological TYPE categories, planktonic taxa represented less of the diatom assemblages from these lakes in comparison to the 'valley' lakes. There are several possible reasons for the comparatively higher abundances of planktonic diatoms in the deep 'valley' lakes. First, 'valley' lakes are typically large, deep graben lakes with steep-sided morphology, and therefore have restricted littoral zones for the growth of benthic diatoms in comparison to similarly deep, non-graben lakes belonging to other TYPE categories. Because the diatom data are expressed as relative abundances, differences in the relative amounts of benthic to planktonic habitats may largely explain the higher proportions of planktonic diatoms in deep 'valley' lakes in comparison to the similarly deep 'plateau', 'direct-runoff' and 'spring-fed' lakes. Low light conditions attributed to high minerogenic turbidity from glacial meltwater inputs also likely contribute to lower representation of planktonic diatoms in some of the deep Icelandic lakes. For example, diatom assemblages from the two deepest lakes, Lagarfljót (59) and Langisjór (57) with maximum depths of 111.5 m and 73.5, respectively, have relatively low percentages of planktonic taxa (Fig. 4a) and are primarily dominated by small benthic *Fragilaria sensu lato* taxa. Lagarfljót (59) is a glacial-fed lake, and therefore receives highly silted melt waters contributing to low light penetration in this lake (Table 1). Lake Langisjór (57) is presently a clear water lake under a strong influence of spring inputs (Table 1), but prior to 1965 it received glacial meltwater inputs from the largest glacier in Iceland, Vatnajökull (Fig. 1). While planktonic diatoms are typically intolerant of low light levels, several small, benthic *Fragilaria sensu lato* species have low light requirements, competing well in lakes with low light penetration associated with ice cover (Smol 1988, Lotter & Bigler 2000), elevated DOC concentrations (Rühland & Smol 2002) and minerogenic turbidity (Karst-Riddoch et al. 2005a,b). Therefore, low light availability in these turbid, glacier-influenced lakes likely accounts for the proliferation of benthic, low-light tolerant *Fragilaria sensu lato* taxa rather than planktonic diatom forms that dominated the assemblages from other deep but clear water lakes. Finally, the greater representation of planktonic diatoms in deep 'valley' lakes than in similarly deep lakes belonging to different ecological lake categories may reflect differences in the degree and duration of ice cover. Increases in planktonic taxa in paleolimnological studies have often been attributed to reduced ice-cover conditions (e.g., Sorvari et al. 2002, Rühland et al. 2003b, 2008, Smol et al. 2005). As previously described, 'valley' lakes are primarily situated in relatively warmer lowland areas of western Iceland, and therefore likely have a shorter ice-covered season than deep lakes elsewhere in Iceland.

Relationships between diatoms and measured environmental variables

The distribution of diatoms among Icelandic lakes is largely influenced by a combination of multiple limnological variables that include lake depth and related factors (such as water clarity, benthic versus planktonic habitat availability, ice cover, stratification patterns), surface water temperature, nutrients and ions (Fig. 5a,b). These relationships between the common diatom taxa and measured environmental variables are largely similar to those observed in other similar studies of subarctic lakes spanning treeline. However, in these other subarctic regions, differences in the chemical properties of lakes that most strongly influence the composition of diatom assemblages has often been attributed to catchment processes related to vegetation gradients across circumpolar or alpine treeline from forest to tundra ecozones. As previously described, similar vegetation gradients do not exist in Iceland, rather vegetation is non-arboreal; the landscape is dominated by mire vegetation mostly of European origin, or is barren due to infertile, desert-like soils and extreme erosion. In the absence of strong vegetation gradients, distinct patterns in the diatom assemblages occur across groups of Icelandic lakes with different TYPE classes. This suggests that the ecological classification scheme proposed by Garðarsson (1979) for Icelandic freshwaters, although qualitatively based on major differences in geographic and topographic location, bedrock geology, and hydrology of the lakes, captures the major environmental conditions influencing ecologically important limnological properties determining the distribution of diatoms (Fig. 5a,b).

