Functional feeding groups of benthic macroinvertebrates in Swedish lakes and streams and the importance of spatial scale

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by

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Table of Contents

Appendix

1. The procedure of partitioning variation in functional feeding groups (FFG) of macroinvertebrates in Swedish streams explained by partial redundancy analysis (RDA) (Table 9).
2. The procedure of partitioning variation in functional feeding groups (FFG) of macroinvertebrates in Swedish lakes explained by partial redundancy analysis (RDA) (Table 10).
3. Parameters in the stream and lake data sets used in statistical analysis (Table 11).
4. Number of individuals of each species or organism group found at the six sample sites in Hågaån (Table 12).

Abstract

Multivariate statistical methods were used to explore the relationships between functional feeding guilds of different macroinvertebrate communities in Swedish streams and lakes.

The most important factor for explaining the composition of functional feeding groups, both in streams and lakes, seemed in Sweden to be geographical position (e.g. altitude and ecoregion) and local scale factors (e.g. substrate).

Principal component analysis (PCA) showed that abiotic factors, like stream velocity and geographical position, seemed to be important both in streams and lakes. Like PCA, redundancy analysis (RDA) showed that geographical factors were important for the functional feeding group composition of benthic communities in lakes. Forest in the catchment area and stream velocity were important for the composition in streams.

Using partial RDA, a total of 39.9% for stream data and 44.0% for lake data were explained. The unique variation of local scale factors seemed to be the most important factor to explain the variability of functional feeding groups, both in streams (59%) and lakes (44%), out of the total variation that could be explained.

Stream velocity in streams and geographical position in lakes also showed, in stepwise multiple regression, to be important factors for the functional feeding group composition. The highest adjusted r^2-value for stream data was shown by passive filter-feeders (0.44), followed by grazers (0.40), detritus feeders (0.35), shredders (0.30), predators (0.28), and active filter-feeders (0.21). For lake data the highest adjusted r^2-value was shown by detritus feeders (0.54), followed by grazers (0.49), predators (0.27), active filter-feeders (0.29), shredders (0.27), and passive filter-feeders (0.15).

The abundance of macroinvertebrates showed for functional feeding groups in lakes, but not in streams, a tendency of increasing values from north to south in the country. Except for the alpine region, the functional feeding group composition of streams did not vary among ecoregions. In lakes, a significant difference in composition of functional feeding groups occured between the middle and southern boreal regions.

A field study comparing functional feeding group composition and fatty acid contents between arable and forested sites within a single stream was also done. No significant differences in functional feeding group composition were found except for active filter-feeders. Fatty acid composition was similar within, but different among the functional feeding groups analyzed between forested and arable sites.

Introduction

At the macroscopic level, the invertebrates provide the highest number of individuals and species, biomass and production in freshwater (Gullan and Cranston 1994). The use of macroinvertebrates as indicators of ecosystem health is today widespread (Johnson 1998). Benthic macroinvertebrates refers to organisms that inhabit the bottom substrates of freshwater habitats, for at least part of their life cycle, and are retained by mesh sizes greater than or equal to 200 to 500 µm (Rosenberg and Resh 1993). Most taxa of benthic macroinvertebrates are relatively sessile organisms and most species have life cycles of one year or more, so they can be used to assess the effects of local and relatively short-term environmental variations (Griffith et al. 1995).

This study deals with the functional feeding aspects of benthic macroinvertebrates, which refers to what and in which way the organisms are feeding. Food webs vary predictably from headwaters to river mouths, caused by the relatively availability of food resources, which also, according to Vannote et al. (1980), changes in a predictable fashion. In this study the benthic macroinvertebrates were divided into six functional feeding groups (shredders, grazers, active and passive filter feeders, detritus feeders and predators). The classification system used is based on a classification by Moog (1995). Functional feeding groups are useful descriptive categories that clarify both the nature and distribution of the food eaten, and the role of the organism in the ecosystem (Palmer et al. 1993).

The focus of this study is placed on bettering our understanding of the parameters that can explain the variance in functional feeding group composition among streams and lakes. A Canadian study of caddiesfly communities from 25 springs showed that grazers and predators are abundant only in springs with relatively high microhabitat diversity, current velocity and pH (Williams 1991). Moreover, Casas (1997) emphasized the importance of natural leaf packs as both a food source and habitat for shredders. The organic periphyton microlayer occuring on stones and other substrates has also been shown to be a food source for aquatic insects (Rounick and Winterbourn 1983). Although much less is known of factors structuring lake littoral communities, in streams a number of studies have shown that abiotic or stochastic variation is important. For example, Barmuta (1990) showed, in a study of interactions between the effects of substratum, stream velocity and stream benthos, that the functional feeding group community is more influenced by stream velocity than substratum size, with riffles having higher total abundances and higher species richness. In regulated streams the abundances of grazers, detritus feeders and predators, but not shredders and filter feeders are negatively affected by increased flow variability (Englund and Malmqvist 1996). Reduced flow and differences in feeding behaviour may probably explain the responses.

Even large scale patterns may be important for explaining the variation in macroinvertebrate community composition. Harding et al. (1997) showed in New Zealand that taxonomic richness, number of species, species dominance and summer faunal densities all differed among ecoregions, but little discrimination was possible using functional feeding groups. Stream faunas were generally similar among forested ecoregions (Harding et al. 1997). In the present study lakes and streams were classified according to six ecoregions (Gustafsson and Ahlén 1996, NMR 1984).

Although functional composition is relatively predictable, it is not always easy to use functional feeding groups as indicators of environmental factors. For instance, Palmer et al. (1996) investigated the potential for using functional feeding groups as indicators of water quality conditions in rivers, and they concluded that functional feeding group classification was unlikely to provide useful indications. In contrast, Camargo (1994) showed that shredders and grazers are the functional feeding groups that are most adversely affected by fish farm effluents in streams.

