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Environmental Science

Investigation into diatom ecology within glacier-fed streams in Iceland

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Contents

Abstract

Milner and Petts (1994) recently proposed a model developed from data on glacier-fed streams outlining zoobenthic community gradients determined by two principal variables, water temperature and channel stability, as a function of distance downstream. This study reviews the physical habitat and ecology of diatoms, in a glacial river with respect to the spatial framework of macroinvertebrates suggested by Milner and Petts. The hydrobiological changes were assessed on a longitudinal scale to a maximum distance of 6300m from glacial snout. The studied lotic system incorporated a proglacial lake along with a highly turbid tributary joining mid-way. Epilithic diatoms were sampled from sites above and below the lake. The diatom assemblages displayed pronounced longitudinal changes in community composition as shown by TWINSPAN and DCA analysis. The majority of diatoms where found to be motile with diversity and abundances very low throughout. Diatoms characteristic of upper sites were found to be smaller species tolerant of fast turbulent flow, with species found at lower sites being larger, forming 'forest like' communities. I propose that flow velocity is the principal variable controlling diatom communities, and not that of temperature. Therefore, when considering diatoms, the effect of the lake and tributary is seen to be of less importance compared to invertebrates.

Introduction

The structure and function of communities in streams and rivers has long been a subject of great interest. Although the hydrology and physicochemical features of glacier-fed rivers has been extensively studied (Tómasson, 1976), their ecology has received comparatively little attention.

Studies on the colonisation and succession of faunal species in freshwater ecosystems are particularly sparse. However, in recent years an increase in ecological research has developed, and a plethora of studies have been undertaken describing patterns of ecological development in glacial systems. Colonisation can be defined as the invasion of species into disturbed and newly created habitats (Mayr, 1965). Fisher (1983) termed succession as the colonisation and the subsequent change of the community. Milner (1987, 1994), examined the colonisation and succession of freshwater macroinvertebrate communities in Glacier Bay, Alaska. It was possible in this situation, due to rapid glacial recession exposing new land, to examine the colonisation and development of communities where temporal variations could be studied on the basis of spatial change. The results from Milner's (1994) study indicated temporal colonisation and succession in a new stream; Wolf Point Creek, between 1978 and 1990. In 1978 the temperature of Wolf Point Creek was typical of a glacial stream at around 2°C, and five out of the six chironomid species were found to be cold tolerant *Diamesia* spp. Eight years later the temperature of the stream had increased to 5-6°C and quantitative sampling indicated that species diversity had increased, with Orthocladiinae species dominating the chironomid community and Baetidae and Chloroperlidae also colonising. By 1990 the temperature had reached 8-9°C and several of the original cold tolerant chironomid species were absent or at greatly reduced abundances. This study, therefore, indicated that the rise in temperature of about 8°C over twelve years resulted in distinct colonisation and successional alterations of the macroinvertebrate community.

Further studies in the Kenai Fjords National Park, Alaska (Milner, 1994), found invertebrate community structures similar to those in Glacier Bay; a domination of *Diamesia* spp. at low temperatures. However, in the Kenai Fjords at an August water temperature of 8-9°C in 1992, the community structure was still dominated by *Diamesia* spp, and the expected colonisation of other taxa, such as Orthocladiinae at temperatures above 5°C had not occurred. Unlike Wolf Point Creek the Kenai Fjord stream possessed an extremely unstable channel, subject to frequent spates (Milner, 1994). This indicated that at least some *Diamesa* species can maintain abundant populations at moderately high temperatures in the presence of low numbers of other taxa (Milner, 1994), and that high streambed disturbance prevented colonisation of other taxa past an early successional stage (Milner & Petts, 1994).

Milner (1987), discovered the same type of successional distribution patterns on a temporal scale that have previously been seen with a longitudinal progression from a glacial margin (Kownaki, 1980, 1985; Ward, 1992, 1994). This successional distribution of macroinvertebrates suggested that certainly in the early stages of aquatic ecosystem development, in Glacier Bay, community alterations are not principally brought about by biotic processes, but are dominated by the influence of the physical environment. The primary abiotic factor is seen to be water temperature, however stability of the channel on varying scales (substrate movement up to channel migration) can also prevail (Anderson, 1992; Milner & Petts, 1994; Milner, 1994). From this information Milner and Petts (1994) developed a generalised qualitative model of zoobenthic community structure in glacial rivers (Figure 1).

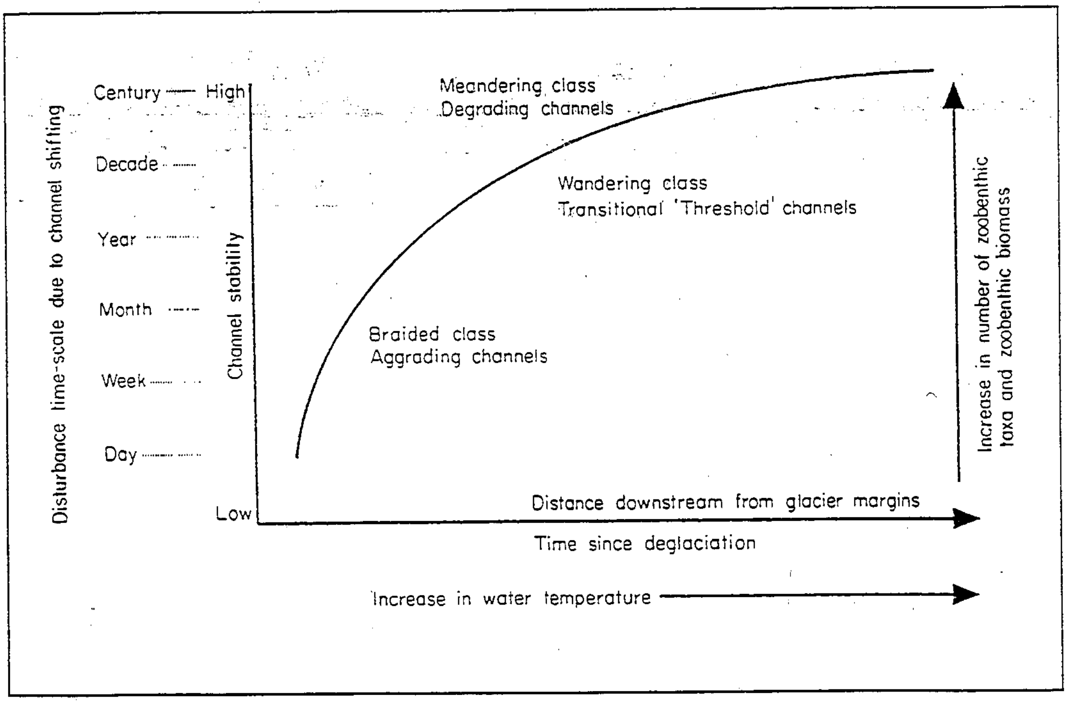

Figure 1 Generalised model of a glacial river showing the relationship between river channel form and stability, the zoobenthos community, temperature and time (Milner & Petts, 1994).

The model proposed a steady increase in diversity and biomass of benthic communities with distance downstream from glacial margins. However, modifiers to this downstream proposal were identified (Milner & Petts, 1994). It was recognised that factors such as changes in channel confinement, lakes and tributary convergence's can alter the water temperature and stability of the lotic system.

These factors influence the biotic community in a way that 'resets' or 'accelerates' the succession of the community in relation to the proposed model.

Milner's (1987) study provided information on the application of ecological theory, including succession, to streams which, as Fisher (1983) highlights, have previously received little attention in freshwater ecology. Milner's (1987) study and many other related studies (Milner, 1994; Milner & Petts, 1994; Ward, 1994) have focused on the ecological theories, principally in respect to macroinvertebrate communities. However, the importance of primary production in glacier-fed streams requires recognition. Although it is well established that many stream

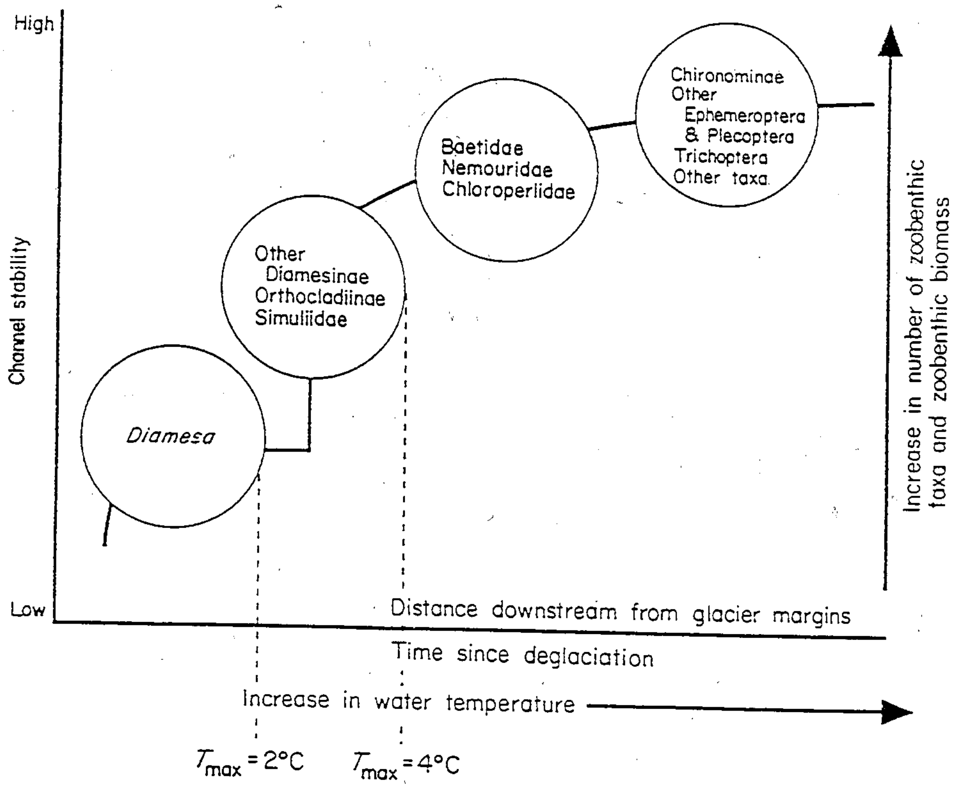

Figure 2 Points along a glacial river channel of increasing stability and water temperature where characteristic invertebrate taxa are typically added to the community (Milner & Petts, 1994)

invertebrates feed on periphytic algae (Brown, 1960; Cummins & Klug, 1979; Anderson & Cummins, 1979), there has been a comparative scarcity of studies focusing on the community structure of periphytic organisms in a natural successional situation, especially so in glacier-fed streams.

Unifying concepts of ecosystem development indicated that successional trends result in an increase in structural complexity, biomass, species diversity, stability and predictability of the community (Allan, 1996). Milner's (1987) study states a relationship between that of the successional changes of zoobenthos in correlation with the colonisation of epilithic organisms. The model proposed by Milner and Petts (1994) describes points along a glacial river channel of increasing stability and water temperature where characteristic invertebrate taxa are typically added to the community (Figure 2). It has been seen in numerous studies (Rounick & Winterbourn, 1983; Winterbourn, 1990; Milner, 1994), that primary production of stream ecosystems has a direct effect on zoobenthic communities as the periphyton acts as food and refugia. However, the scarcity of natural successional studies on diatom communities in glacier-fed streams, negates proposals to be formed for the downstream variation of diatom communities in the same context as that of the macroinvertebrate model. In particular there is a lack of detailed records of stream attributes with detailed knowledge on the structure and function of diatom communities (taxonomy, ecology and life histories) and their relation to faunal communities. The floral benthic communities of running waters include biofilm assemblages within the organic layer which coats all solid surfaces. This biofilm is a heterogeneous assemblage of attached algae, bacteria, fungi, protozoans and micrometazoans (Allan, 1996). In glacial rivers the main constituent of this biofilm is diatoms (Milner & Petts, 1994). Diatoms occur throughout the range of freshwater habitats, from standing and flowing waters to damp terrestrial sites. Some grow in the water column itself, as members of the phytoplankton, while others are associated with different types of substrata. The specificity of certain algae for particular substrata has allowed the recognition of different benthic communities; epilithon, epiphyton, epipelon, epipsammon, metaphyton, and if different components of freshwater are sampled contrasting communities can be found (Cox, 1996).

The present study concentrates on a glacial river system in the highlands region of Iceland during early July, 1997. The river channel studied is a glacial-fed stream which feeds a post glacial lake. Glacial streams in this region were classified by Peterson *et al* (1995), as alpine/arctic, the flow is observed to increase in May and peak in July and August due to snow and ice-melt; then the flow gradually decreases in September and is usually low in winter, with a few exceptions caused by rain in the autumn. Although the area is influenced by the Gulf Stream, the relatively high altitude and latitude results in low annual air temperatures of around 6°C in July and a mean annual air temperature of -1.5°C (Einarsson, 1979). While there is considerable information suggesting that the epilithic algal communities of alpine/arctic rivers thrives even under extremely harsh conditions and that primary production is important to the stream, there is no quantitative information on abundance or productivity for these streams (Petersen *et al.*, 1995).

The alpine and arctic rivers of Iceland lack any riparian vegetation within the highlands. The riparian substrate consists entirely of rocks covered with a patchwork of lichens. An organic soil, if present, is unstable and supports only patchy vegetation (Peterson *et al,* 1995). It has in some cases (Steffan, 1971) been established that invertebrate communities in close proximity to glacial snouts feed on organic matter released from the glacial ice during melting. However, in the Icelandic case there is comparatively little organic matter available to be blown onto the ice sheets. It can, therefore, be assumed that the meltwater of the Icelandic glaciers probably do not release enough organic matter to support invertebrate communities (Gíslason, Unpub. data). Due to the relative lack of plant cover, the amount of allocthonous material entering streams is quantitatively small for alpine rivers although it is thought that the input of allocthonous material may still play an important role in stream ecosystems (Petersen *et al.*, 1995). However, the autocthonous production is of greater importance, especially in the headwaters of glacier-fed streams, is important.

In glacier-fed arctic streams the physical habitat is extremely harsh. The temperature variation in streams is influenced by factors that operate at different temporal and spatial scales. In most freshwater periphyton habitats, water temperature is determined primarily by direct solar radiation, and on a larger spatial scale, factors such as source (most influential in glacial-fed streams), latitude, elevation, continentality and morphometry determine the overall temperature regime (Hutchinson, 1957). Substrate stability and channel morphology are also highly variable in arctic streams. For example, large outcrops and boulders offer substrata of a greater dependability and generally remain stationary through flood scouring events. In contrast, small rocks and sediments move with current action. Such environments would select for motile microalgae, such as diatoms, as opposed to large populations of sessile algae that would be more easily buried or crushed (Hynes, 1970; Whitton, 1975).