Ecological preferences of small benthic *Fragilaria sensu lato* taxa for relatively higher nutrient concentrations (TN, SiO_2), alkalinity, and conductivity among shallow, cold Icelandic lakes may have important implications for diatom-based paleolimnological investigations from cold subarctic and Arctic environments. Small benthic *Fragilaria sensu lato* taxa are typically described as generalists as they often occur in high abundances over a wide range of habitats. In cold subarctic, Arctic and alpine regions, sedimentary diatom assemblages are frequently dominated by *Fragilaria sensu lato* spp., which has been mostly attributed to their tolerance of prolonged ice cover and other harsh environmental conditions (e.g. Smol 1988, Douglas & Smol, 1999, Lotter & Bigler 2000). For this reason, changes in the relative abundances of *Fragilaria sensu lato* diatoms from sedimentary records are often interpreted as an indication of changes in the duration and extent of ice cover in Arctic, subarctic and alpine lakes. However, based on the above distribution patterns of benthic *Fragilaria sensu lato* from subarctic Icelandic lakes, as well as similar observations from lakes spanning treeline in the Central Canadian Arctic (Rühland et al. 2003a), downcore shifts in the abundance of this group of diatoms may also reflect changes in limnological conditions associated with nutrient and ion concentrations.

Determination of ecological differences among species of benthic *Fragilaria* is of interest for diatom-based paleolimnological studies, particularly when *Fragilaria* taxa dominate the sedimentary record, and when the most significant changes in the diatom assemblages occur within this group. For example, in a *Fragilaria*-dominated sedimentary record from East Greenland, shifts between *F. pinnata* and *F. construens* were concurrent with temperature changes inferred from the Renland ice core (Cremer et al. 2001). Based on these results, Cremer et al. (2001) suggested that *Fragilaria pinnata* and *F. construens* might be temperature-sensitive species, with the former indicative of warmer conditions. Similarly, benthic *Fragilaria* dominated the diatom assemblages in a sediment core from Lake Myvatn in Iceland (Einarsson et al. 2004), but causes of major shifts between species of *Fragilaria* over the past ~2,300 years were not able to be discerned. Among Icelandic lakes in this study, small benthic *Fragilaria* taxa displayed weak or little ecological preferences for the other measured environmental variables, as evidenced by their close positioning in the CCA (Fig. 5a,b). This is further supported by a lack of clearly defined differences in the distribution patterns of individual *Fragilaria* taxa across single measured environmental variables (including surface water temperature) (Fig. 6), as well as results from a series of CCAs constrained to a single variable at a time. However, as expected, *F. pinnata* and *F. construens* var. *venter*, two taxa often associated with more severe ice conditions in Arctic lakes, did tend to be more common in colder waters (Fig. 6c,d). Our overall conclusions would remain, based on the available data, that many of these small benthic *Fragilaria* taxa are ecological generalists, but are especially competitive in colder, more ice-covered environmental conditions, as occur in some Arctic lakes (e.g. Douglas & Smol 1999).

The affinity of larger pennate diatoms for the deep, oligotrophic Icelandic lakes in this data set is likely related to the greater availability of rocky littoral habitat suitable for the growth of these relatively larger attached diatom forms. Many similar taxa (e.g., *Diploneis ovalis, Nitzschia sigmoidea, Synedra ulna, Tabellaria flocculosa*) were also identified in the epilithic algal communities from the stony littoral zone (0–10 m depth) in Lake Thingvallavatn, a large deep valley lake located in southwest Iceland (Jónsson 1992). In Lake Thingvallavatn, estimated net epilithic production was high (188 g C m^{-2} yr^{-1}) in comparison to other oligotrophic systems, with diatoms contributing approximately 50 % of the productivity (95 g C m^{-2} yr^{-1}) of the epilithic community from 0 to 18 m depth (Jónsson 1992). Together with the predominance of relatively large pennate diatoms in the assemblages from most of the deeper oligotrophic Icelandic lakes in this study, this suggests that the contribution of the epilithic diatom community may be especially important to the productivity of deep oligotrophic Icelandic lakes.

Comparison of diatom assemblages amongst the Icelandic ecological lake TYPE categories

Comparisons between pairs of ecological lake TYPE categories reveal that diatom assemblages from 'spring-fed' lakes differ from those of both 'direct-runoff' and 'valley' lakes, while 'valley' and 'plateau' lakes have significantly different assemblages (Table 6). The diatom assemblages from the more nutrient rich, ionically concentrated 'spring-fed' lakes have higher abundances of *Fragilaria* spp. and lower abundances of *Achnanthes*, *Cyclotella* and *Aulacoseira* spp. than both the oligotrophic, dilute 'direct-runoff' and 'valley' lakes (Table 7). These differences in diatom species account for 68 % and 60 % of the dissimilarity between the diatom assemblages from 'spring-fed' and 'direct-runoff' and 'spring-fed' and 'valley' lakes, respectively. Similar relationships are observed between the diatom assemblages of the 'plateau' lakes with highly variable nutrient and ion concentrations and the deeper, oligotrophic 'valley' lakes. Higher relative abundances of small benthic *Fragilaria sensu lato* taxa and lower abundances of *Achnanthes, Cyclotella* and *Aulacoseira* spp. in the 'plateau' lakes relative to the 'valley' lakes account for 60 % of the dissimilarity between their diatom assemblages.