Angradi (1996) showed that community structure is more similar among habitats than among streams and similarly that functional organisation also differs among habitats. In riffles all functional feeding groups are generally well represented. However, microdistribution patterns do exist. Although detritus feeders are generally the most abundant group, filter feeders, grazers and detritus feeders are often more common on rock faces, while shredders and predators often predominate the biomass in pools (Angradi 1996). Robinson and Minshall (1990) showed that distribution patterns were due to both microhabitat and food availability. These authors showed an initial buildup and then decline of filter feeder densities downstream from the outlets of three oligotrophic lakes, and concluded that these longitudinal patterns were related to differences in food quantity and quality and microhabitat. Lastly, in a new man-made lake, filter feeders colonized first followed by grazers, detritus feeders, predators and shredders, respectively (Malmqvist et al. 1991).

Fatty acid content, in particular biomarker fatty acids, are also interesting in connection with functional feeding groups, since the composition of fatty acids in insect tissues has been shown to differ with diet (Barlow 1966; Hanson et al 1983). Hence, dietary differences between representatives of different functional feeding groups should be manifested in their fatty acid composition. If differences in food acquisition mechanisms between functional feeding groups result in different diets for the groups, their fatty acid composition should also be expected to differ. Food quality may have strong effects on ecosystem functioning (Ederington et al. 1995) and may be more important than food quantity for survival, growth and reproduction in animal populations (Xu et al. 1993, D'Abramo and Sheen 1993, Vanderploeg, Lieblig and Gluck 1996). According to Kaneda (1991) the branched *iso-* and *anteiso-* forms of 15C and 17C fatty acids indicate a diet of bacterial origin. Large dietary amounts of these fatty acids are also considered to be of low food quality (Kaneda 1991). Highly unsaturated fatty acids (fatty acids with many double bonds) are an important adaption to the aquatic environment (Hanson et al. 1985).

The aim of the present study was to explore the relationships between functional feeding aspects of different macroinvertebrate communities in Swedish lakes and streams. This study addressed several questions: (1) Which environmental variables correlated best with different functional feeding groups?; (2) How were the different parameters related to each other?; (3) How much of the variance was explained?; and (4) Were there any differences in composition of functional feeding groups between different ecoregions and between lakes and streams?

A field study testing the linkage between land use and functional response of streams macroinvertebrate communities was also done. Here it also was tested if fatty acid composition varied by functional feeding group.

Material and methods

Data set

Data for this study was taken from the national survey of lakes and streams done in the autumn 1995 (Wilander et al. 1998). The data set consists of macroinvertebrate data and physical and chemical variables (Table 11, appendix 3) for the 694 sites sampled in streams (riffle habitats) and the 532 sites sampled in lakes (wind-exposed littoral habitats). Benthic macroinvertebrate samples were collected using standardised kick-sampling with a handnet with a 0.5 mm mesh size (SS EN 27 828). Taxonomic identification was done to a predetermined level, most of the taxa to species, but some to a higher taxonomic level (e.g. Chironomidae or Oligochaeta) (see Wilander et al. 1998 for a complete taxa list). Samples for water chemistry of lakes was generally done in mid-lake, often using helicopter. Samples were, if possible, taken directly into the sample bottles, otherwise samples were taken with a metal free Ruttner-sampler. In streams, the chemistry samples were taken in connection with the macroinvertebrate collection, generally directly into the sample bottles. Characteristics of the sites sampled were recorded in the field (see Wilander et al. 1998).

For studying the relationships between functional feeding groups and environmental variables only lakes and streams considered unaffected by human activity were used. First 19 lakes and 38 streams in Väster Norrland were excluded, because the samples had not been taken according to the sampling protocol. Lakes and streams directly or indirectly affected by liming were removed; 79 (lakes) and 99 (streams), respectively. Finally, 24 lakes and 96 streams, classified as eutrophicated, with ≥20% arable land in the catchment area and 52 lakes and 33 streams, deemed as acidified with an exceedance of critical load for sulfur acidity (Henriksen et al. 1992 and 1998), were removed. The remaining data set consisted of 364 lakes and 428 streams.

Classification of functional feeding groups

Classification of macroinvertebrates into different functional feeding groups was done using Fauna Aquatica Austriaca (Moog 1995) (Table 1). Categorization was based on the food consumed, the morphological adaptions of the feeding structures (mouthparts, legs) and the behaviour that drives these structures (e.g. modes of attachment that allow individuals positioned in the stream current to manipulate a filtering structure, and the construction of capture nets). Moog (1995) uses ten classes of functional feeding groups, but since one of the groups was not represented in the data set (leaf borers) and three of the groups were represented only by a few individuals (xylophagous, parasites and other feeding types), only six classes were used in this study.

The 10 point system for explaining how much a species belongs to a specific functional feeding group was used to classify the functional feeding of individual taxa and communities. For example a species with a very narrow range of food selection might receive a score of 10 for only one class (e.g. all Odonata are strictly predators and will be given a score of 10 for predators) (Table 2). Conversely, a species may belong to several feeding classes and will receive scores lower than 10 in more than one class, but with the sum total equal to 10. Table 2 shows for example that *Somatochlora metallica* (Odonata) is classified as a strict predator, while *Phryganea grandis* (Trichoptera) is mostly a predator (score = 6), but during part of its life history this animal is also classified as a shredder (2), grazer (1) and detritus feeder (1). Similarly, *Hydropsyche* spp. (Trichoptera) is considered being mostly passive filter-feeders (5), but this species group is also classified as predators (3) and shredders (2).

Table 1. A classification of macroinvertebrates into different functional feeding groups based on the classification scheme in Fauna Aquatica Austriaca (Moog 1995) (see text). * = Mostly shredder.

Functional feeding groups	Feeding mechanisms	Dominant food resources	Particle size Range of food (mm)	Example of genus
Shredders	Chew conditioned or live vascular plant tissue, or gouge wood	Fallen leaves, plant tissue, coarse particulate organic matter (CPOM)	>1.9	*Gammarus**, *Nemoura**
Grazers	Graze mineral and organic surfaces	Epilithic algal tissues, biofilm, partially POM	0.01-1.0	*Theodoxus*
Active filter-feeders	Suspension feeders, filter particles actively with sediment or brush loose surface deposits	Suspended fine particulate organic matter (FPOM), CPOM, prey	0.01-1.0	*Ephemera, Sphaerium*
Passive filter-feeders	Suspension feeders, filter particles brought by flowing water current	Suspended FPOM, CPOM, prey	0.01-1.0	*Simulium*
Detritus feeders	Deposit feeders, ingest sediment or brush loose surface deposits	Sedimented FPOM	0.05-1.0	*Leptophlebia, Caenis, Tubifex*
Predators	Capture and engulf prey or ingest body fluids	Prey, living animal tissue	>0.5	*Helobdella, Somatochlora, Rhyacophila*

Table 2. Example of scores for functional feeding groups.