Within this study, the community composition and ecological significance of the diatom species and abundance was investigated qualitatively with a level of quantitative analysis. Within the glacier-fed stream system studied, the diatom community gradient is hypothesised to follow a pattern similar to that of macroinvertebrates proposed by Milner and Petts (1994); colonisation by a small number of 'early coloniser' species followed by an increase in abundance and diversity, controlled by biotic and abiotic factors. Also carried out by a colleague (J. Ray) during the same expedition was an extensive study on the macroinvertebrate communities of the Icelandic river in the context with the proposed model (Milner & Petts, 1994), allowing comparisons of diatom and invertebrate communities to be made in an analogous situation. Within the stream system studied there was a postglacial lake and tributaries present. This allowed assessment of the ecological impact of potential modifiers on diatom community composition, with comparisons to that of invertebrates in relation to the generalised model of the association between river channel form and stability, the zoobenthos community, temperature and time (Milner & Petts, 1994). Milner and Petts (1994), considered temperature to be the dominant variable influencing invertebrate community structure in glacial rivers at the scale of the entire river channel, with downstream variations in channel stability also holding a level of influence on invertebrate communities. This dominance of temperature as the overriding factor in community control may not hold fast when concerning diatom communities. It is hypothesised here that the physical forces of flow are the main environmental factors controlling the diatom assemblages. Therefore, morphological adaptations of diatoms will be important in colonisation. Also increased streambed stability and decreased disturbance regime in a downstream direction would be important in controlling the diatom communities and would result in more abundant and diverse algal communities at lower more stable sites. An apparent preference for rough surfaced substrata has been attributed to greater heterogeneity providing greater diversity of microhabitats and increased protection from sloughing (Antoine & Benson-Evans, 1985). Where turbulence and scour is greatest firmly attached organisms dominate, as shear stress decreases an increasingly complex floristic 'forest like' structure with adnate, pedunculate and motile forms occuring (Round, 1993). It can therefore, be hypothesized that a diatom community of small, firmly attached species will dominate the high flow conditions of the stream headwaters, with introductions of larger adnate, pedunculate and motile forms in a downstream direction. Diatoms are the most ubiquitous of the lotic algae in glacial stream headwaters and can generally be found up to the glacial snout (Strøm, 1926). These diatoms are likely to be of particular value as food sources for invertebrates since organic inputs from allocthonous sources are usually low (Milner & Petts, 1994). It is, therefore, the overall aim of this research exercise to examine the physical habitat and the ecology of diatoms in a glacial river with respect to the spatial framework of successional patterns seen in macroinvertebrates suggested by Milner and Petts (1994). Comments on the relationship of the model proposed by Milner and Petts (1994) for invertebrates and the downstream patterns in diatom assemblages will be made with reference to similar models being constructed for gradients of epilithic diatom communities.

Study Sites

Iceland, with a latitude of 63° 25'N-66° 32'N is situated between the Atlantic Ocean and the Arctic Sea, with its northern promontories just reaching the Arctic Circle (Eythorsson, 1949). The island with an area of approximately 103,300km^2 (Gíslason & Adalsteinsson, 1996) consists mainly of highland plateau, more than 400m a.s.l.. Generally the lowland areas encroach a comparatively short distance inland, with the valley regions furthest from the coast reaching approximately 40- 80km inland (Gíslason & Adalsteinsson, 1996).

Iceland is built of basalt originating from volcanic activity, mainly in fissure complexes. The active volcanic zones are situated between two plates that drift apart, and divide the island into basalt formations of different ages (Gíslason & Adalsteinsson, 1996). The majority of the central highland area, including the region of study, is made up of Upper Pleistocene formations (0.7-0.01 Myr).

The location of Iceland means it is an area subject to high cyclonic activity at the border of cold polar air masses and warm air masses of tropical origin (Björnsson, 1979). The climate is further affected by the confluence of warm and cold oceanic currents, namely a branch of the Gulf Stream and the polar East Greenland Current (Björnsson, 1979). The climate of Iceland is oceanic, characterised by relatively warm winters and cool summers. Mean air temperatures in the central highlands in January range from -8 to -10°C (Gíslason & Adalsteinsson, 1996). In July, the warmest month of the year, the mean temperature for the highlands at 600m a.s.l. is 6-8°C (Einarsson, 1979). Easterly winds are the closest to typifying the prevalent wind direction, however southerly winds bring the majority of the precipitation (Sigurdsson & Jónsson, 1995). These climatic conditions and the topographical features result in high glacieration. Glaciers cover 11,300km^2 (11%), with freshwater covering 2,300km^2 (2.2%) (Landmælinger Íslands, 1993).

Due to climatic variations many Icelandic glaciers attained their historical maximum extension in the latter part of the 19th century (Björnsson, 1979). This period of maximum glacial extension was followed by a period of overall climatic warming and glacial retreat until the middle of the twentieth century. However, many of the glaciers in the south, north and central regions of the country have been advancing rapidly since the late 1960s and early 1970s (Sigurdsson & Jónsson, 1995).

Four large ice caps, each with many outlet glaciers, constitute over 95% of the total glacierated area (Sigurdsson & Jónsson, 1995). Langjökull, situated in central Iceland, with an area of around 950km^2, has southern outlets which, like most of the other large ice caps are active compared to the northern ones, with snouts terminating at around 600m a.s.l. (Björnsson, 1979).

The glacier of study was one of a number of small branches that due to topographic restrictions, break from the southern lateral edge of Eystri-Hagafellsjökull, a main glacier stretching from the Langjökull ice field (Figure 3). The snout of the small glacier studied (510m a.s.l., 20°14'N, 64°30'W) is situated in a narrow bedrock gorge (about 8m across), with the glacier flowing down a steep gradient from Eystri-Hagafellsjökull. This small branching glacier has a direct catchment area of around 1.5km^2, up to around 760m a.s.l., although it forms part of the Eystri-

Hagafellsjökull catchment which itself comprises of possibly up to 30% (300km^2) of the ice field reaching a greatest altitude of 1316m a.s.l.

The meltwater stream flowing from the small glacier stretches about 1800m before reaching a post glacial lake, Hagavatn (4.5km^2, 439m a.s.l.). The confinement of the stream above the lake varies greatly. The upper 100m of the stream was extremely confined in a bedrock gorge, study closer than 50m to the glacial snout was not possible due to valley constraints. As the distance from the glacial snout increases the confinement of the channel decreases. However, the confinement through certain stretches was not due to bedrock constraints but large levels of glacial moraine material. This moraine formed unstable banks up to 2.5m high. Although the stream channel was visibly confined the presence of a number (up to three) of dry channels indicated that the streams path is not stable, but dynamic. As the stream approaches the lake the channel confinement was very low with some meandering braided sections. The last 200-300m of the stream before the lake was slower flowing as the gradient visibly decreased and the channel morphology was increasingly braided. The valley widens up to a distance of around 300m and a small delta system is present with large areas of saturated unconsolidated land, due to an increasing input of melt water from the main stem of Eystri-Hagafellsjökull. In addition to the studied meltwater stream, Hagavatn is also fed by the melt-water streams of the main stem of Eystri-Hagafellsjökull along with the other main glacial outlet of the region, Vestari-Hagafellsjökull. The lake outlet allows the River Far to gush rapidly through a small gap in the bedrock and over a series of falls. The

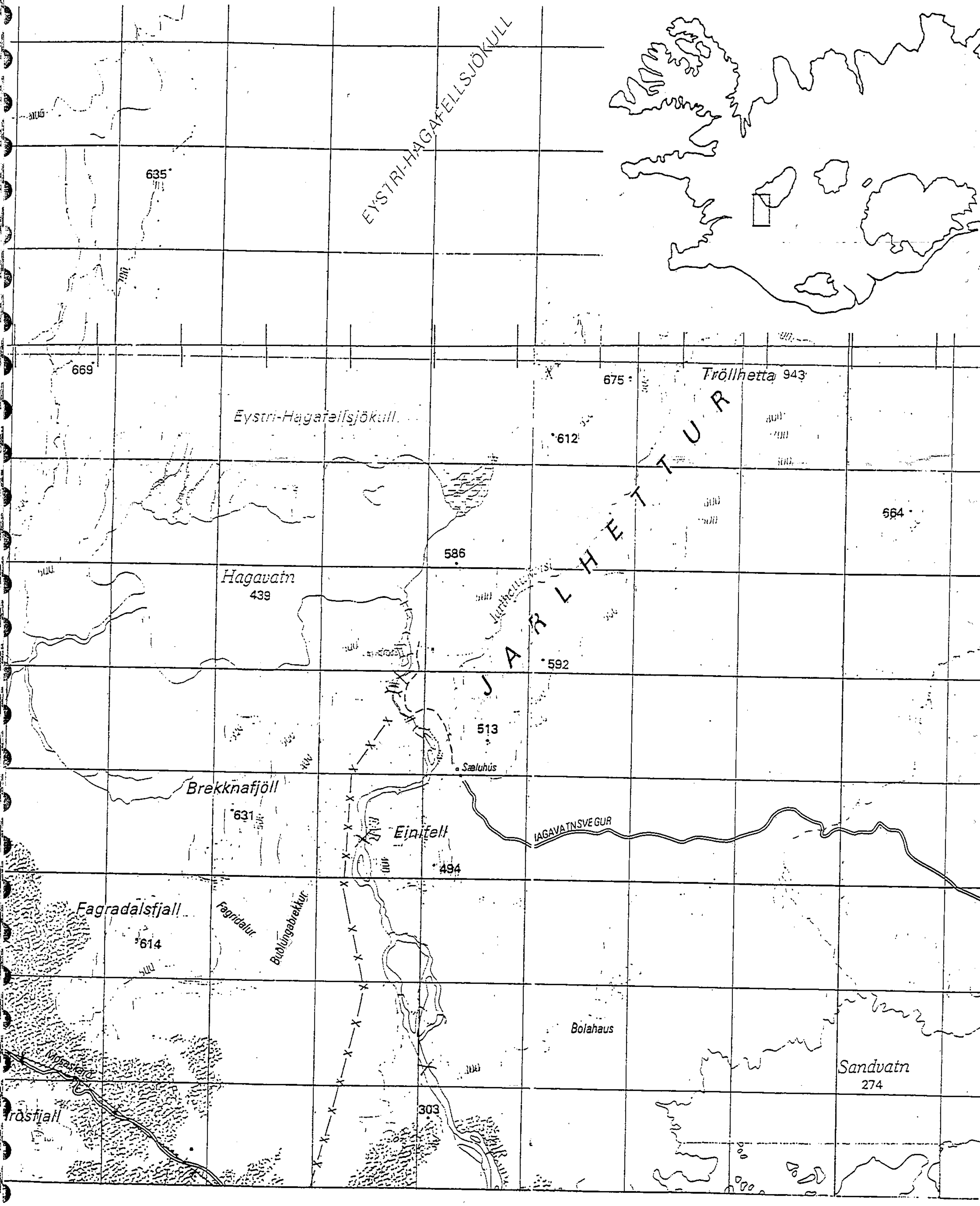

Figure 3 Map of River Far, with Hagavatn and glacier-fed stream showing the locations of the six sampling sites. Insert: the location of the River Far in Iceland.

River Far then winds down through a valley caused by a series of basalt peaks formed by an old fissure, and onto a relatively flat plateau before reaching a second larger lake, Sandvatn (274m a.s.l.). Eventually the river system joins with the River Hvítá, the main river system of the area. All sampling for this study was undertaken above the second lake, Sandvatn.

Methods and Materials

The difficulty in sampling in remote areas requires recognition. It was necessary as a team of undergraduates, with limited financial assistance, to minimise expenditure. As a result, access to the study area was through public transport into the highlands coupled with a 15km walk across hard terrain. All resources and equipment that were required for three weeks needed to be carried in back packs. As it was essential that diatoms were sampled, it was not realistic for much of the equipment needed for recording physicochemical parameters to be taken on site. As a result data from literature sources and semi-quantitative field assessments were unavoidably used in some instances. At each site a 15m representative reach was marked within which all sampling took place.

The fieldwork studies on the glacial-fed stream were carried out between July 7 and 15, 1997. During this sampling period the weather was overcast and rain was present at least every other day.

Physicochemical Sampling

General site observations and descriptions were made using maps and site observations. The average channel depth was measured using a metre rule, with average channel width recorded using a 15m measure. For each selected 15m reach and its adjacent valley floor a scale morphological map was produced (Appendix 1) and photographs were taken for reference if required (Appendix 2). The channel bed-sediment within the survey reach was assessed visually as percentages of boulders (>20cm), coarse gravel (5-20cm), fine gravels (0.2-5cm), inorganic sand (0.01-0.2cm), inorganic silt (<0.01) and mud (organic silt and clay <0.01cm). Thirty stone tracers were prepared varying in size but representative of the site substrate. The tracers were placed in riffle zones and their original position was recorded. Their locations were then surveyed 5 days after their placement providing an indicator of short term stability (AASER, 1997). The stability of the reach habitat was also classified according to the bottom component of the Pfankuch index (Appendix 3).

Temperature was recorded using a TINYTALK temperature recorder. Only one TINYTALK recorder was available for the measurements, so a systematic movement of the probe from one site to the next had to be used. Recordings were made at each site for a duration of at least 48 hours. A recording frequency of 10 minutes was used to monitor the water temperature.

Flow velocity was measured using an SDC meter. Six 10 second replicates were taken within the reach at riffle sites, at 0.6 of total depth. The measurements were taken at 15:00 when flow was approximately the daily maximum.

The level of aquatic vegetation was assessed using a subjective ranking system (absent, present, abundant) for biofilm, green filamentous algae, mosses and aquatic macrophytes.

Biotic Sampling

The epilithic assemblages of diatoms were favoured for sampling as within headwater streams in Iceland this was the only possible widespread media to sample from, and is suited to quantitative measurement (Round, 1993).

Within the stream reach, riffles were favoured for sampling as they provide an increased consistency in physical conditions and are an important habitat to diatom production (Kelly *et al.*, 1995). This is especially the case in unproductive mountain streams (Poff, 1990). Kelly *et al* (1995) found that stone size influenced taxa present, probably due to differences in susceptibility to disturbance, although no obvious differences in assessment scores were apparent between large and small stones. Round (1993), stated that despite inevitable local variation due to microhabitat differences (stone orientation, roughness and composition) stone type is not of critical importance. Literature suggests (Watanabe *et al*, 1988; Round, 1993) that more representative samples are obtained by collecting stones at intervals rather than juxtaposed. In the situation of the upper reaches of glacial-fed streams of the Icelandic highlands, the overall biotic diversity and productivity is low in comparison with regions of lower latitudes (Rohde, 1992). This coupled with the location of the study in glacial headwater streams indicates that the diversity and abundance of diatom communities can be expected to be low.

Following the AASER (1997) protocol ten sample stones were selected from water depths of not exceeding 40 cm throughout all sites. All sample stones were situated in riffles with flow velocity varying from site to site. The stones were randomly selected from suitable stream habitats at sites 1, 2 and 3 and were therefore morphologically representative of each site. At sites 4, 5 and 6 stone types were preferentially selected against heavy coatings of filamentous green algae, a method advocated by Round (1991) when studying epilithon assemblages. Stone orientation, roughness and composition were again random and representative of the site.