Significant differences were not found when comparing the diatom assemblages from 'plateau' with either 'spring-fed' or 'direct-runoff' lakes (Table 6). The lack of observed differences between these lake TYPE categories is likely due to the highly variable limnological conditions of the 'plateau' lakes relative to the other lake TYPE categories (Figs 2, 3 and 5). As previously described, the limnological conditions and diatom assemblages of 'plateau' lakes appear to be strongly influenced by geographic location (Fig. 5a,b). 'Plateau' lakes situated in colder, drier regions in northeast Iceland are typically nutrient-poor, alkaline, and possess diatom assemblages dominated by larger, more heavily-silicified periphytic taxa. By contrast, in warmer wetter climates of the north and northwest of Iceland, diatom assemblages from more nutrient-rich and ionically dilute 'plateau' lakes are characterized by higher abundances of lightly-silicified small benthic *Fragilaria sensu lato, Achnanthes* and *Navicula* taxa.

Summary and conclusions

Analyses of modern limnological conditions and the distribution of sedimentary diatom assemblages revealed important ecological features of subarctic Icelandic lakes with a wide range of typologies. Based on measurements of 16 environmental variables, the lakes differed primarily along gradients of ionic composition and nutrient concentrations as well as lake depth. Deep lakes were generally oligotrophic with relatively low conductivity and concentrations of associated ions, while shallow lakes (< 5 m) exhibited a wide range of nutrient and ionic composition. Differences in limnological conditions of the lakes appear to be strongly related to local climatic conditions, bedrock geology, hydrology and lake morphometry. The wide range of limnological settings with variable habitats for diatom growth is reflected in the taxonomic diversity of the diatoms. Distribution of diatom taxa among lakes was best described by measured limnological gradients of mean depth, conductivity, nutrients (TOC, SiO_2, TN), alkalinity, and surface water temperature. Small, benthic *Fragilaria sensu lato* taxa were important components of the diatom assemblages from most of the lakes, consistent with the overall cold conditions and extended periods of ice cover that characterize lakes in this subarctic environment. Importantly, diatoms within this complex displayed similar preferences for the measured environmental variables in this study, suggesting that differences in their relative abundances are not closely related to, for example, concentrations of major ions and nutrients in subarctic Icelandic lakes. As suggested in previous paleolimnological studies from polar regions, these taxa are likely generalists that can survive harsh environmental conditions, and so they may often thrive in, for example, ice covered lakes, as other diatom taxa are less competitive in these environments.

Limnological conditions and sedimentary diatom assemblages were similar among lakes within ecological classes of freshwater Icelandic lakes (i.e., 'valley', 'spring-fed', 'plateau' and 'direct-runoff') initially proposed by Garðarsson (1979). 'Valley' lakes are large, deep, oligotrophic basins primarily located in narrow valleys in western Iceland. Diatom assemblages from the 'valley' lakes are characterized by high abundances of centric diatoms reflecting the availability of clear water planktonic habitats, as well as relatively large pennate taxa that occupy rocky littoral habitats surrounding the lakes. 'Spring-fed' lakes found predominately in the southwest, south and northeast of Iceland are relatively rich in dissolved nutrients most likely originating from the cold-water springs that feed them. Elevated ion concentrations in these lakes are most likely due to inputs from weathering of soluble bedrock that dominates in their catchments. Relatively