	Functional feeding group					
Species	Shredders	Grazers	Active filter-feeders	Passive filter-feeders	Detritus feeders	Predators
Somatochlora metallica	-	-	-	-	-	10
Phryganea grandis	2	1	-	-	1	6
Hydropsyche spp.	2	-	-	5	-	3

Ecoregions

A categorization using six ecoregions, based on the Nordic Council of Ministers (NMR 1984), is used for division of the country into smaller parts (Fig. 1). NMR (1984) uses eight classes of ecoregions, but in the present study the arctic region has been combined with the alpine region and the northern boreal region has been combined with the northern-southern boreal region (see Gustafsson and Ahlén 1996). The six ecoregions used in this study are then the: (1) alpine zone, with heath and alpine vegetation; (2) northern boreal zone, with open coniferous forests and mountain birch forests; (3) middle boreal zone, with coniferous forests; (4) southern boreal zone, with coniferous forests and also occurring decidiuous trees; (5) boreo-nemoral zone, with mixed forests of spruce, pine and decidiuous trees and large areas of arable land; and (6) nemoral zone, with deciduous forests and large areas of arable land. The northern border of the boreo-nemoral zone coincides with the northern natural spreading of oak, and is called *Limes Norrlandicus* (see Gustafsson and Ahlén 1996). Characteristics from each of the different ecoregions are listed in Table 3. Ecoregion classification was used to test if differences in the composition of functional feeding groups varied among ecoregions.

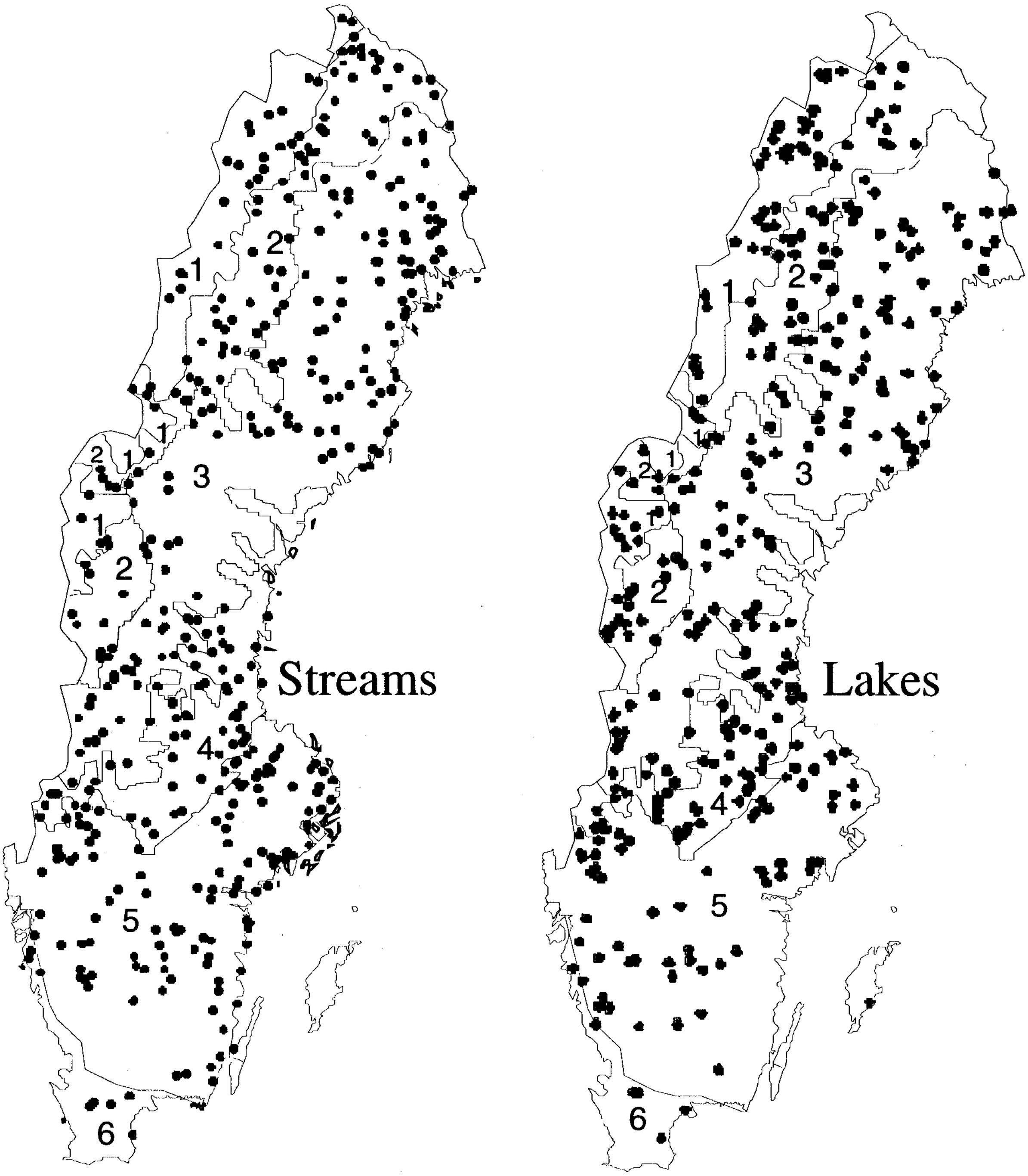

Figure 1. Map over Sweden divided into six ecoregions (NMR 1984) with sample sites for streams and lakes. Regions: 1=alpine, 2=northern boreal, 3=middle boreal, 4=southern boreal, 5=boreo-nemoral and 6=nemoral.

Table 3. Selected characteristics of the six ecoregions (NMR 1984).