On removing a selected stone, it was gently washed in the stream flow to remove any potentially contaminant lightly attached organisms (Kelly *et al*, 1995). The stones were then transferred to a white plastic tray. If any organic material was removed during handling it was washed off and added to the sample water. Diatom sampling was performed by firmly brushing, using a stiff nylon brush, over the upper surface of the stones making sure removed material was washed off and transferred to the sample water. After algal sampling, the dimensions of each stone was roughly recorded by drawing round the stone on 1cm^2 paper. This sampling technique obtains diatom assemblages from important microhabitats of the stones which are exposed to varying current regimes. The level of quantitative accuracy was not extremely high due to the difficulty of precise stone measurements and complete community removal. The water and the suspended material removed from the ten stones was pooled (due to limited number of containers) and transferred to plastic containers and preserved on site in formaldehyde to a final concentration of around 2%. Valuable information can be obtained by viewing the ratio of live to dead diatom frustrules, however, this was not possible due to the remoteness of the sampling area.

The biofilm samples were concentrated through settling and decanting methods, then placed in an oven at 450oC for 2 hours, burning off all organic matter leaving the siliceous cell wall (frustrule). Samples were mounted using the mounting medium of high refractive index, Naphrax. Identification was performed under light microscopy at x1000 using a freshwater diatom key developed in Iceland (Foged, 1974). Within this study, as is the case in many studies, a fix count of a predetermined number of cells is used. Researchers have advised counts of 400 cells (Prygiel & Coste, 1993; Jüttner *et al.*,1996) and 200 cells (Kelly *et al.*, 1995). Round (1991) however, considers the identification of 50-100 frustrules as adequate to determine dominant taxa that characterise the habitat. Round (1991) argues that sites are generally dominated by very few taxa, excessive counting increases numbers of rare taxa identified which is time consuming and merely increases representation of contaminant flora. Based on Round's (1991) consideration and bearing in mind the very low diatom abundance of the study stream, only 50 frustrules were identified to species within each site sample.

Data Analysis

The diatom data was ordinated using Detrended Correspondance Analysis (DCA) in CONACO, and classified by two way indicator species analysis (TWINSPAN). Pseudospecies cut levels were arranged at 0, 2, 5, 10, 20. Algal cell densities (cells per cm^2 of substrate surface) were obtained through volumetric calculations.

Niche breadth (Steinman & Lamberti, 1988) for each taxon was calculated from the expression:

$$B_i = \exp\left[-\sum_{k} (P_{ij}/R_i)\log(P_{ij}/R_i)\right]$$

where P_{ij} is the proportion of the total abundance associated with the i-th taxon in the j-th sample, k is the total number of samples and R_i is Σp_{ij}. Values of B_i can vary from 1, when a taxon is present only in one sample, to a maximum value of k, when its proportional abundance is the same in all samples under consideration (Steinman & Lamberti, 1988). The community diversity, H, and evenness, E, were also calculated using the Shannon & Weaver diversity index. Community richness was also calculated.

$$H = -\sum_{i=1}^{S} Pi \ln Pi \qquad E = \frac{-\sum_{i=1}^{S} Pi \ln Pi}{\ln S}$$

Results

Physicochemistry

Data for the general study area and the glacial river site studies is summarised in Tables 1 and 2 respectively, with substrate composition at the six sites also shown (Figure 4). For ease of description the sites can be separated into two groups; those above the lake (1-3) and those below (4-6).

On return to Birmingham, England, it was discovered that the TINYTALK temperature recorder was set up incorrectly, and the data recovered from it after downloading was incorrect. As a result of this, no temperature data was obtained during the study. It was therefore necessary to refer to literature for a basis of temperature in similar glacier-fed meltwater streams. The outcome of this research was that it could be assumed that the maximum temperature of the stream system at sites above the lake was around 3°C (Milner, personal communication). Below the lake, estimations of temperature can be based on data provided by Gíslason (Unpub. data) from June 1996, in which a study recorded maximum stream temperatures of 6.6°C at site 5.

Table 1 Summary of physical characteristics of general study site

Maximum height of watershed (m a.s.l.)	1355
Altitude of valley floor at glacial snout (m a.s.l.)	510
Altitude of valley floor at downstream limit of study area (m a.s.l.)	290
Distance between glacial snout and downstream limit of study area (km)	6.3
Dominant rock type	Basalt
Valley orientation looking downstream (degrees): above postglacial lake	210-220
below postglacial lake	180
Valley floor morphology (evidence of flood plain reworking) : above postglacial lake	present
below postglacial lake	absent
Level of riparian vegetation	none

Table 2 Measurements and observations of physical and floral characteristics of glacial-fed river at each of the six sites.

Characteristic	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Altitude of site (m a.s.l.)	505	460	450	370	330	290
Distance from glacial snout (m)	50	270	1300	2600	4300	6300
Average channel width (m)	1.50	2.50	2.00	10.00	11.50	16.00
Average channel depth (m)	0.16	0.21	0.22	0.70	1.02	0.92
Average flow velocity at 15:00 (ms^{-1})	2.23	1.43	1.30	1.58	1.33	1.38
Level of channel confinement	Extremely high	Moderate to high	Very low	Moderate	Moderate to low	Low
Valley floor vegetation	Barren	Barren	Extremely sparse	Sparse	Sparse	Sparse
Number of stone tracers recovered	0	1	3	0	0	0
Pfankuch scale scores: Rock angularity	2	2	3	2	1	1
Brightness[1]	4	3	4	2	1	1
Consolidation or particle	2	6	6	4	4	4
Percentage of stable materials	4	12	16	8	8	8
Scouring and deposition[2]	-	-	-	-	-	-
Aquatic vegetation, mosses and algae	4	4	4	2	2	2
TOTAL stability score	18	27	33	18	16	16
Visible aquatic vegetation (o=absent, x=present, xx=abundant):						
Biofilm	o	x	x	x	xx	xx
Green filamentous algae	o	o	o	x	x	x
Mosses	o	o	o	o	x	x
Aquatic macrophytes	o	o	o	o	o	o

Sites 1-3

These sites were typified by a relatively narrow channel not exceeding an average width of 2.5m, with an average depth of between 0.16 - 0.22m. The greatest flow velocity was seen at site 1 with an average flow at 15:00 of over 2.2ms^{-1}, site 2 had a flow of 1.43ms^{-1} with site 3 lower again, at 1.3ms^{-1}. The short term stability was seen to be very unstable as a very low recovery rate of stone markers was seen. Although few stone markers were recovered it was noted that the stream substrate was, in fact, very stable at sites 1, 2 and 4 due to compacting and the channel bed was at site 1, extremely armoured.

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[1] Modification of this measure was undertaken due to the difficulty in classifying the brightness of volcanic rocks. Therefore, the level of staining due to algae of rocks was used as the primary measure of brightness.

[2] Score allocation for scouring and deposition was inappropriate for headwater streams

The substrate composition of the upper sites was dominated by boulders at site 1 and 2 with coarse gravel dominating site 3 (Figure 4). The level of stability as measured by the Pfankuch Scale was high at site 1 with sites 2 and 3 far less stable with site 3 the most unstable with a score of 33. The level of vegetation at the sites was minimal. There was no riparian vegetation with the valley floor vegetation barren or extremely sparse. Very little aquatic vegetation was also found, with only biofilm present at these upper sites. At site 1 the biofilm was not clearly visible, however, at sites 2 and 3 an organic layer could be seen or identified through touch on at least some of the stream substrate.

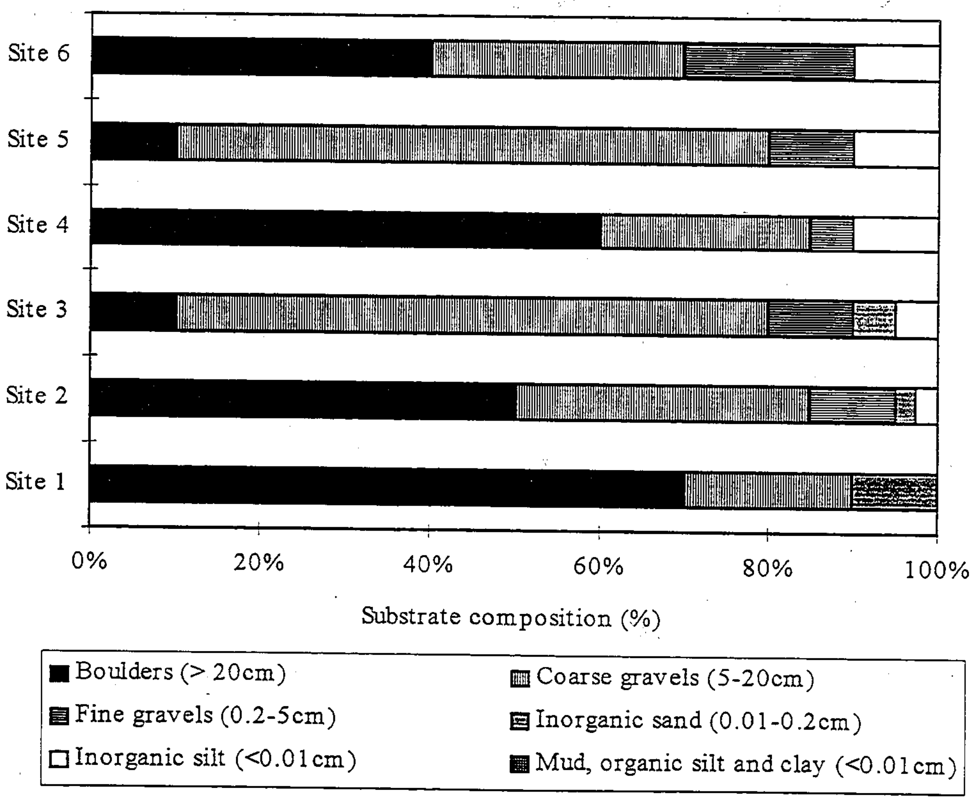

Figure 4 Chart showing the percentage substrate composition at each site.

Sites 4-6

These lower sites were typified by a much wider channel up to 15.0m at site 6, with a greater depth of between 0.7-1.02m. Flow velocities did not vary to the same extent as those above the Hagavatn, with maximums found at site 4 of 1.58ms^{-1}, and site 5 and 6 between 1.33-1.38ms^{-1}. The level of channel confinement was low to moderate with sparse valley floor vegetation. The substrate composition was again dominated by boulders and coarse gravel (Figure 4). After the lake there was a distinct lack of inorganic sand (0.01-0.2cm), in comparison to the sites above the lake. The Pfankuch Scale produced relatively low scores of between 18 and 16. The level of aquatic vegetation was far greater at these sites, with biofilm present or abundant and green filamentous algae present at all the sites. Mosses were also present at sites 5 and 6.

Diatoms

Twenty-four diatoms species or subspecies were identified from the six sites (Table 3). Abundances of total number of diatoms found at each site showed a general trend of increasing with distance from the glacial snout (Figure 5). However, this trend was notstraight forward as low abundances of 1313 diatoms m^{-2} were found at site 4 compared to abundances of 6762 and 10714 diatoms m^{-2} at sites 3 and 5 respectively. At the extreme headwaters of the glacier-fed stream (Site 1) there was a clear dominance of the genus *Pinnularia* with *P. parva* v. *minuta* forming almost 50% of the communities composition. Also *P.cruciformis* and *P. borealis* were

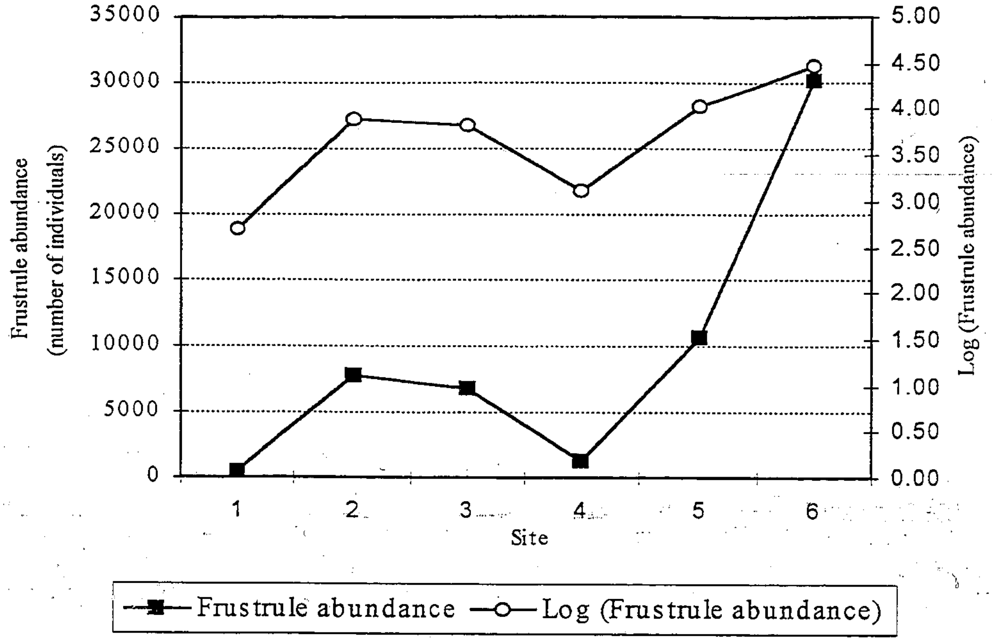

Figure 5 Abundance and Log_{10} (Abundance) of diatom frustrules.

found to be abundant in the upper reaches of the stream. *P. parva* v. *minuta* and *P.cruciformis* are the most widespread species found throughout the entire study with the highest niche breadths (1.96 and 2.10 respectively). The diversity at this uppermost site is the lowest of study (1.42) with a low species richness of 6 and a evenness value of 0.79. At site 2 there is a large increase in species richness as many more species are represented. The dominance remains with *P. parva* v. *minuta* at 50% and the diversity increases to 1.79. The presence of many species at a low abundance decreases the evenness of the community to 0.70. At the last site before the lake, there was again an increase in community evenness to the highest value observed (0.91). The species richness remains similar to site 2, however, the species present differ somewhat and the diversity increases substantially to 2.26. The number of genera represented by more than one individual increases from 2 and 3 at sites 1 and 2 respectively to 7 at site 3. The dominance of *P. parva* v. *minuta* and *P.cruciformis* is greatly reduced to 25% or less with *P. borealis* no longer represented.

Table 3 List of diatom species collected from aquatic habitats at each of the sites. Included for each species is a measure of niche breadth (B_i), and for each site a measure of diversity and richness.