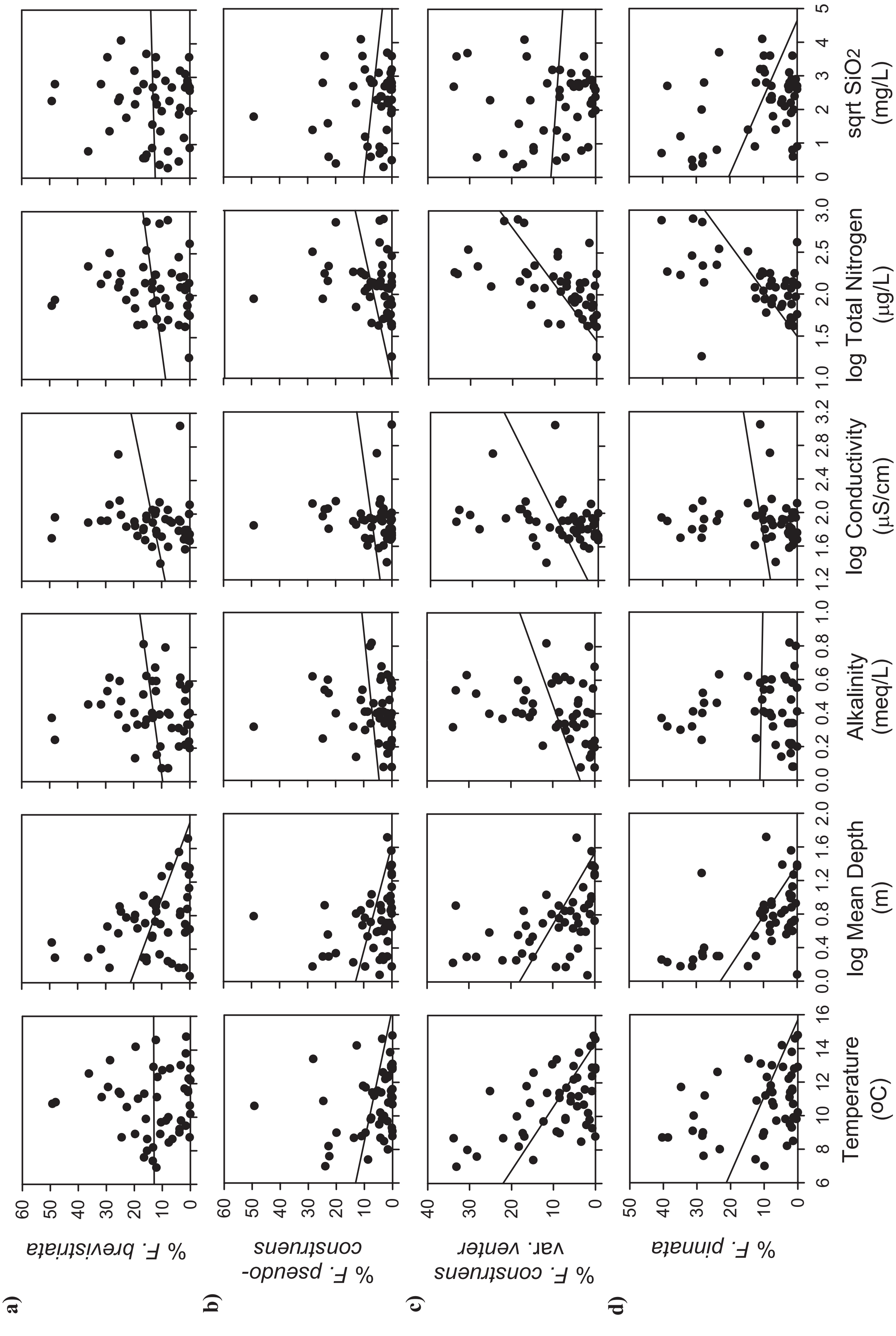

Fig. 6. Scatterplots showing the lack of relationship (Pearson correlation, $p > 0.05$) between relative abundances of **a)** *Fragilaria brevistriata*, **b)** *F. pseudoconstruens*, **c)** *F. construens* var. *venter*, and **d)** *F. pinnata* and selected environmental variables.

high ion and nutrient concentrations, in combination with cold environmental conditions, provide suitable habitats for small benthic *Fragilaria sensu lato* diatoms that dominate the assemblages from 'spring-fed' lakes. The limnological conditions and diatom assemblages of 'plateau' lakes that are mostly situated in the unpopulated highlands (~200–400 m a.s.l.) of western and northeastern Iceland vary with respect to geographic location. In colder, drier regions of northeast Iceland, 'plateau' lakes are nutrient-poor, alkaline, and possess diatom assemblages dominated by larger, more heavily-silicified periphytic taxa. By contrast, small benthic diatoms (primarily of the genera *Fragilaria, Achnanthes* and *Navicula*) dominate the assemblages from more nutrient-rich and ionically dilute 'plateau' lakes in relatively warmer, wetter climates of the north and northwest of Iceland. 'Direct-runoff' lakes have similar limnic properties and diatom assemblages as 'plateau' lakes in north and northwest. Refinement of the Garðarsson's (1979) classification system as a tool for lake management practices in Iceland may be achieved by including more precise morphometric data, especially lake depth and basin form, as well as better-defined local climatic conditions and broader categories of lake water origin.