Ecoregion	Number of streams used in this study	Number of lakes used in this study	Mean annual temperature (°C)	The yearly precipitation (mm)	Growing season (days)
Alpine	37	43	-4 – 5	<500 – >4000	110 – 140
Northern boreal	78	81	-3 – 5	<500 – >4000	110 – 140
Middle boreal	137	119	-1 – 5	<500 – 1000	120 – 160
Southern boreal	55	50	2 – 6	<500 – 1000	140 – 180
Boreo-nemoral	113	63	2 – >7	<500 – 2500	160 – 200
Nemoral	8	8	5 – >7	<500 – 2000	180 – 210

Statistical analysis

Principal component analysis (PCA) was done (The Unscrambler 6.11, PC version) to visually analyse correlations between different parameters and to outline general structure of the data, both for lakes and streams.

Redundancy analysis (RDA) was applied (Canoco 3.15, Mac. version) to visualize the structure of the functional feeding group data in relation to the most important environmental variables.

A partial RDA technique (Canoco 3.15, Mac. version) was used to clarify the relationships between functional feeding groups and the different habitat factors. The procedure of the variation partitioning was used according to Liu (1997) (appendix 1 & 2) and was carried out by two steps (Table 9, appendix 1 & Table 10, appendix 2). In order to explain spatial patterns of functional feeding groups, the data set was divided into three groups including regional (longitude, latitude, altitude and ecoregions), catchment (landuse in the catchment area and catchment area) and local (landuse in the riparian zone, chemical variables, substrate and vegetation) environmental variables. In the first step, RDA was run using functional feeding groups (FFG) as response (FFG are the responder in the whole procedure) and all three groups of environmental variables as explanatory variables and no covariables and hence the total amount of variation explained by the three environmental variable groups was obtained. In the second step, partial RDA was run using one of the three environmental variable groups as explanatory variables and the remaining two groups as covariables, and the other way around, with and without covariables. The RDA was thus run four times within each combination of environmental variable groups. After this the pure effect of regional, catchment and local scale, the joint effect of catchment and local scale, regional and local scale and regional and catchment scale were obtained. Finally the procedure of variation decomposition was accomplished with the aid of two sets of equations (appendix 1 & 2).

Stepwise multiple regression was done to determine which parameters could explain significant differences in functional feeding groups (JMP 3.2.2, Mac. Version).

One way ANOVA (JMP 3.2.2, Mac. Version) was used to test for different composition of functional feeding groups among different ecoregions. If a difference was found, post-hoc tests were applied using Tukey-Kramer honestly significant difference test (JMP 3.2.2, Mac. Version). Descriptive statistics with quartiles were also used to visualize the differences between the ecoregions.

In all statistical tests α was set at 0.05 and Bonferroni corrections were applied.

Field study

Hågaån, a stream east of Uppsala, which is 25 km in length and drains Lake Fibysjön, was chosen for the field study. The catchment area is 104 km^2 and consists of 56% forested land, 3% wetland, 37% arable and meadowland and also 4 % other land. The mean current velocity is 0.8 m^3/s (Brunberg and Blomqvist 1998).

The fieldwork consisted of two parts. Firstly, a field study was done to obtain an overview over the benthic macroinvertebrate community (i.e. taxonomic and functional composition of the stream) (Table 12, appendix 4). Samples were collected at six sites (Table 4) along the stream, using standardised kick sampling with a handnet (0.5 mm mesh size) (SS EN 27 828). Three of the sites were situated in forested land and three were found on arable land. Latitude and longitude were recorded for the sample sites with a GPS instrument (Lowrance GlobalNav 212). The organisms were immediately preserved in 70% ethanol after collection, and sorted and identified according to SWEDAC certified procedures (Naturvårdsverket 1996).

Sites were blocked by riparian type with three sites in forested land and three sites in arable land. For statistical analysis, a General Linear Model (GLM) of ANOVA (Minitab 12.2, PC version), with α set to 5% was used. To test if the composition of functional feeding groups differed between the sites the data set was transformed into absolute numbers of individuals per functional feeding group using Moog's (1995) 10 point system. The data were log-transformed. The sample sites were compared to each other, both between forested and agricultural land, and between all the six sample sites.

Table 4. The six sample sites in order up streams to down streams.

Site (order)	Site (name)	Dominating land use	Latitude	Longitude	Distance from Lake Fibysjön (km)
1	Fiby urskog	Forest	66°41′N	15°86′E	2
2	Stora Kil	Arable	66°40′N	15°88′E	3.5
3	Forsbacka	Arable	66°37′N	15°97′E	11.5
4	Kvarnbo	Forest	66°37′N	15°98′E	13
5	Hågadalen	Arable	66°33′N	16°00′E	23
6	Lurbo	Forest	66°32′N	16°01′E	24.5

Secondly, a field study, based on the results of the first field study was done to determine the fatty acid composition of three different functional feeding groups at two of the earlier visited sites (Fiby urskog and Stora Kil, Table 4). A handnet with 0.5 mm mesh size was used for kick sampling. The organisms were kept alive in aerated water and after sorting of the organisms according to taxa, they were kept in the dark at 4°C to empty their guts. After about 18-20 hours the water solution was removed and the organisms were counted, weighed and then transferred to vials and placed in a freezer at -20°C. After approximately two weeks the organisms were freeze dried for 4 days. The dry weights of the organisms was recorded (±0.1 mg) measured and then the organisms were placed in glass vials (Ø=24 mm and height=24 mm), filled with N_2-gas and closed with a plastic snap-cap. Fatty acid analyses were done by the Clinic of Geriatrics at Uppsala University hospital in Uppsala.

Fatty acids were measured as their methyl esters by gas chromatography (GC) according to the procedure described by Ahlgren et al. (1994). The fatty acids were quantified ($mg \cdot g^{-1}$ dry mass) by injecting fixed volumes of the dissolved, pre-weighed samples into the GC, and comparing the area of the peaks with the peaks of an internal standard (0.05, 0.10 or 0.20 mg per sample of tricosanoic acid, 23:0). Butylated hydroxytoluene was used as an antioxidant. Individual fatty acids were identified by comparing their retention times with those of several commercially available standard mixtures, mixed with fish oil or separate standard fatty acids. Total fatty acids were calculated from the total area under the curve in the chromatograms minus the peaks for the added antioxidant and standard.