Species	S1	S2	S3	S4	S5	S6	B_i value
Achnanthes kolbei Hust.				1		2	1.32
Ceratoneis arcus (Ehr.) Kütz.[3]					1	19	1.09
Cyclotella spp.			2				1.00
Diploneis pseudovalis Hust.		1					1.00
Eunotia exigua (Bréb.) Rabh. v. *compacta* Hust.				4		2	1.32
Eunotia rhomboidea Hust.			2	1	3	8	1.62
Fragilaria bidens Heiberg		2	2	3	1	7	1.83
Navicula dicephela (Ehr.) W. Smith			2	1	5		1.48
Navicula occulta Krasske			2	12			1.20
Navicula similis Krasske		1	2	2			1.58
Nitzschia ignorata Krasske	3		5			2	1.56
Nitzschia palustris Hust.	3	1	4				1.53
Nitzschia spp.			2			1	1.37
Nitzschia stagnorum Rabh.		1		1			1.35
Nitzschia sigmoidea (Ehr.) W. Smith			8		20	1	1.37
Pinnularia borealis Ehr.	9	7					1.35
Pinnularia cruciformis Donk.v.*faeroeensis* Østrup	11	5	10	14	15	5	2.10
Pinnularia islandica Østrup		1					1.00
Pinnularia parva (Greg.) Cleve v. *minuta* Østrup	23	25	9	11	4	3	1.96
Pinnularia parva (Greg.) Cleve v.*lagerstedtii* Cleve		1					1.00
Pinnularia spp.	1	2					1.32
Pinnularia subcapitata Greg.		1					1.00
Synedra spp.		2					1.00
Synedra ulna (Nitszch) Ehr.					1		1.00
Shannon Diversity	1.42	1.79	2.26	1.85	1.56	1.89	
Evenness	0.79	0.70	0.91	0.80	0.75	0.82	
Richness	6	13	12	10	8	10	

After the lake, at site 4, the diversity decreases to 1.85, as the richness also decreases. Three species are dominant, those dominant at sites 1 and 2 along with *Navicula occulta*. However, *N. occulta* is no longer present at any of the lower

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[3] Foged (1974) described this species as *Ceratoneis arcus*, however later descriptions place the species within *Fragilaria* (Cox, 1996). For the purpose of this study *C.arcus* will be used as all original identification was performed based on Foged's (1974) work in Iceland.

sites and *Nitzschia sigmoidea* becomes the most dominant species. The evenness and diversity of site 5 are low along with a richness value of 8. The dominant diatom species changes once more at site 6 as *Ceratoneis arcus* is found at a level of almost 40%. This last site has a diversity value of 1.89 with 10 species represented.

Overall, the richness of the diatom communities is very low (Figure 6), with a site maximum of 13 (site 2). This poor richness is also represented in low diversity values (Figure 7) with species niche breadths also very low, with Steinman and Lamberti (1988) classing niche breadths below 2 as rare and above 10 as ubiquitous.

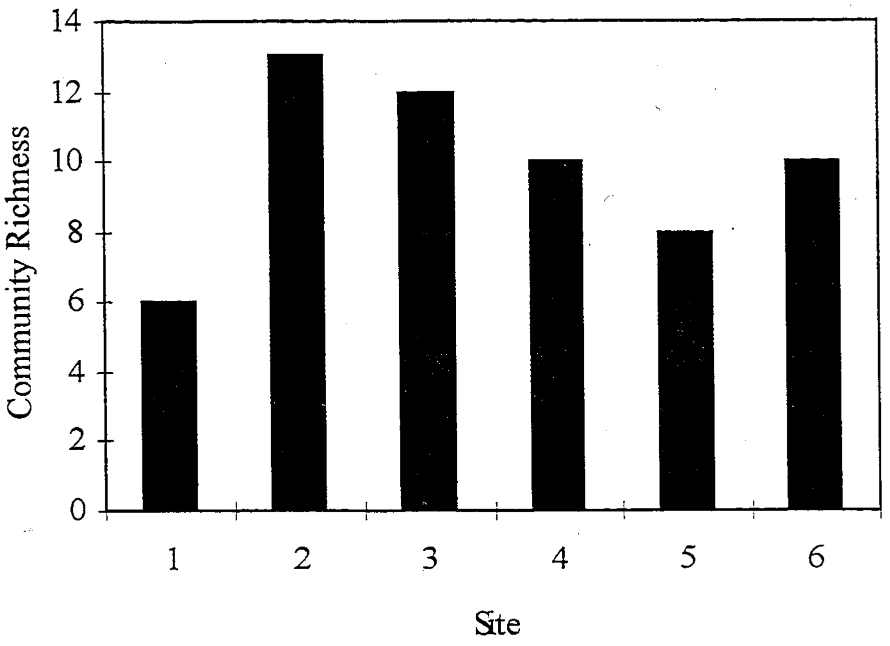

Figure 6 Graph showing Richness at each of the six sites.

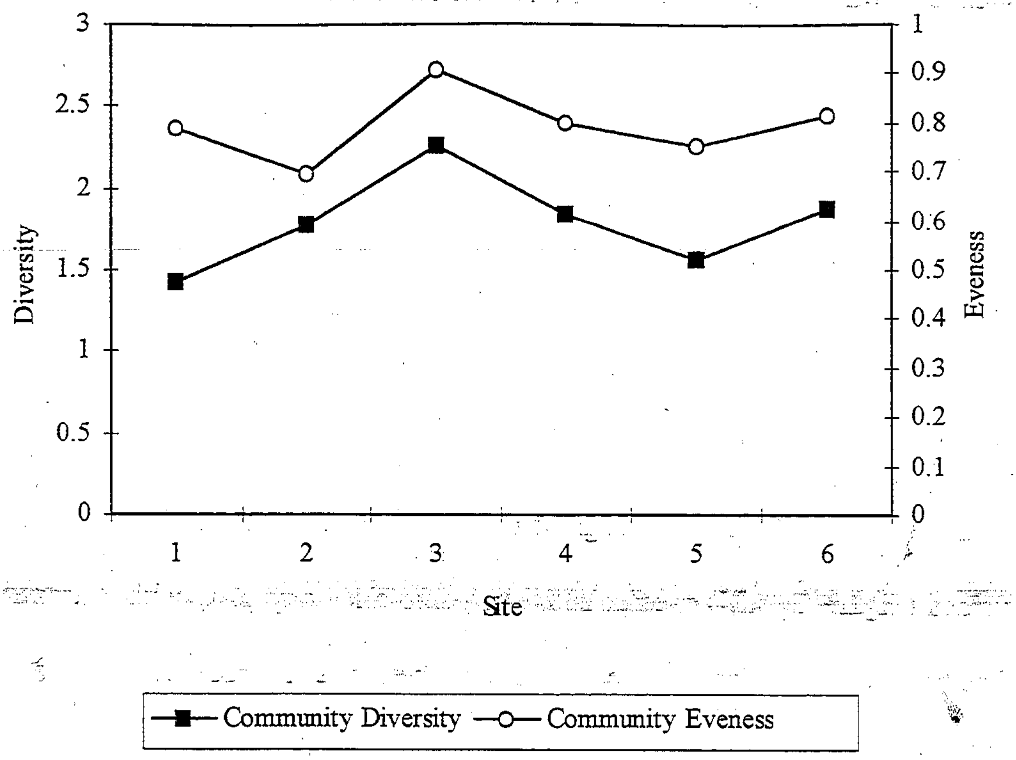

Figure 7 Shannon diversity and Evenness at each of the six sites.

Site assemblages were clearly separated between upstream and downstream sites, although the separation occurred between sites 2 and 3, not sites 3 and 4 as might of been expected. This pattern was also reflected in the results from the Detrended Correspondance Analysis (DCA) with three groupings of sites clearly visible (Figure 8). Sites 1 and 2 were strongly separated from sites 3-6 along axis 1. Sites 4 and 6 were also separated from sites 3 and 5 along axis 2. A plot of the abundant diatom species (>10% of the total assemblage) and rare diatoms species (<10% of the total assemblage) on DCA axis 1 and 2 shows that there is no clear grouping identifiable (Figure 9). A plot of the major environmental parameters; flow velocity, Pfankuch stability score, distance of site from glacial snout, and altitude was plotted (Figure 10). It can be seen that flow velocity and distance from glacial snout are the most significant parameters defining axis 1. Flow velocity is opposed to that of distance from glacial snout. It is negatively correlated with the organic parameters. Axis 2 is most strongly defined by the Pfankuch scale score.

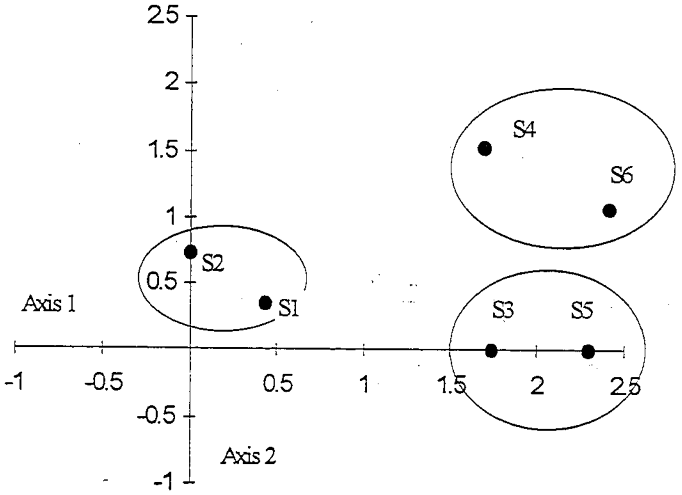

Figure 8 Ordination diagram (Detrended Correspondance Analysis) showing the association of site samples. Groupings shown.

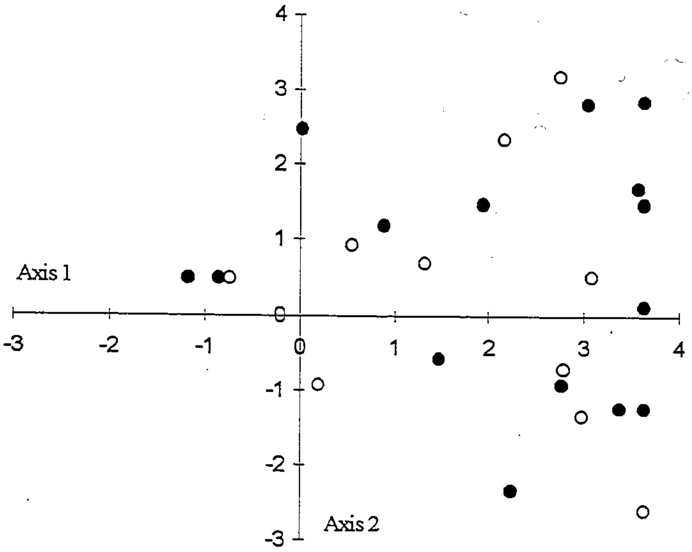

Figure 9 Ordination diagram (DCA) showing the association of species; abundant species (>10% of total assemblage - open circle) and sparse species (<10% of total assemblage - closed circle). No clear grouping occurred.

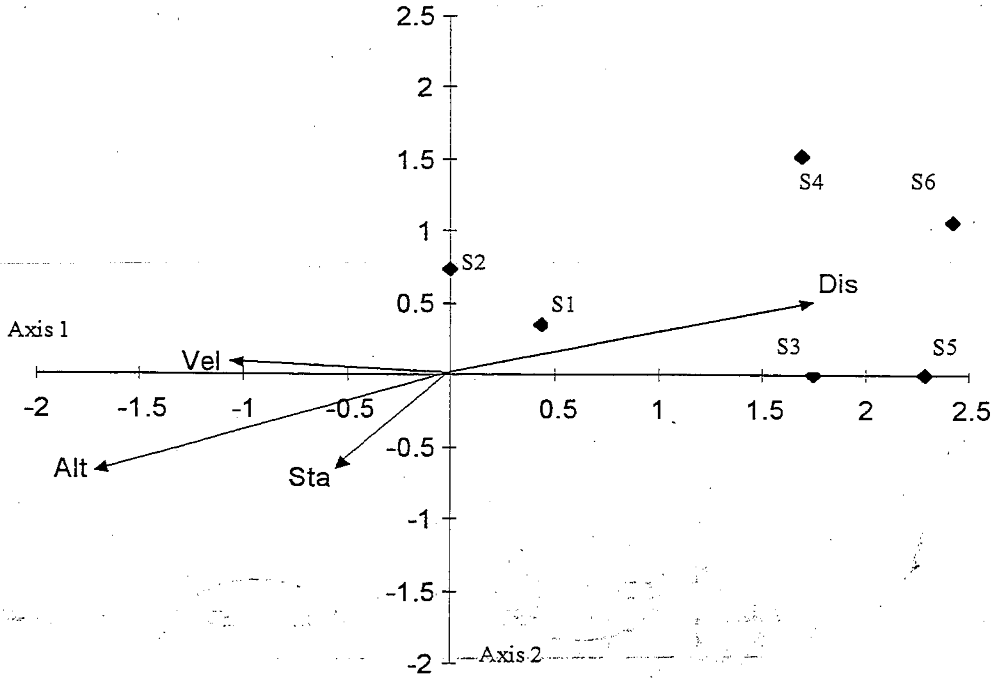

Figure 10 Ordination diagram (DCA) showing the association of site samples, with correlation coefficient (x2) of ecological parameters; flow velocity (Vel), Pfankuch stability (Sta), distance of site from glacial snout (Dis) and altitude (Alt).

The TWINSPAN classification showed that there was a distinct community change present in a downstream direction (Figure 11). TWINSPAN separated the six sites into 2 clusters; sites 1 and 2, and sites 3, 4, 5 and 6 (Figure 12). This was in line with the results from the DCA analysis, and followed that there is a distinct downstream pattern to structure and abundances of the epilithic diatom assemblages.