Distinct limnological conditions and composition of the sedimentary diatom assemblages from lakes within ecological type classes (i.e., 'valley', 'spring-fed', 'plateau' and 'direct-runoff') suggest that classification of Icelandic lakes based on major topographic, geological and hydrological features may indeed capture important limnological and ecological differences of the lakes. These findings are especially important for lake management strategies because of the individualistic responses and differing sensitivities of Arctic and alpine lakes to climatic and environmental change (Anderson et al. 2004, Karst-Riddoch et al. 2005b). Therefore, Icelandic lakes that are limnologically and ecologically similar (with the same ecological TYPE category) are more likely to respond in a comparable way to climate change. However, the response of Icelandic lakes within these different ecological TYPE categories to past environmental changes remains largely unknown, but can now be determined using diatom-based paleolimnological investigations and the diatom autecological information gained in this study.

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References

Aðalsteinsson, H., Rist, S., Hermannsson, S. & Pálsson, S., 1989: Lakes in Iceland. A list of lakes larger than 0.1 km^2. National Energy Authority. Report no. OS-890004/VOD-02. 48 pp. (in Icelandic).

Anderson, N. J., Ryves, D. B., Grauert, M. & McGowan, S., 2004: Holocene palaeolimnology of Greenland and the northern north Atlantic islands. – In: Pienitz, R., Douglas, M. S. V. & Smol, J. P. (eds): Long-Term Environmental Change in Arctic and Antarctic Lakes. – Kluwer Academic Publishers, Dordrecht, pp. 319–347.

Andrews, J. T., Caseldine, C., Weiner, N. J. & Hatton, J., 2001a: Late Holocene (ca. 4 ka) marine and terrestrial environmental change in Reykjarfjordur, north Iceland: climate and/or settlement? – J. Quat. Sci. **16:** 133–143.

Andrews, J. T. & Giraudeau, J., 2003: Multi-proxy records showing significant Holocene environmental variability: the inner N. Iceland shelf (Hunafloi). – Quat. Sci. Rev. **22:** 175–193.

Andrews, J. T., Helgadottir, G., Geirsdottir, A. & Jennings, A. E., 2001b: Multicentury-scale records of carbonate (hydrographic?) variability on the northern Iceland margin over the last 5000 years. – Quat. Res. **56:** 199–206.

Arnalds, Ó., 1999: Invited lecture: Soils and soil erosion in Iceland. – Geochemistry of the Earth's Surface. – Balkema, Rotterdam, pp. 135–138.

Bigler, C. & Hall, R. I., 2002: Diatoms as indicators of climatic and limnological change in Swedish Lapland: a 100-lake calibration set and its validation for paleoecological reconstructions. – J. Paleolimnol. **27:** 97–115.

Birks, H. J. B., Line, J. M., Juggins, S., Stevenson, A. C. & ter Braak, C. F. J., 1990: Diatoms and pH reconstruction. – Philos. Trans. R. Soc. Lond. **327:** 263–278.

Bjarnasson, Á. H., 1978: Erosion, tree growth and land regeneration in Iceland. – In: Holdgate, M. W. & Woodman, M. J. (eds): The Breakdown and Restoration of Ecosystems. – Plenum Press, New York, pp. 241–248.

Brooks, S. J. A. & Birks, H. J. B., 2000: Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Kråkenes Lake, western Norway. – J. Paleolimnol. **23:** 77–89.

Caseldine, C., Langdon, P. & Holmes, N., 2006: Early Holocene climate variability and the timing and extent of the Holocene thermal maximum (HTM) in northern Iceland. – Quat. Sci. Rev. **25:** 2314–2331.

Clarke, K. R. & Warwick, R. M., 1994: Change in marine communities: An approach to statistical analysis and interpretation. – Natural Environment Research Council, UK, 144 pp.

Cremer, H., Melles, M. & Wagner, B., 2001: Holocene climate changes reflected in a diatom succession from Basaltø, East Greenland. – Can. J. Bot. **79:** 649–656.

Doner, L., 2003: Late-Holocene paleoenvironments of northwest Iceland from lake sediments. – Palaeogeogr. Palaeoclimatol. Palaeoecol. **193:** 535–560.

Douglas, M. S. V. & Smol, J. P., 1999: Freshwater diatoms as indicators of environmental change in the High Arctic. – In: Stoermer, E. F. & Smol, J. P. (eds): The diatoms: applications for the environmental and earth sciences. – Cambridge University Press, Cambridge, pp. 227–244.

Einarsson, M. Á., 1984: Climate of Iceland. – In: Van Loon, H. (ed.): World Survey of Climatology, Climates of the Oceans, volume 15. – Elsevier Science Publishers, Amsterdam, pp. 673–695.

Einarsson, P., 1986: Seismicity along the eastern margin of the North American Plate. – In: Vogt, P. R. & Tucholke, B. E. (eds): The Geology of North America, Volume M, The Western North Atlantic Region. – Geological Society of America, pp. 99–116.