Results

Principal component analysis (PCA)

The first three PCA axes for streams (Fig. 2) explained 19%, 7% and 6% of the total variation, respectively, indicating a weak collinearity among the variables. For lakes, the first three PCA axes (Fig. 3) explained 15%, 8% and 7% of the total variation, respectively, also indicating a weak collinearity among the variables. Neither in lakes nor streams did the functional feeding group composition show very strong correlation with any of the environmental variables in the principal component analysis. Abiotic factors, like stream velocity and geographical position, seemed however to be the most important factors for functional feeding group composition both in streams and lakes.

The first PCA axis (Fig. 2) for the stream data accounted for variance in geographical factors (latitude and altitude), chemical factors (total phosphorous and total nitrogen), substrate factors (block - silt) and vegetation factors (filamentous algae - emergent plants) and the second axis represented land use (forest - alpine) both in the catchment area and in the riparian zone. Stream velocity showed the closest correlation with the functional feeding groups. There appeared to be a strong north-south gradient along the first PCA axis (Fig. 2). PCA showed that streams in the northern part of the country were often characterized as having block substrate, situated at higher altitudes and having more alpine vegetation. In contrast, streams in the south were characterized by high nitrogen and phosphorus levels, low stream velocities, more emergent plants and generally finer substrates, like silt. Not surprisingly stream velocity was also higher in the northern part of the country, in particular at higher altitudes.

The first PCA axis (Fig. 3) of the lake data showed that geographical factors (ecoregion - latitude/altitude) explained a large portion of the variance, while the second axis represented land use (alpine – forest) and partly substrate factors (block) and vegetation factors (emergent plants). In contrast to streams, in lakes, functional feeding groups were more closely correlated with geographical factors. Even for lake data, there was a strong north-south gradient along the first PCA axis (Fig. 3). Similar to streams, there was more block substrate in lakes in the northern part of the country and more emergent plants in the southern part of the country.

Redundancy analysis (RDA)

The first two RDA axes for streams explained 14% and 6% of the total variation, respectively (Fig. 4a). For lakes the first two RDA axes explained 23% and 3% of the total variation, respectively (Fig. 4b). Variables that could explain a significant portion of the variance among functional feeding groups were plotted in the ordinations (Fig. 4). The RDA showed, like PCA, that geographical factors were important for the functional feeding group composition in lakes, whereas factors such as the type of forest in the catchment area, stream velocity, and altitude were important predictors for the functional feeding group composition in streams. For example, in lakes all functional feeding groups were more abundant at lower altitudes and lower latitudes (i.e. in the southern part of the country) (Fig. 4b). Wetland in the riparian zone was also important for the functional feeding group composition. For streams, all functional feeding groups were also more abundant at lower altitudes and with large areas of forested land in the catchment area in streams (Fig. 4a), but stream velocity seemed to be the single most important factor.

Variation partitioning by partial RDA

Using data in Tables 8 and 9, the total explained variation was partitioned into seven parts: (1) the pure effect of regional scale; (2) the pure effect of catchment scale; (3) the pure effect of local scale; (4) the joint effect of regional and catchment scale; (5) the joint effect of regional and local scale; (6) the joint effect of catchment and local scale; and (7) the joint effect of the three scale variable groups (appendix 1 & 2).

$$\text{Total explained variance for stream data} = \overbrace{0.044}^{\substack{\text{Joint variation}\\ \text{Reg, Cat and Loc}}} + \underbrace{0.037 + 0.011 + 0.006}_{\substack{\text{Partial joint variation}\\ \text{Reg and Cat}\\ \text{Reg and Loc}\\ \text{Loc and Cat}}} + \overbrace{0.027 + 0.035 + 0.236}^{\substack{\text{Unique variation}\\ \text{Reg, Cat, Loc}}} = 0.396$$

$$\text{Total explained variance for lake data} = \overbrace{0.153}^{\substack{\text{Joint variation}\\ \text{Reg, Cat and Loc}}} + \underbrace{0.012 + 0.039 + 0.013}_{\substack{\text{Partial joint variation}\\ \text{Reg and Cat}\\ \text{Reg and Loc}\\ \text{Loc and Cat}}} + \overbrace{0.012 + 0.020 + 0.191}^{\substack{\text{Unique variation}\\ \text{Reg, Cat, Loc}}} = 0.440$$

Figure 5. The equation for total explained variance (eigenvalues), including the joint variation of regional scale (Reg), catchment scale (Cat) and local scale (Loc) and the partial variation of Reg and Cat, Reg and Loc and Loc and Cat and the unique variation of Reg, Cat and Loc.

The first run of partial RDA for stream data showed that 39.9% of the total variation in functional feeding group data was explained by the three groups of environmental scale variables and for lake data the first run showed that 43.9% of the variance was explained by these three groups of variables. In subsequent runs regional scale variables explained 7% of the total explained variance of streams (0.396) and 3% of lakes (0.439) (Table 9–10, appendix 1–2). Catchment scale variables explained 9% (streams) and 5% (lakes). Local scale factors explained 59% (streams) and 44% (lakes). The pure effect of joint catchment and local scale (69% and 51% for streams and lakes, respectively) (the pure effect from each group is still included, the same for the following two), regional and local scale (69% and 55 %) and regional and catchment scale (25% and 10%) were obtained.

Figure 5 shows the equations for total explained variation partitioned into the three parts; the common component, the partial common component and the unique component. The unique variation of local scale seemed to be the most important factor to explain the variability of functional feeding groups both in streams and lakes.