The indicator species group together showing a correlation with the site communities (Figure 13). Group 4 is representative of sites 1 and 2 with *P.borealis*, which is only found at these sites along with *Pinnularia* spp. Groups 2 and 3 are

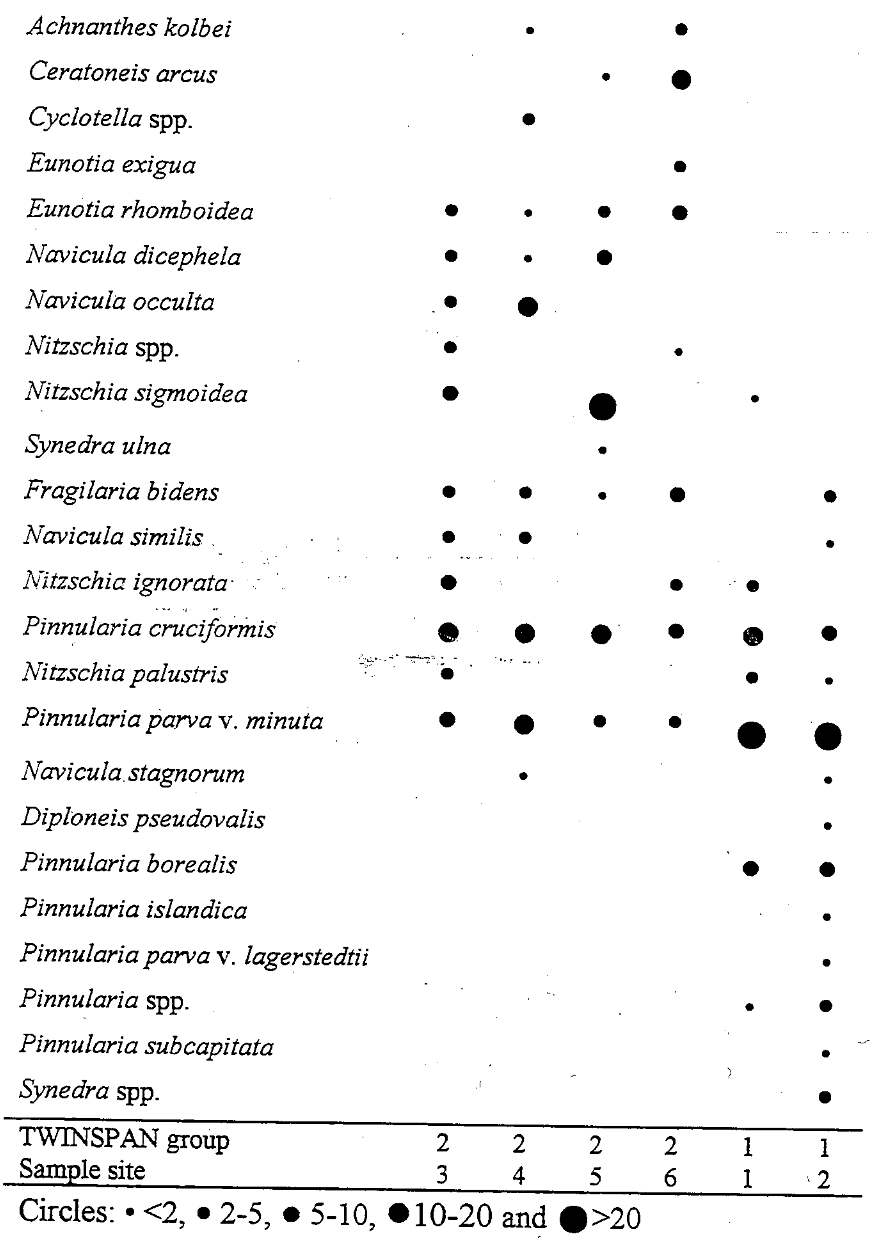

Figure 11 TWINSPAN classification of diatom species from the six sites. Circles represent the abundance of each species at the sites with pseudospecies cut off limits set at 0, 2, 5, 10 and 20.

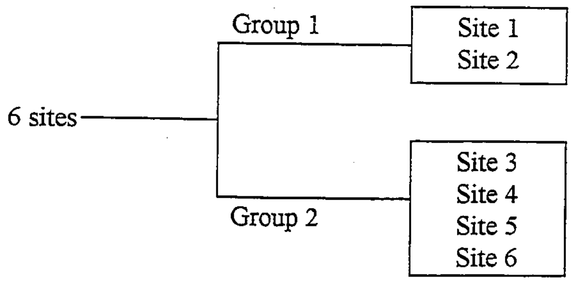

Figure 12 TWINSPAN classification of 6 sites on the glacier-fed stream based on diatom species.

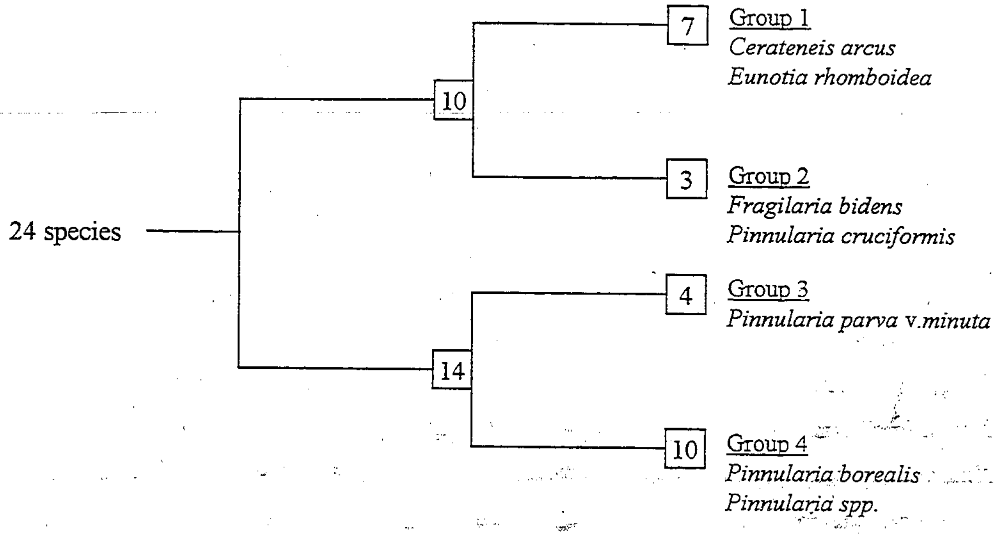

Figure 13 TWINSPAN classification of 24 species collected from six sites. Indicator species for each group are shown.

less distinct in their grouping with indicator species that are found throughout the six sites. However, *Pinnularia parva* v.*minuta* is found with higher abundances at sites above the lake than sites below the lake, whereas *P.cruciformis* and *Fragilaria bidens* are found at greater abundance at sites below the lake. Therefore, it appears that group 3 and 4 are representative of all sites with emphasis on sites above and below the lake respectively. Group 1, however, has a strong correlation with species found at site 6 i.e. *Ceratoneis arcus*.

A number of gut analyses were also undertaken. Gut anlyses did not identify any diatom material. This may be due to the small nature of the invertebrate guts and as invertebrates were not preserved on site in formaldehyde (invertebrates were preserved in ethanol) silaceous material may have been lost.

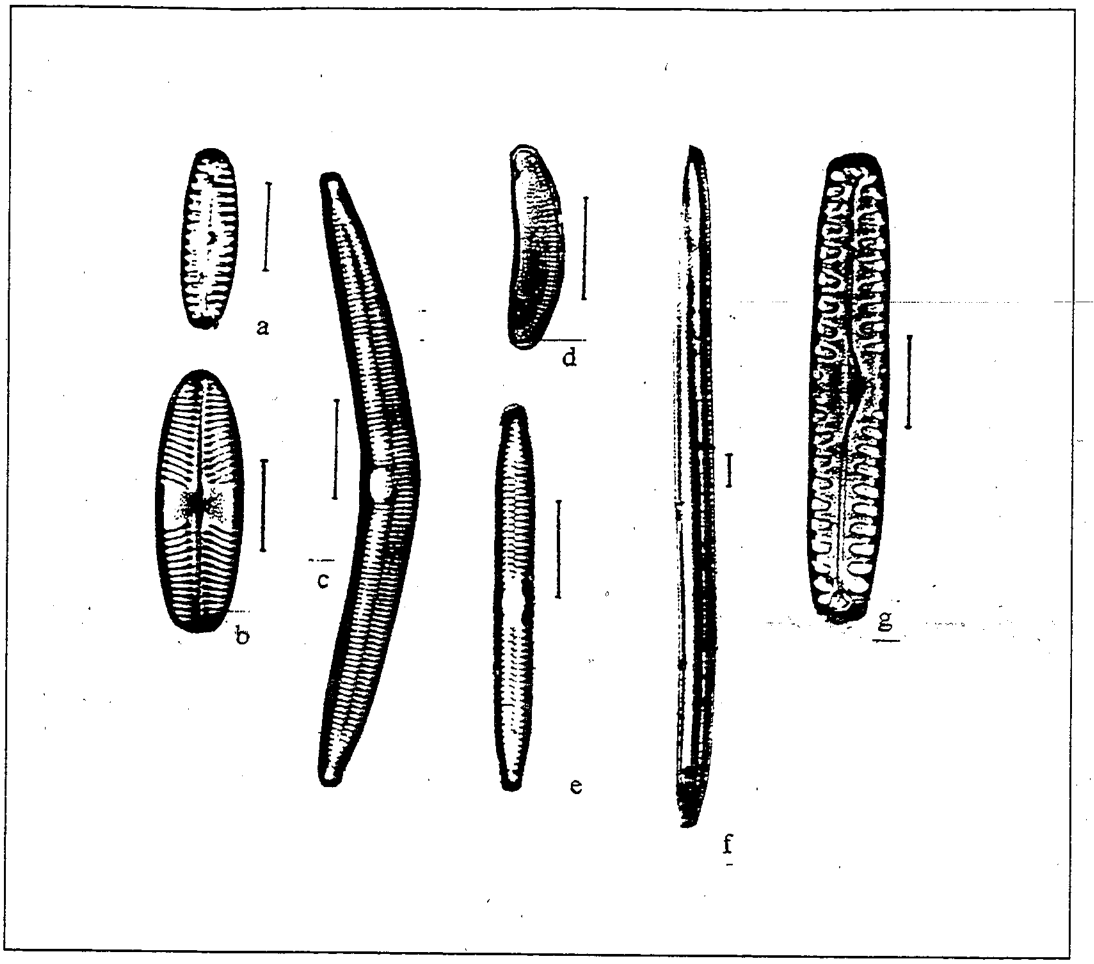

Plate 1 Diatoms found to be indicator species; a)*Pinnularia parva* v.*minuta*, b)*Pinnularia cruciformis*, c) *Ceratoneis arcus*, d) *Eunotia rhomboidea*, e) *Fragilaria bidens* f) *Nitzschia sigmoidea*. and *Pinnularia borealis* (scales 10μm). (Foged, 1974)

Discussion

The data from the glacier-fed river system in Iceland show that changes in diatom community: richness, abundance, diversity and species composition occur with increased distance from the glacial snout. Almost certainly a range of factors are involved in mediating such patterns. Thus, transition from the extreme headwaters of the glacier-fed stream in the Icelandic included changes in flow velocity, channel stability, substrate composition, invertebrate populations, aquatic vegetation and channel width and depth.

Consideration of the types of species that occurred at different spatial scales illustrates some of the ecological changes that occur along the profile of the high latitude glacier-fed lotic system. Within Iceland, it must be taken into consideration that the level of diversity present on any biotic scale is very low. This is due to the comparatively short existence of the island and the degree of its isolation. The methods by which the colonisation of extreme aquatic habitats by diatoms occur is important. The dispersal of algae has been recognised to occur using two mechanisms: (i) dispersal of suspended dissemules by winds, and (ii) passive overland transport of dissemules by aquatic or water frequenting animals (Stewart & Schlichting, 1966). It is possible for both of these methods to allow the colonisation of remote habitats.

At the extreme upper reaches of the study (site 1) there was a dominance of the genera *Pinnularia.* This is a large genus in which many of the species are widespread and vary in apparent habitat preference. *P. parva* v.*minuta* is the smallest species found within the study at around 20 μm in length. Foged (1974), found *P. parva* v.*minuta* to be found extensively throughout Iceland with its main habitat in streams and rivers of pH levels between 6.5 and 7.4. Gíslason recorded pH levels of 6.68 at site 5 (unpub. data), supporting the habitat preferences of this species. The only other species abundant at site 1 is *P. cruciformis* and *P. borealis,* the former of these two species is again a small diatom (30μm). Silvester and Sleigh (1985) recognised that diatoms on substrates exposed to higher velocities tend to be small, flattened forms. Since these small diatoms only project a few μm above the surface, they will only be subjected to a very small proportion (<1% of stream velocity) of the bulk velocity, although at very high flow speeds the boundary layer is reduced and this proportion may increase. A positive effect of current velocity on immigration, increasing impingement rates, has been shown by the immigration of some small diatoms being enhanced by current (Stevenson, 1983). Peterson and Stevenson (1990), identified the irregularities of natural substrata as important in serving as refugia from scour for microalgal cells. They also recognised that the ability of an alga to remain attached through periods of scour is affected by its location with respect to the substratum refugia, but may also vary with cell size, growth form, and attachment strength.

The clear dominance of *P. parva* v. *minuta* and *P. cruciformis* at site 1 indicates that small frustrules can withstand high flow and cold temperatures (<2°C) whereas many other species cannot. Therefore, it can be argued that these very small *Pinnularia* species can be considered as fugitive pioneer species, although the specific dispersal ability and speed of colonisation is not known for these species.

However it must be noted that in these extreme aquatic habitats the productivity and resulting abundance is very low.

However, *P. borealis* is not a particularly small diatom (>50μm). Foged (1974) and Cox (1996), described this species as being aerophilous and often associated with subaerial habitats e.g. on mosses, walls and damp earth, as well as margins of standing and flowing water. It is possible that *P. borealis* is capable of surviving on and within glacial ice as dissemules or frustrules. This could provide an extremely sparse, but continual addition of *P. borealis* to the glacial meltwater streams incrteasing chance of colonisation. Their colonisation may also be aided by the presence of pitted substrata allowing a relatively large boundary layer to form.

As distance from glacial snout increases the dominance of the three *Pinnularia* species no longer remains, and there is no clear dominant species present as richness increases. This richness is somewhat unstable as five of the species present at site 2 were represented at this site only and were found at very low abundances. Along this comparatively short stretch of stream from the glacial snout to the lake margin, the temperature can be assumed not to exceed 3°C, and the stability of the stream was seen to decrease due to meandering channels, braiding and the decrease in boulders, which tend to be the first and most colonised substrata in glacier-fed streams (Milner & Petts, 1994). It must be noted that this decrease in stability on a longitudinal scale can be considered unusual for glacier-fed streams, as channel stability is usually seen to be, least stable close to the glacial snout, and increases with distance. The morphology of the valley at site 1 caused very high channel confinement, and although the flow was very high the channel stability was also high due to compacting and armouring (although introduced substrata would be extremely unstable). As stability decreased, diversity of diatom communities increased. This indicates that stability may not control the flora of the glacier-fed streams to the same extent as Milner and Petts (1994) hypothesised for invertebrates. It appears to be the case that flow has a greater controlling factor over the floral community.

The presence of the proglacial lake within the lotic system causes an increase in temperature and the attainment of a relatively stable single thread, meandering channel (Milner & Petts, 1994). The lake also acts as a flow regulator by attenuating floods and sustaining low flows as well as trapping the majority of the systems coarse sediment load. The effect of the lake on the microflora is difficult to quantify from this single study. Although it may be the case that the increase in temperature allows the dominance of certain species, as there is a decrease in both community diversity and richness. However, these decreases are more likely to be caused by the increase in flow due to the large output and steep gradient of the stream immediately after the lake. The lake outflow point is relatively narrow and the large outflow is due to the large catchment input from the meltwater streams of the main southern glaciers of Langjökull. This results in an extremely high flow from the lake and in conjunction with the falls causes the channel water at site 4 to be extremely turbulent.