Einarsson, Á., Stefánsdóttir, G., Jóhannesson, H., Ólafsson, J. S., Gíslason, G. M., Wakana, I., Gudbergsson, G. & Gardarsson, G., 2004: The ecology of Lake Mývatn and the River Laxá: variation in space and time. – Aquat. Ecol. **38:** 317–348.

Fallu, M. A., Allaire, N. & Pienitz, R., 2002: Distribution of freshwater diatoms in 64 Labrador (Canada) lakes: species-environment relationships along latitudinal gradients and reconstruction models for water colour and alkalinity. – Can. J. Fish. Aquat. Sci. **59:** 329–349.

Foged, N., 1974: Freshwater Diatoms in Iceland. – Bibliotheca Phycologica, Band 15. – J. Cramer, Vaduz, 118 pp.

Foged, N., 1981: Diatoms in Alaska. – J. Cramer Verlag, Vaduz, 317 pp.

Garðarsson, A., 1979: A classification of Icelandic freshwaters. – Týli, **9:** 1–10. (in Icelandic, with English summary).

Gerrard, J., 1991: An assessment of some of the factors involved in recent landscape change in Iceland. – In: Maizels, J. K. & Caseldine, C. J. (eds): Environmental Change in Iceland: Past and Present. – Kluwer Academic Publishers, Dordrecht, pp. 237–254.

Gislason, S. R., Arnorsson, S. & Armannsson, H., 1996: Chemical weathering of basalt in southwest Iceland: Effects of runoff, age of rocks and vegetative/glacial cover. – Amer. J. Sci. **296:** 837–907.

Gíslason, G. M., Ólafsson, J. S. & Aðalsteinsson, H., 1998: Animal communities in Icelandic rivers in relation to catchment characteristics and water chemistry. Preliminary results. – Nordic Hydrol. **29:** 129–148.

Gregory-Eaves, I., Smol, J. P., Finney, B. P. & Edwards, M. E., 1999: Diatom-based transfer functions for inferring past climatic and environmental changes in Alaska, U. S.A. – Arct. Antarct. Alp. Res. **31:** 353–365.

Gudmundsson, H. J., 1997: A review of the Holocene environmental history of Iceland. – Quat. Sci. Rev. **16:** 81–92.

Hall, R. I. & Smol, J. P., 1992: A weighted-averaging regression-calibration model for inferring total phosphorus concentration from diatoms in British Columbia (Canada) lakes. – Freshwat. Biol. **27:** 417–434.

Hallgrímsson, H., 2007: A list of freshwater and terrestrial algae recorded from Iceland. – The Icelandic Institute of Natural History. Report no. 48. 94 pp. (in Icelandic, with English summary).

Hanna, E., Jónsson, T. & Box, J. E., 2004: An analysis of Icelandic climate since the nineteenth century. – Internat. J. Climatol. **24:** 1193–2004.

Hill, M. O. & Gauch, H. G., 1980: Detrended correspondence-analysis – an improved ordination technique. – Vegetatio **42:** 47–58.

Jennings, A. E., Hagen, S., Hardardottir, J., Stein, R., Ogilvie, A. E. J. & Jonsdottir, I., 2001: Oceanographic change and terrestrial human impacts in a post AD1400 sediment record from the southwest Iceland shelf. – Climat. Chang. **48:** 83–100.

Jóhannesson, H. & Saemundsson, K., 1998: Geological map of Iceland. 1:500 000. – Bedrock Geology, 2nd edition. Icelandic Institute of Natural History, Reykjavík.

Jongman, R. H. G., ter Braak, C. J. F. & van Tongeren, O. F. R. (eds), 1995: Data Analysis in Community and Landscape Ecology. – Cambridge University Press, Cambridge, 299 pp.

Jónsson, G., 1992: Photosynthesis and production of epilithic algal communities in Thingvallavatn. – Oikos **64:** 222–240.

Karst-Riddoch, T. L., 2004: Sedimentary diatoms from sensitive alpine (northwest Canada) and subarctic (Iceland) lakes as indicators of Environmental and climatic conditions. – Ph.D. Thesis. Queen's University, Kingston, 194 pp.

Karst-Riddoch, T. L., Pisaric, M. F. J., Youngblut, D. K. & Smol, J. P., 2005a: Postglacial record of diatom assemblage changes related to climate in an alpine lake from the northern Rocky Mountains, Canada. – Can. J. Bot. **83:** 968–982.