Stepwise multiple regression

Stepwise multiple regression was used to fit environmental variables to functional feeding groups. Passive filter-feeders showed the highest adjusted r^2-value for stream data (44%) (Table 5), followed by grazers (40%) and detritus feeders (35%). For lake data (Table 6),

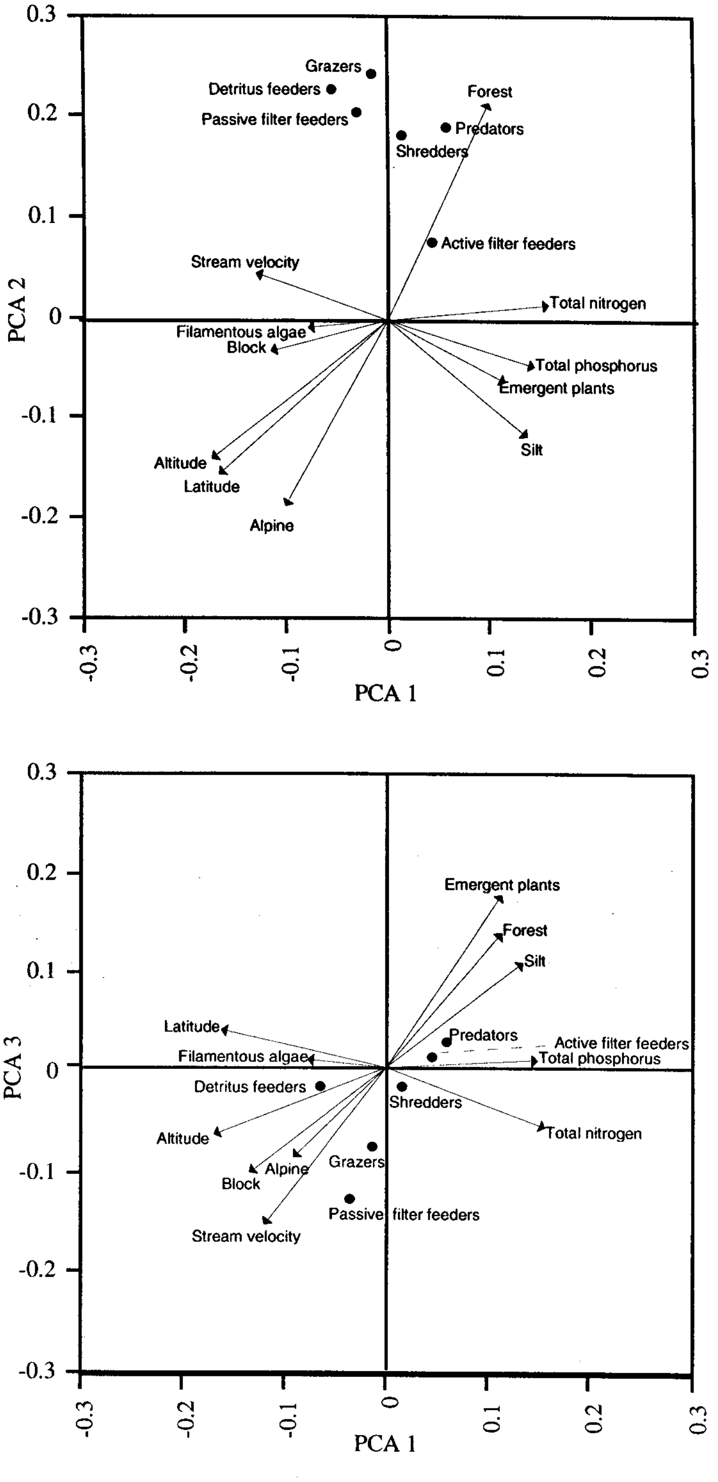

Figure 2. Ordination of parameters in 428 streams along the first three principal component axes.

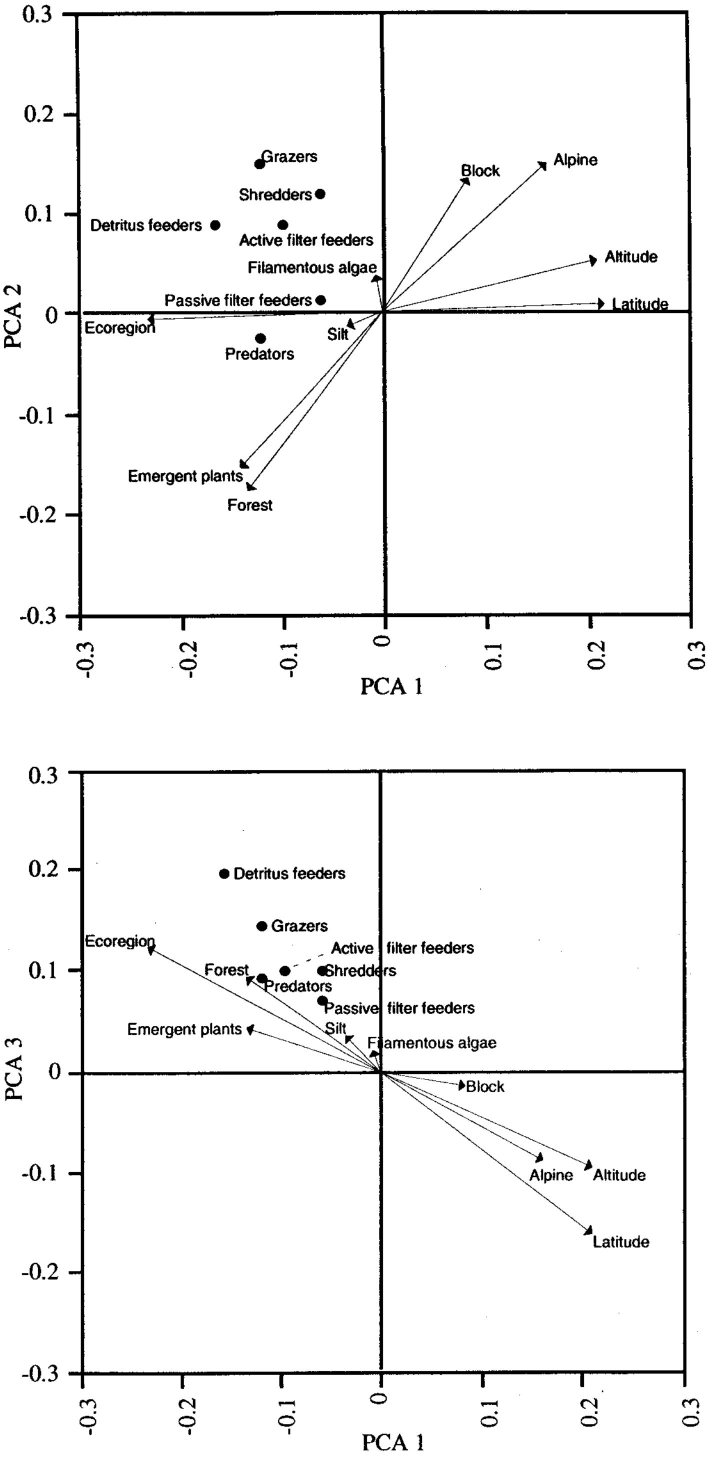

Figure 3. Ordination of parameters in 364 lakes along the first three principal component axes.