The species composition after the lake returned to a dominance of *P. Parva* v. *minuta* and *P.cruciformis* along with *Navicula occulta. N. occulta* is very similar in shape to that of the two *Pinnularia* species. It is very small (15µm) and consequently is adapted to surviving in high flows. After the lake there was also a dramatic decline in the abundance of diatoms the reasons for which, may be due to a combination of the high flows and the turbulent nature of the stream, and is discussed in detail later.

Further down the stream at sites 5 and 6 the flow is less turbulent and slower. At site 5 there remains the dominance of *P. cruciformis*, however *P. parva* v.*minuta* is no longer a dominant diatom. The most abundant species at site 5 was seen to be *Nitzschia sigmoidea*, this species is far larger than any of the other dominant species (>160µm) and is seen to be widespread and relatively common in mesotrophic waters of high electrolyte content, often epipelic in slow flowing waters (Cox, 1996). Foged (1974), described *N.sigmoidea* in many habitats including many streams of pH 6.5-7.4. After site 4 a glacier-fed tributary joins the study river. The sediment load of this tributary was very high. This increase in sediment was noticeable at site 5, but less so, at site 6. The increase in sediment may have favoured the growth of *N. Sigmoidea,* as electrolyte content is also high. It is unlikely that this input of colder water affected the diatom community as a shift to cold water community composition (those found above the lake) was not observed.

At the last site of study there was again a change in the species composition of the diatom assemblages, with a slight increase in diversity and a large increase in abundance. At this site the flow was similar to the previous site along with stability. The dominant species was now seen to be *Ceratoneis arcus* with smaller species no longer represented in large numbers. Round *et al.* (1990) described the arcuate cells of *C. arcus* as sometimes free living, but often in clusters or short colonies; attached to rocks in freshwater streams particularly in mountainous areas. *Eunotia rhomboidea* is also found at site 6, and is a relatively small species (20µm) and is typical of oligotrophic waters (Cox, 1996). At this site there is an increasing variation in sizes of diatoms present indicating a reduction in the stress induced by flow allowing an increasing 'forest like' floristic complex to occur (Round, 1993).

The abundance of epilithic diatoms within the glacial meltwater catchment is seen to increase in a downstream direction with maximum production furthest away from the glacial snout. Low abundances close to the glacial snout are probably due to the high flows, scouring the majority of species from the substrate along with the low rate of colonisation. Site 4 does not follow the pattern of abundance increase and population numbers are similar to those at the first site. Even though the flow at site 4 is less than that recorded at site 1, this flow is likely to be relatively constant due to the presence of the lake which acts as a buffer for flow. In contrast at sites above the lake the flow will vary diurnally. Although it has been stated that it is the maximum free-stream velocity that plays a major role in influencing assemblage species composition and development (Poff *et al.,* 1990), there is an increase in the turbulence at site 4, which may increase shear stress. Stevenson (1983), studied the effects of current and microhabitats on benthic diatom immigration and found that impingement rates of diatoms are dependent on the depth of the laminar sublayer because diatoms must sink through it to the substrate. Thus, the impingement rate increases with current velocity as turbulence increases and depth of the laminar sublayer decreases. The composition of the diatom assemblages at site 4 would, therefore, be expected to be diverse and of an equal or increased productivity than upstream sites. This does not aid the explanation of low diversity and low abundance at this site. It may be the case that although the impingement rate is increased, the turbulent nature of the flow may be too great and restricts successful diatom colonisation and growth due to excessive shear forces. Poff *et al.*, (1990) described species with specialised attachment mechanisms such as pores (e.g., *Ceratoneis arcus*) or raphe(s) (e.g. *Cocconeis placentula*) as more abundant in ‘fast-rough’ hydraulic situations, suggesting that higher inferred shear stress in high velocity regimes retarded the successful colonisation of many other species, especially araphid species. Quantification of this was not possible due to the very low percentage of araphid diatoms throughout the study.

This unexpected dominance of mobile raphid diatoms throughout the entire study may be due to an adaptation for living in very turbid waters. The motility allows continual migration, if necessary, to higher, shallower positions where the light attenuation is less and the level of irradiance is greater, although light reduction of up to 60-80% has not been found to affect the taxonomic structure of diatom communities in many systems (Sullivan, 1979; O’Quinn & Sullivan, 1983). There are surprisingly few studies on the effect of depth (light climate) on occurrence and growth characteristics (in contrast to studies on planktonic species) (Round, 1993). Bothwell *et al.*, (1989) undertook an extensive experiment to test dark avoidance by algal species. If dark avoidance is a widespread phenomenon, it may prove to be an important mechanism contributing to species succession in lotic environments, especially in high latitude lotic systems where due to seasonality the annual light regime changes dramatically with long periods of daylight (24 hours during mid-summer) and equally long periods of darkness or very reduced light intensities during the arctic winter. Light restriction at the upper sites may also occur in the form of complete channel covering by snow. It is possible that the low abundances above the lake, where the stream is narrow enough to be covered by snow, may be due to the lack of light for several weeks of the year. This may greatly effect the abundances of the upper sites and even select for species capable of long periods of darkness.

As abundances of diatoms increase it can be hypothesised that autogenically induced modifications of adsorptive characteristics and flow interruption near the substrate will enhance the probability of successful immigration of some species more than others (Stevenson, 1983). It was also observed by Stevenson (1983) that invertebrate grazers may reflect patterns of diatom immigration, such as microhabitat selection.

The results from the accompanied study of benthic macroinvertebrates providing some interesting results. With respect to diatom ecology it was important that invertebrates were found close to the glacial snout at site 1. A large proportion of invertebrates food source is often obtained from diatom assemblages, with larval invertebrate species such as *Apatania zonella* (Zett.), Iceland's commonest Trichoptera, feeding almost exclusively on diatoms (Gíslason & Sigfússon, 1987). It has been seen in studies that a number of the common stream invertebrates are capable of feeding effectively on very thin organic layers incorporating very low abundances of algae (Walter & Knight, 1987), such as those found at the upper sites of the study. Although gut analysis was not successful in identifying diatom contents, many studies have observed the use of diatom assemblages by invertebrates for food (Gíslason & Sigfusson, 1987; Steinman, *et al.*, 1987). Whether such herbivory alters the species composition of diatom communities in upper reaches of glacier-fed streams depends on several factors, including the feeding selectivity (preferential selection of larger frustrules is often seen) of the grazers and the relative competitive abilities of their algal "prey" (Lubchenco & Gaines, 1981). Steinman *et al.*, (1987) described the grazing of algal communities on stream benthos is analogous to that of terrestrial systems, where grazing has been shown to set back succession (Brown, 1985).

Conclusion

The classification and ordination of sites in the study by TWINSPAN and DCA respectively related to types of ecological factors, particularly flow. This suggests that regardless of what autogenic processes are occurring among these assemblages with respect to downstream gradients and succession, the physical effects still have a distinct influence on the diatom community structure. This data is consistent with the idea that glacier-fed stream ecosystems are closely linked to the abiotic properties of the stream channel and the surrounding watershed (Hynes, 1975; Milner & Petts, 1994).

In summary, the taxonomic structure of lotic diatom assemblages is primarily determined by the physical environment in the form of current velocity. Morphological characteristics of diatom frustrules therefore are seen as adaptations for different flow conditions, small frustrules dominating regions of high flow velocity, with larger diatoms colonising areas of lower flow. From this study other factors involved in the determination of diatom assemblages appeared to be that of distance from glacial snout, and that of stability and herbivory. It was not possible to clearly distinguish the dominant variable influencing diatom community structure in glacial rivers at the scale of the entire river channel. However, this paper acknowledges that an existence of a downstream, qualitative pattern may exist for epilithic diatoms in glacial rivers. This downstream pattern, however, is likely to be influenced greatly by the flow velocity of the lotic system. However, the model proposed by Milner and Petts (1994) regards temperature to be the dominant variable controlling invertebrate communities, which has a fundamental gradient from the very cold temperatures close to a glacial snout, increasing with distance from snout. Flow velocity does not necessarily follow a fundamental gradient of change from the glacial snout in a downstream direction. Therefore, if predictive modelling is developed, information on factors effecting flow velocity, such as channel morphology and confinement must be considered in detail.

It is clearly not possible from a single study of an Icelandic glacier-fed lotic system to begin constructing predictive qualitative models for diatoms such as the one proposed by Milner and Petts (1994) for invertebrates. However, it is hoped that from this study the recognition of changes in diatom communities in relation to abiotic factors along with biotic influences, are important within glacial systems and the comparative plethora of information on invertebrates in glacier-fed lotic systems will be accompanied by an increased understanding of the ecology of primary production in glacier-fed streams and rivers.

Finally it is clear that there is a need for intensive studies of specific aspects, e.g. effect of current velocity, substrate stability, seasonality, depth in water and grazing, in sites which can be sampled intensively. Although it must not be overlooked that wider surveys to provide a geographical framework of diatom distributional data related broad scale nutrient/chemical status of habitats is also essential (Round 1991).

Acknowledgements

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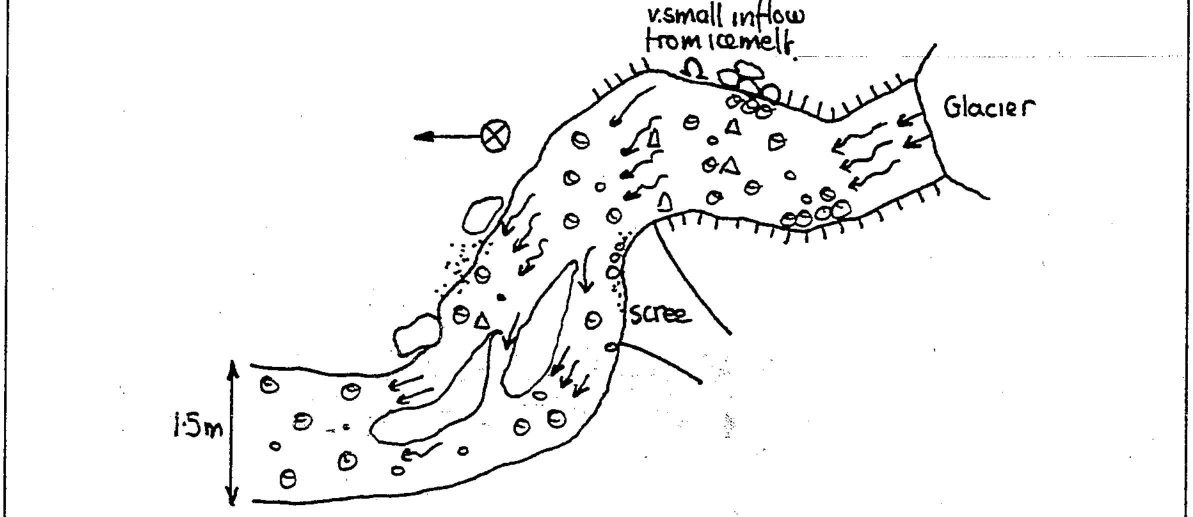
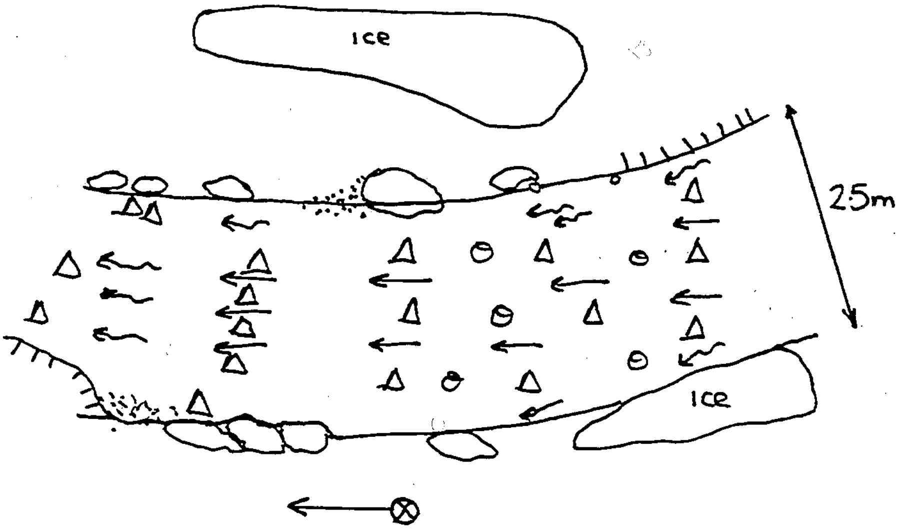
Appendix