Karst-Riddoch, T. L., Pisaric M. J. & Smol, J. P., 2005b: Diatom responses to 20th century climate-related environmental changes in high-elevation mountain lakes of the northern Canadian Cordillera. – J. Paleolimnol. **33:**265–283.

Krammer, K. & Lange-Bertalot, H. 1986–1991: Bacillariophyceae. – In: Ehl, H., Gerloff, J., Heynig, H. & Mollenhauer, D. (eds): Süßwasserflora von Mitteleuropa Band 2 (1–4). – Gustav Fisher Verlag, Stuttgart/Jena.

Lotter, A. F. & Bigler, C., 2000: Do diatoms in the Swiss Alps reflect the length of ice-cover? – Aquat. Sci. **62:** 125–41.

Maizels, J. & Caseldine, C., 1991: Environmental change in Iceland: past and present. An introduction. – In: Maizels, J. & Caseldine, C. J. (eds): Environmental Change in Iceland: Past and Present. – Kluwer Academic Publishers, Dordrecht, pp. 1–9.

Malmquist, H. J., 1997: Existing monitoring programmes in Iceland relevant to the project: Nature Monitoring in Nordic Rivers and Lakes. – In: Friberg N. (ed.): Pre-project: Nature monitoring in Nordic rivers and lakes National Environment Research Institute, Silkeborg, Denmark, pp. 13–21.

Malmquist, H. J., 1998: Rivers and lakes in Iceland: Ecology and wetland interactions. – In: Ólafsson J. S. (ed.): Icelandic wetlands, conservation and utilization University of Iceland Publication, Reykjavík, pp. 37–55. (in Icelandic, with English summary).

Malmquist, H. J., Antonsson, T. H., Guðbergsson, G., Skúlason, S. & Snorrason, S. S., 2000: Biodiversity of macroinvertebrates on rocky substrate in the surf zone of Icelandic lakes. – Verh. Internat. Verein. Limnol. **27:** 121–127.

Malmquist, H. J., Appelberg, M., Diepenrik, C., Hesthagen, T. & Rask, M., 2001: Fish. – In: Skriver, J. (ed.): Biological Monitoring of Nordic Rivers and Lakes. – TemaNord **513:** 61–71.

Malmquist, H. J., Ingimarsson, F., Ingvason, H. R., Stefánsson. S. M., 2008: Lake Þingvallavatn monitoring project. Data report for year 2007. Workpackage 2: Biology and physico-chemical factors in the pelagic habitat. – Natural History Museum of Kópavogur. Report 2–08, 38 pp. (in Icelandic with English summary)

Malmquist, H. J., Antonsson., Th., Ingvason, H. R., Ingimarsson, F. & Arnason, F., in press: Salmonid fish and warming of shallow lake Ellidavatn in SW-Iceland. – Verh. Internat. Verein. Limnol. **30:** (in press).

Martin, H. E., Whalley, W. B. & Caseldine, C. J., 1991: Glacier fluctuations and rock glaciers in Tröllaskagi, northern Iceland, with special reference to 1946–1986. – In: Maizels, J. K. & Caseldine, C. J. (eds): Environmental Change in Iceland: Past and Present. – Kluwer Academic Publishers, Dordrecht, pp. 255–265.

Ólafsdóttir, R. & Gudmundsson, H. J., 2002: Holocene land degradation and climatic change in northeastern Iceland. – Holocene **12:** 159–167.

Ólafsson, J. S., Aðalsteinsson, H. & Gíslason, G. M., 2001: Classification of running waters in Iceland, based on catchment characteristics. – In: Bäck, S. & Karttunen, K. (eds): Classification of Ecological Status of Lakes and Rivers. – TemaNord **584:** 57–59.

Ólafsson, J. S., Aðalsteinsson, H., Gíslason, G. M., Hansen, I. & Hrafnsdóttir, Th., 2002b: Spatial heterogeneity in lotic chironomids and simuliids in relation to catchment characteristics in Iceland. – Verh. Int. Verein. Limnol. **28:** 157–163.

Ólafsson, J. S., Gíslason, G. M. & Aðalsteinsson, H., 2002a: Icelandic running waters; anthropological impact and their ecological status. – TemaNord **566:** 86–88.

Pienitz, R., Douglas, M. S. V. & Smol, J. P. (eds), 2004: Long-Term Environmental Change in Arctic and Antarctic Lakes. – Springer, Dordrecht, 562 pp.

Pienitz, R. & Smol, J. P., 1993: Diatom assemblages and their relationship to environmental variables in lakes from the boreal forest-tundra ecotone near Yellowknife, Northwest Territories, Canada. – Hydrobiologia **269/270:** 391–404.