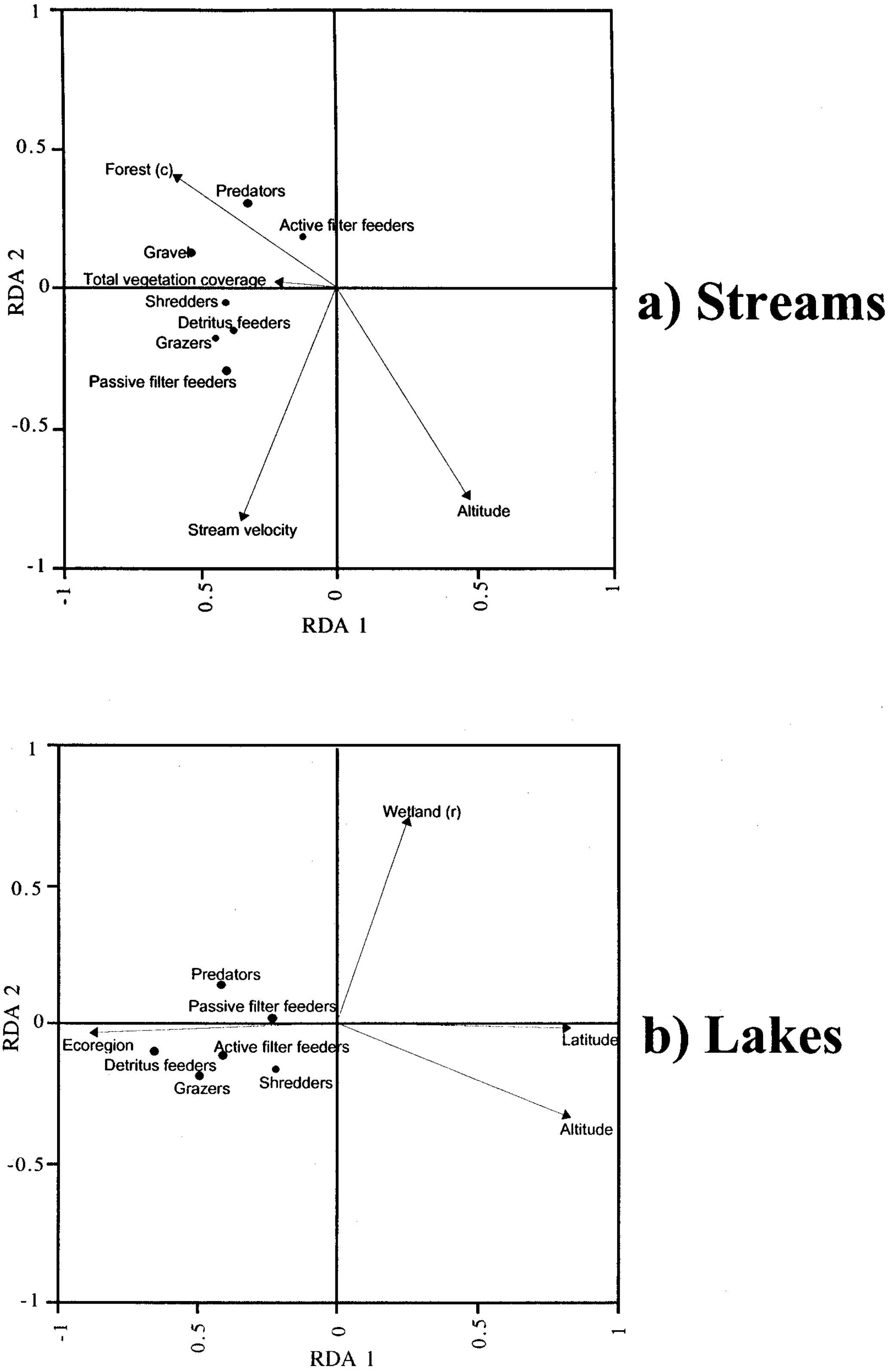

Figure 4. RDA ordination of functional feeding groups and selected parameters along the first two component axes for streams (a) and lakes (b). (r = in the riparian zone; c = in the catchment area)

Table 5. Stepwise multiple regressions, connections between functional feeding groups and factors in and around streams. r^2-, adjusted r^2- & accumulated r^2-values and p-values are shown.

SHREDDERS

r^2	r^2 *adjusted*
0.339	0.297

Parameter	r^2 *accum.*	*p-value*
Forest^{C}	0.053	0.000
Stream velocity	0.127	0.000
Fontinalis	0.154	0.000
Depth	0.173	0.002
Block	0.192	0.002

GRAZERS

r^2	r^2 *adjusted*
0.430	0.400

Parameter	r^2 *accum.*	*p-value*
Fontinalis	0.102	0.000
Stream velocity	0.163	0.000
Forest^{C}	0.231	0.000
pH	0.262	0.000
Floating leaved plants	0.289	0.000
Si	0.312	0.000

ACTIVE FILTER FEEDERS

r^2	r^2 *adjusted*
0.256	0.212

Parameter	r^2 *accum.*	*p-value*
Ecoregion	0.055	0.000
Catchment area	0.085	0.000
Coniferous forest^{R}	0.103	0.003
Block	0.122	0.003

PASSIVE FILTER FEEDERS

r^2	r^2 *adjusted*
0.470	0.436

Parameter	r^2 *accum.*	*p-value*
Stream velocity	0.179	0.000
Forest^{C}	0.247	0.000
Coarse detritus	0.311	0.000
Decidious forest^{R}	0.331	0.000
Depth	0.347	0.002

DETRITUS FEEDERS

r^2	r^2 *adjusted*
0.387	0.349

Parameter	r^2 *accum.*	*p-value*
Silt	0.102	0.000
Forest^{C}	0.165	0.000
Floating leaved plants	0.199	0.000
Mire^{C}	0.225	0.000
Total P	0.245	0.001
pH	0.263	0.001

PREDATORS

r^2	r^2 *adjusted*
0.316	0.277

Parameter	r^2 *accum.*	*p-value*
Altitude	0.149	0.000
Gravel	0.184	0.000
Fine leaved submergent plants	0.197	0.009

Table 6. Stepwise multiple regressions, connections between functional feeding groups and factors in and around lakes. r^2-, adjusted r^2- & accumulated r^2-values and p-values are shown.