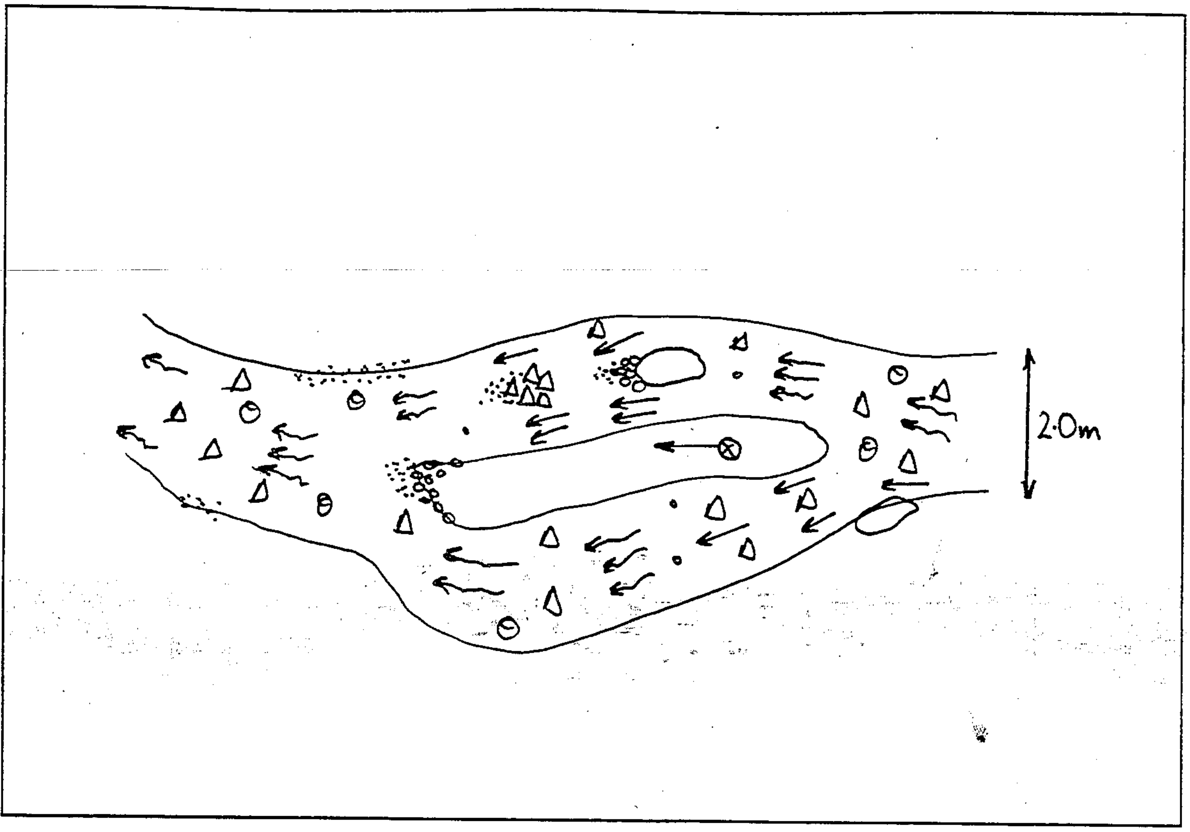
Appendix 1



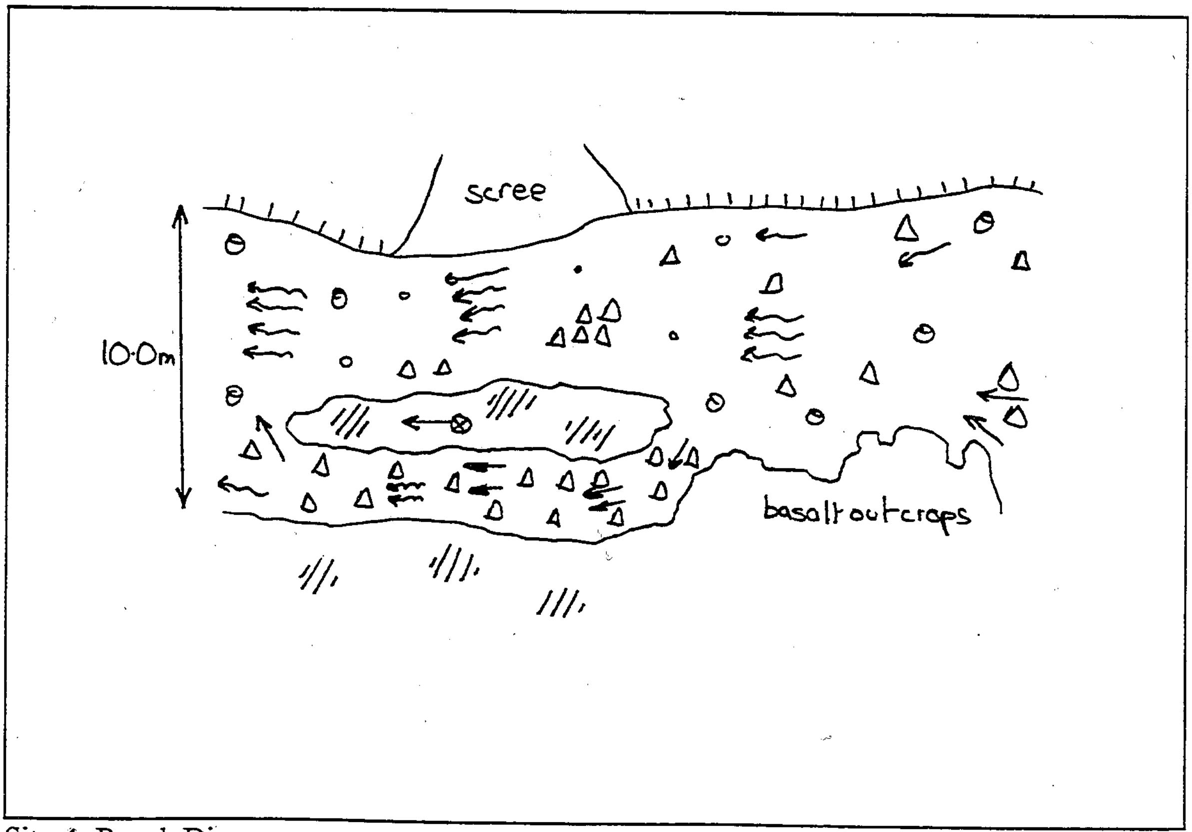
Site 1: Reach Diagram



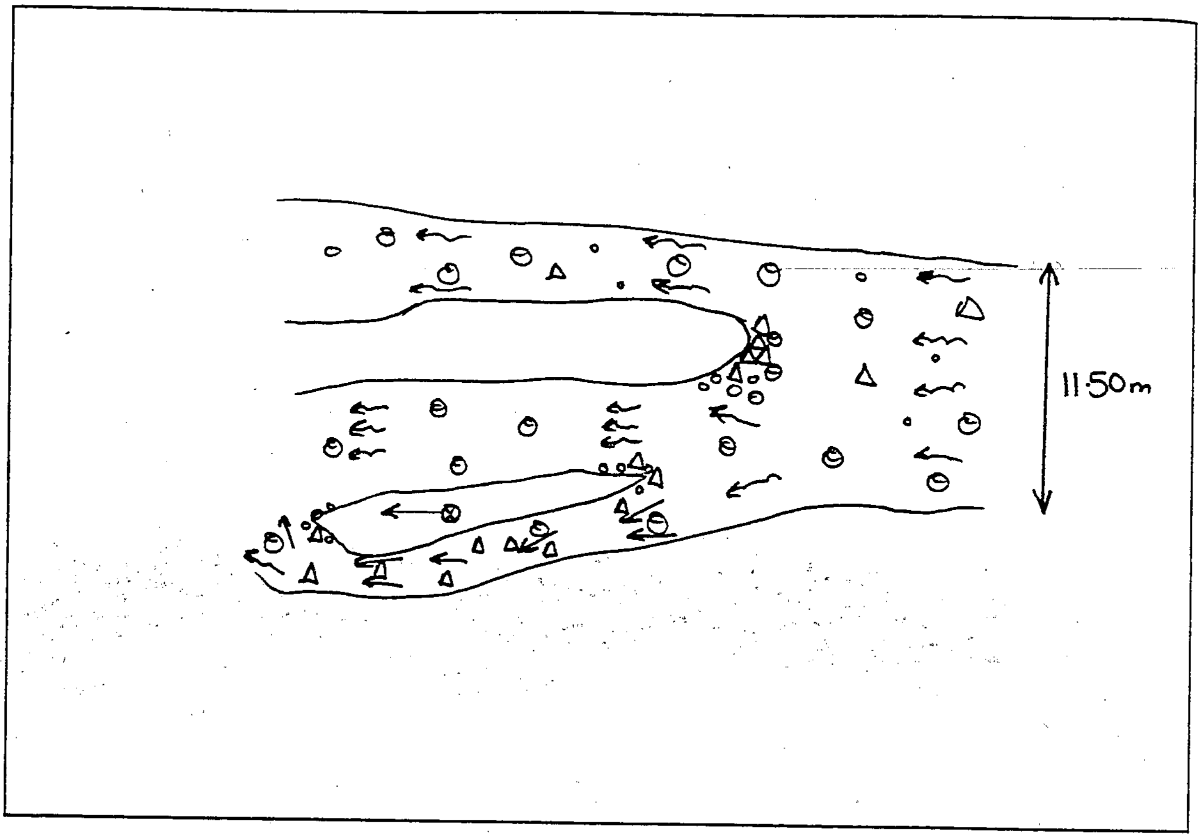
Site 2: Reach Diagram



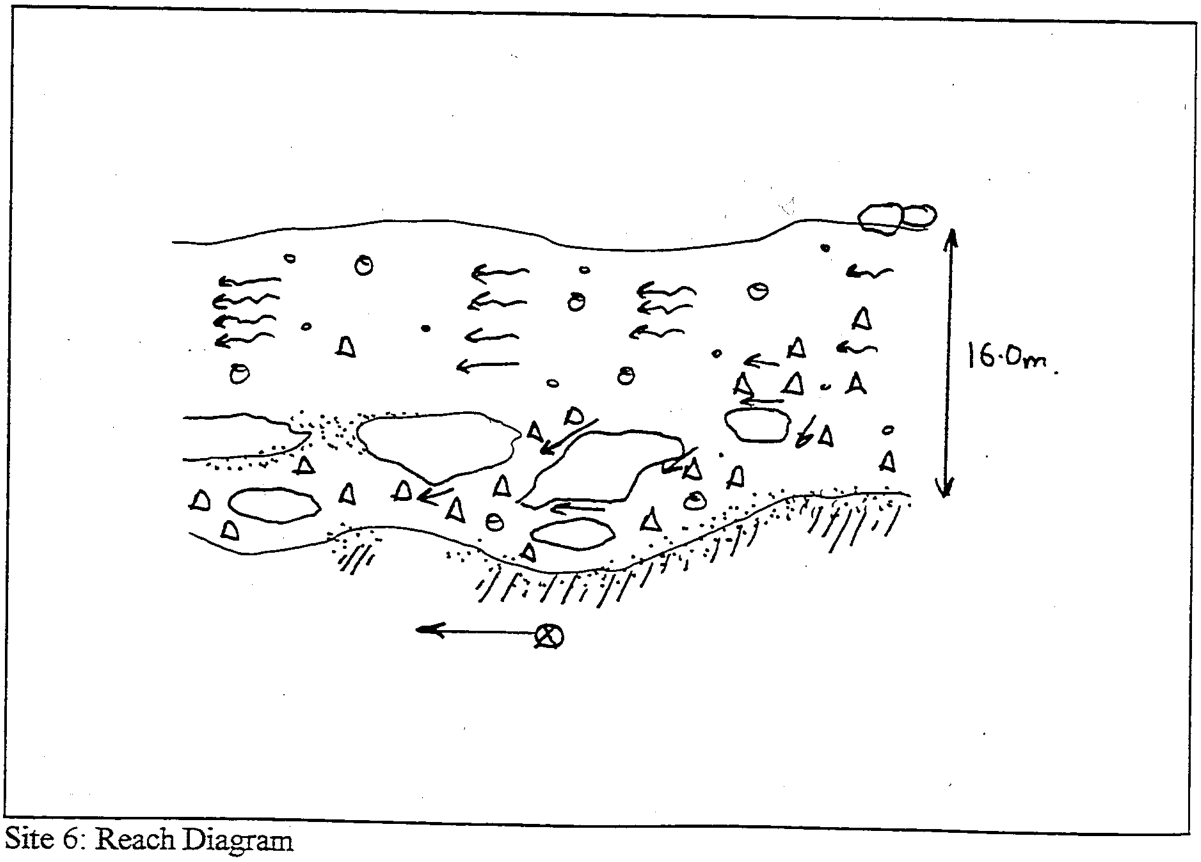
Site 3: Reach Diagram



Site 4: Reach Diagram



Site 5: Reach Diagram



Site 6: Reach Diagram

Appendix 2: Site photographs

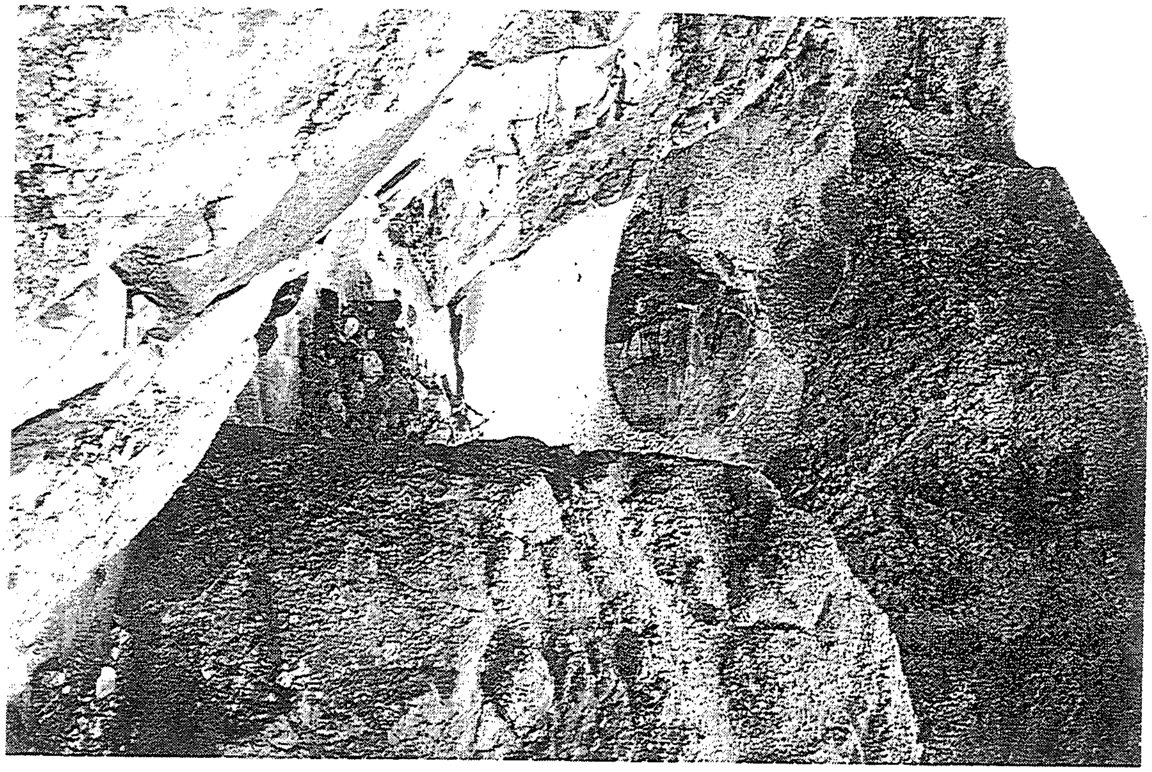


Plate 2: Site 1

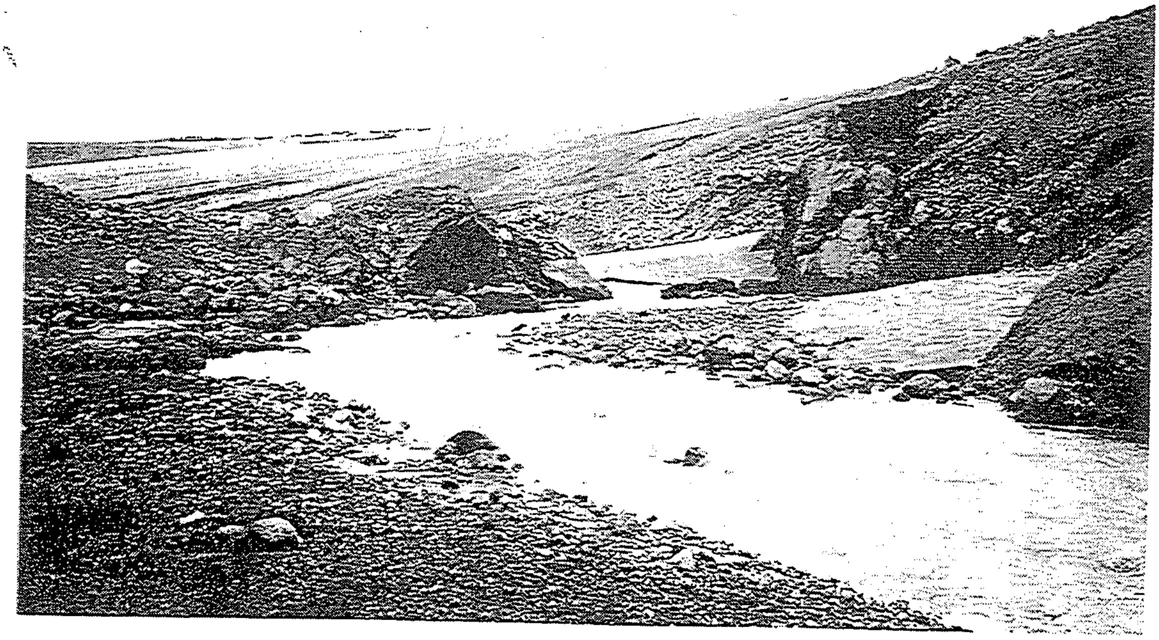


Plate 3: Site 2

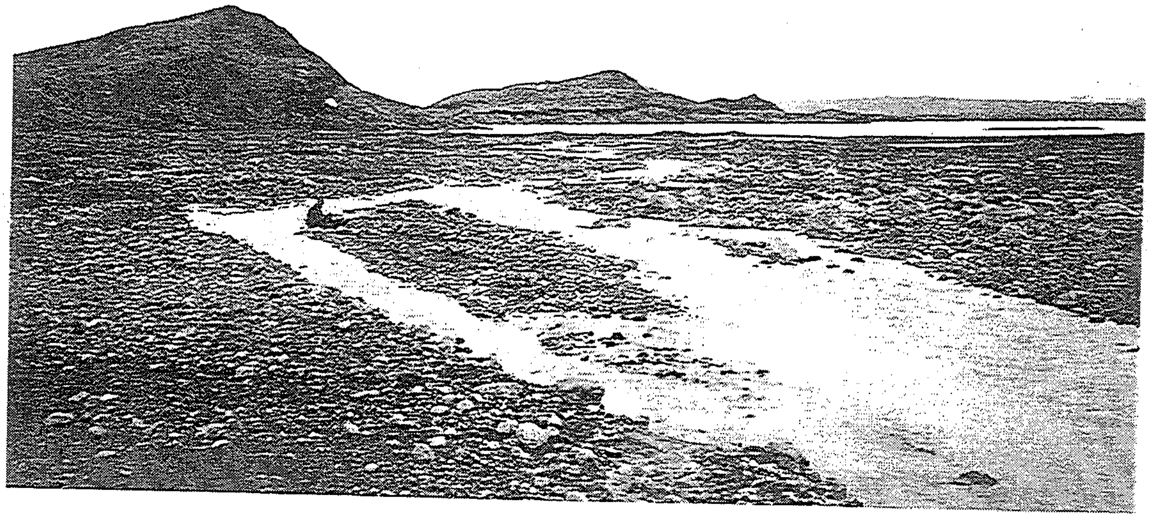


Plate 4: Site 3

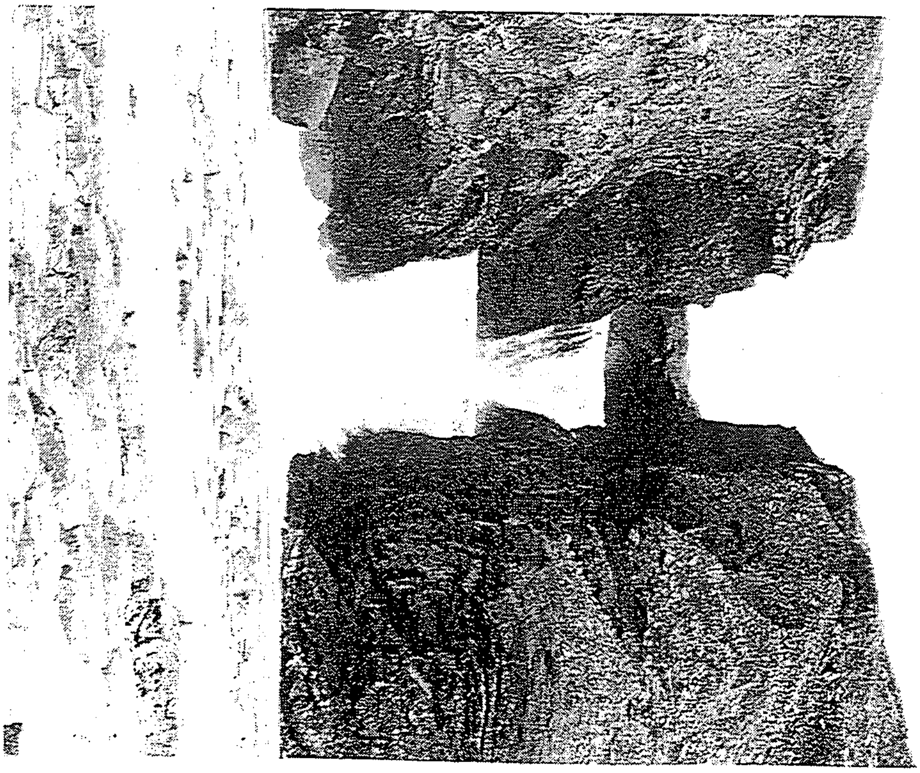


Plate 5: Site 4

Plate 6: Site 5

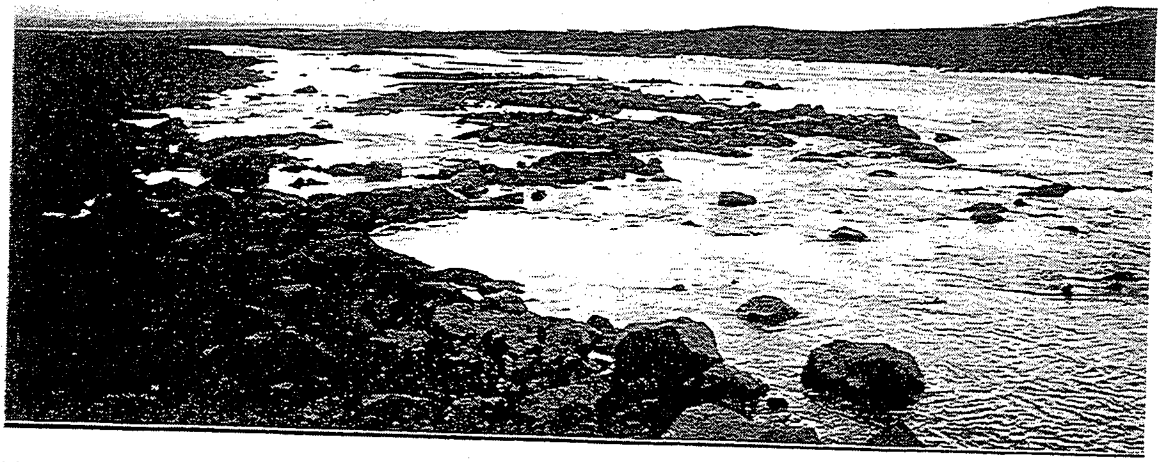


Plate 7: Site 6

Appendix 3: Pfankuch Scale (Bottom component only was used).

LOWER BANKS	EXCELLENT		GOOD		FAIR		POOR	
Channel Capacity	ample for present some increases. Peak flows contained Width to depth ratio <7.	1	Adequate. overbank flows rare width to depth ratio 15-Aug	2	Barely contains Occasional overbank floods. Width to depth ratio 15-25.	3	Inadequate. Over-bank flows common. Width to depth ratio >25.	4
Bank Rock Content	>65% rocks with large angular boulders >30cm numerous.	2	40-65% rock, mostly small boulders to cobbles 15 to 30cm	4	20-40%. with most in the 8 to 15cm diameter class, although larger ones maybe present	6	<20% of rock fragments of gravel sizes. 2.5 to 8cm or less.	8
Obstructions /flow deflectors / sediment traps.	Rocks & old logs firmly embedded. Flow pattern without cutting or deposition. Pools and riffles stable.	2	Some present causing erosive cross currents & minor pool filling. Obstructions & deflectors newer and less firm.	4	Moderate frequent. Moderately unstable obstructions & deflectors move with high water causing bank cutting & filling in of pools.	6	Frequent obstructions & deflectors cause bank erosion year long. Sediment trps full, channel migration occurring.	8
Cutting	Little or none evident. Infrequent raw banks less than 15cm high generally.	4	Some, intermittently at outcurves & constrictions Raw banks maybe up to 30cm high.	8	Significant. Cuts 30-60cm high. Root mat overhangs and sloughing evident.	12	Almost continous cuts some over 60cm high. Failure of overhangs frequent.	16
Deposition	Little or no enlargement of channel or point bars.	4	Some new increases in bar formation mostly of coarse gravels.	8	Moderate depostion of new gravel & coarse sand on old and some new bars	12	Extensive deposits of predominantly fine particles. Accelerated bar development.	16
SUB - TOTAL								

BOTTOM	EXCELLENT		GOOD		FAIR		POOR	
Rock Angularity	Sharp edges & corners plane surfaces roughened.	1	Rounded corners and edges. Surfaces smooth and flat.	2	Corners and edges well rounded in 2 dimensions	3	Well rounded in all dimensions. surfaces smooth.	4
Brightness	Surface dull, darkened stained by algae or minerals. Bright surfaces <5% of area.	1	Mostly dull but may have up to 35% bright surfaces, some dull on larger rocks.	2	Mixture 50-50% dull and bright -- 15% (ie. 35-65%)	3	Predominantly bright >65% exposed or scoured surfaces.	4
Consolidation or particle??? of substrate	Assorted sizes tightly packed and or overlapping	2	Moderatley packed with some overlapping	4	Mostly a loose assortment with no apperent overlap	6	No packing evident. loose assortment easily moved.	8
% Stable Materials.	Stable materials 80-100%	4	Stable materials 50-80%	8	Stable materials 20-50%	12	Stable materials 0-20%	16