Pienitz, R., Smol, J. P. & Birks, H. J. B., 1995: Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. – J. Paleolimnol. **13:** 21–49.

Rühland, K., Paterson, A. M. & Smol, J. P., 2008: Hemispheric-scale patterns of climate-induced shifts in planktonic diatoms from North American and European lakes. – Global Change Biol. **14:** 2740–2745.

Rühland, K., Priesnitz, A. & Smol, J. P., 2003b: Paleolimnological evidence from diatoms for recent environmental changes in 50 lakes across Canadian Arctic treeline. – Arct. Antarct. Alp. Res. **35:** 111–124.

Rühland, K. M. & Smol, J. P., 2002: Freshwater diatoms from the Canadian arctic treeline and development of paleolimnological inference models. – J. Phycol. **38:** 249–264.

Rühland, K. M., Smol, J. P. & Pienitz, R., 2003a: Ecology and spatial distributions of surface–sediment diatoms from 77 lakes in the subarctic Canadian treeline region. – Can. J. Bot. **81:** 57–73.

Saemundsson, K., 1986: Subaerial volcanism in the western North Atlantic. – In: Vogt, P. R. & Tucholke, B. E. (eds): The Geology of North America, Volume M, The Western North Atlantic Region. – Geological Society of America, pp. 69–86.

Saemundsson, K., 1992: Geology of the Thingvallavatn Area. – Oikos **64:** 40–68.

Schindler, D. W. & Smol, J. P. 2006: Cumulative effects of climate warming and other human activities on freshwaters of Arctic and Subarctic North America. – Ambio **35:** 160–168.

Smol, J. P., 1988: Paleoclimate proxy from freshwater arctic diatoms. – Verh. Internat. Verein. Limnol **23:** 837–44.

Smol, J. P., 2008: Pollution of Lakes and Rivers: A Paleoenvironmental Perspective – 2nd Edition. Blackwell Publishing, Oxford, 383 pp.

Smol, J. P., Wolfe, A. P., Birks, H. J. B., Douglas, M. S. V., Jones, V. J, Korhola, A., Pienitz, R., Rühland, K., Sorvari, S., Antoniades, D., Brooks, S. J., Fallu, M.-A., Hughes, M., Keatley, B. E., Laing, T. E., Michelutti, N., Nazarova, L., Nyman, M., Paterson, A. M., Perren, B., Quinlan, R., Rautio, M., Saulnier-Talbot, É., Siitonen, S., Solovieva, N. & Weckström, J., 2005: Climate-driven regime shifts in the biological communities of arctic lakes. – Proc. National Acad. Sci. **102:** 4397–4402.

Sorvari, S., Korhola, A. & Thompson, R., 2002: Lake diatom response to recent Arctic warming in Finnish Lapland. – Global Change Biol. **8:** 171–81.

Stoermer, E. F. & Smol, J. P. (eds), 1999: The Diatoms: Applications for the Environmental and Earth Sciences. – Cambridge University Press, Cambridge, 481 pp.

ter Braak, C. J. F. & Šmilauer, P., 1998: CANOCO for Windows. – Centre for Biometry, Wageningen, The Netherlands.

Thórarinsson, S., 1962: L'érosion éolienne en Islande à la lumière des études tephrochronologiques. – Rev. Geomorph. Dyn. **13:** 107–124.

Thorsteinsson, I. & Arnalds, Ó., 1992: The vegetation and soils of the Thingvallavatn area. – Oikos **64:** 105–116.

Wada, K., 1985: The distinctive properties of Andosols. – Adv. Soil Sc. **2:** 173–229.

Weckström, J., Korhola, A. & Blom, T., 1997: The relationship between diatoms and water temperature in thirty subarctic Fennoscandian lakes. – Arctic Alpine Res. **29:** 75–92.

Wilson, S. E. & Gajewski, K., 2002: Surface-sediment diatom assemblages and water chemistry from 42 subarctic lakes in the southwestern Yukon and northern British Columbia, Canada. – Ecoscience **9:** 256–270.

Wooller, M., Wang, Y. & Axford, Y., 2008: A multiple stable isotope record of Late Quaternary limnological changes and chironomid paleoecology from northeastern Iceland. – J. Paleolimnol. **40:** 63–77.

WWF, 2001: The Status of Wild Atlantic Salmon: A River by River Assessment. pp. 108–110. Chapter 7.7. Iceland. Report by World Wildlife Fund. Printed in Canada. 179 p. http://www.worldwildlife.org/oceans/pdfs/atlantic_salmon.pdf

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