Scouring and Deposition.	<5% of the channel length affected by scouring & deposition	6	5-30% affected. Scour at constrictions & where grade steepens. Some deposition in pools and backwaters.	12	30-50% affected. Deposits & scour at obstructions. constrictions & bends. Some filling of pools.	18	>50% of the bottom in a state of flux or change nearly year long.	24
Clinging aquatic vegetation (mosses and algae).	Abundant. Growth largly moss-like. dark green, year-round. In swift water to.	1	Common. Algae forms in low velocity and pool areas.Moss here too and in swift waters.	2	Present but spotty. Mostly in backwater areas Seasonal blooms make rocks slick.	3	perennial types scarce or absent. Yellow-green short term bloom may be present.	4
SUB - TOTAL								

TOTAL STABILITY SCORE = SUM O F SUB-TOTALS

USE BOTTO.M COMPONENT ONLY

Appendix 4: General data.

Substrate composition

Substrate composition: Boulders (>20cm)	70	50	10	60	10	40
Coarse gravel (5-20cm)	20	35	70	25	70	30
Fine gravels (0.2-5cm)	0	10	10	5	10	20
Inorganic sand (0.01-0.2cm)	10	2.5	5	0	0	0
Inorganic silt (<0.01cm)	0	2.5	5	10	10	10
Mud; organic silt and clay (<0.01cm)	0	0	0	0	0	0

Abundances of total diatoms at each site using data on laboratory processes and multiplying numbers up to give the abundance per unit area of substrate at each site.

Site	1.00	2.00	3.00	4.00	5.00	6.00
Volume of water (ml)	2.00	2.00	2.00	2.00	2.00	2.00
Volume of sediment (ml)	0.75	0.25	0.25	0.75	0.40	0.25
Number of drops added to slide	3.00	3.00	3.00	3.00	3.00	3.00
Average no. of diatoms on slide	2.00	14.75	9.60	22.00	54.00	68.00
Number of diatoms in sample	82.96	5506.67	3584.00	912.59	7875.00	25386.67
Total surface area of rock sampled (m^2)	0.1680	0.7100	0.5300	0.6950	0.7350	0.8400
Number of diatoms (m^{-2})	494	7756	6762	1313	10714	30222

Results from Detrended Correspondance Analysis (DCA)

Diatom Species *EIG*	Axis 1 *0.4823*	Axis 2 *0.2133*
Achnanthes (cf) kolbei	3.0463	2.829
Ceratoneis arcus	3.5725	1.6857
Cyclotella spp.	2.2392	-2.3412
Diploneis pseudovalis	-1.1767	0.4922
Eunotia exigua	2.7386	3.1971
Eunotia rhomboidea	3.0814	0.5182
Fragilaria bidens	1.9423	1.4765
Navicula dicephela	2.7833	-0.7209
Navicula occulta	2.1648	2.3497
Navicula similis	0.8867	1.2076
Navicula stagnorum	0.0206	2.4756
Nitzschia ignorata	1.4646	-0.5879
Nitzschia palustris	0.2049	-0.9344
Nitzschia spp.	2.7738	-0.9192
Nitzschia (cf) sigmoidea	2.9791	-1.354
Pinnularia borealis	-0.7535	0.4922
Pinnularia cruciformis	1.3201	0.7022
Pinnularia islandica	-1.1767	0.4922
Pinnularia parva (v. lagerstedtii)	-1.1767	0.4922
Pinnularia parva (v. minuta)	0.5532	0.9219
Pinnularia spp.	-0.8651	0.4922
Pinnularia subcapitata	-1.1767	0.4922
Synedra spp.	-1.1767	0.4922
Synedra ulna	3.3666	-1.2536

SITES		
EIG	*0.4823*	*0.2133*
S1	0.439	0.3533
S2	0	0.737
S3	1.7441	0
S4	1.6935	1.5231
S5	2.2891	0.0046
S6	2.4183	1.0701

Summary list of invertebrate species collected from aquatic sites identical in location to the sites used for diatom sampling (Ray, unpublished data).

Invertebrate Taxa	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
D.lindrothi/latitarsis A	20	40	112	0	0	0
Diamesa 1	0	4	8	79	24	16
D.lindrothi/latitarsis B	0	0	40	30	42	58
Diamesa bertrami	0	0	0	6	9	19
Diamesa 2	0	0	0	0	0	8
Diamesa aberrata	0	0	0	6	0	11
Eukiefferiella minor	0	0	0	65	72	38
Eukiefferiella claripennis	0	0	0	10	37	0
Orthocladius orthocladius/euorthocladius	0	0	0	0	24	37
Simuliidae	0	0	0	0	24	20
Tipuliidae	0	0	0	0	12	12
Hydracarina (mites)	0	0	0	0	2	5
Total	20	44	160	196	246	224
Diversity	0.00	-0.30	-0.75	-1.38	-1.93	-2.07
Evenness	0.05	0.027	0.011	0.017	0.024	0.030
Richness	1	2	3	6	8	10

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