SHREDDERS

r^2	r^2 *adjusted*
0.336	0.269

Parameter	r^2 *accum.*	*p-value*
Decidious forest^{R}	0.105	0.000
Ecoregion	0.128	0.005
Block	0.154	0.003

GRAZERS

r^2	r^2 *adjusted*
0.534	0.490

Parameter	r^2 *accum.*	*p-value*
Ecoregion	0.219	0.000
Wetland^{R}	0.288	0.000
Cobble	0.319	0.000
Grazing ground^{C}	0.343	0.002
NH$_4$-N	0.368	0.001

ACTIVE FILTER FEEDERS

r^2	r^2 *adjusted*
0.350	0.293

Parameter	r^2 *accum.*	*p-value*
Ecoregion	0.141	0.000
Isoetids	0.175	0.001
Wetland^{R}	0.199	0.003

PASSIVE FILTER FEEDERS

r^2	r^2 *adjusted*
0.184	0.155

Parameter	r^2 *accum.*	*p-value*
Altitude	0.076	0.000
Lake area	0.111	0.001

DETRITUS FEEDERS

r^2	r^2 *adjusted*
0.576	0.538

Parameter	r^2 *accum.*	*p-value*
Ecoregion	0.362	0.000
Wetland^{R}	0.413	0.000
NH$_4$-N	0.443	0.000
Latitude	0.468	0.000

PREDATORS

r^2	r^2 *adjusted*
0.322	0.272

Parameter	r^2 *accum.*	*p-value*
Altitude	0.154	0.000
Heath^{R}	0.189	0.000
Total vegetation coverage	0.212	0.004

C = Landuse in the catchment area; R = Landuse in the riparian zone

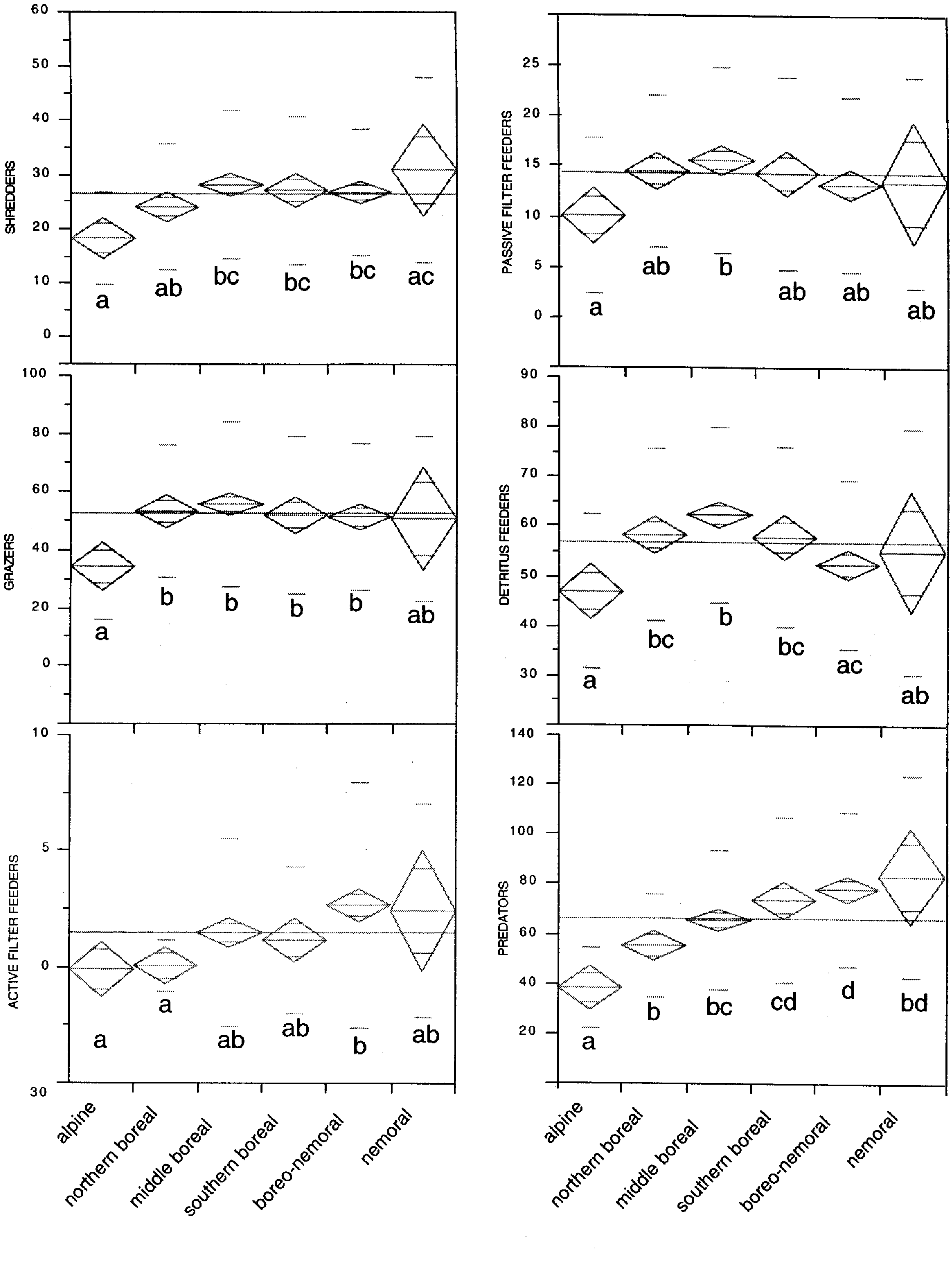

Figure 6. Mean number of functional feeding group scores in streams within each ecoregion. Diamonds represents a 95% confidence interval and the standard deviation is shown as dashed lines above and below the diamonds. Ecoregions denoted with the same letter are not significantly different (Tukey-Kramer HSD-test).

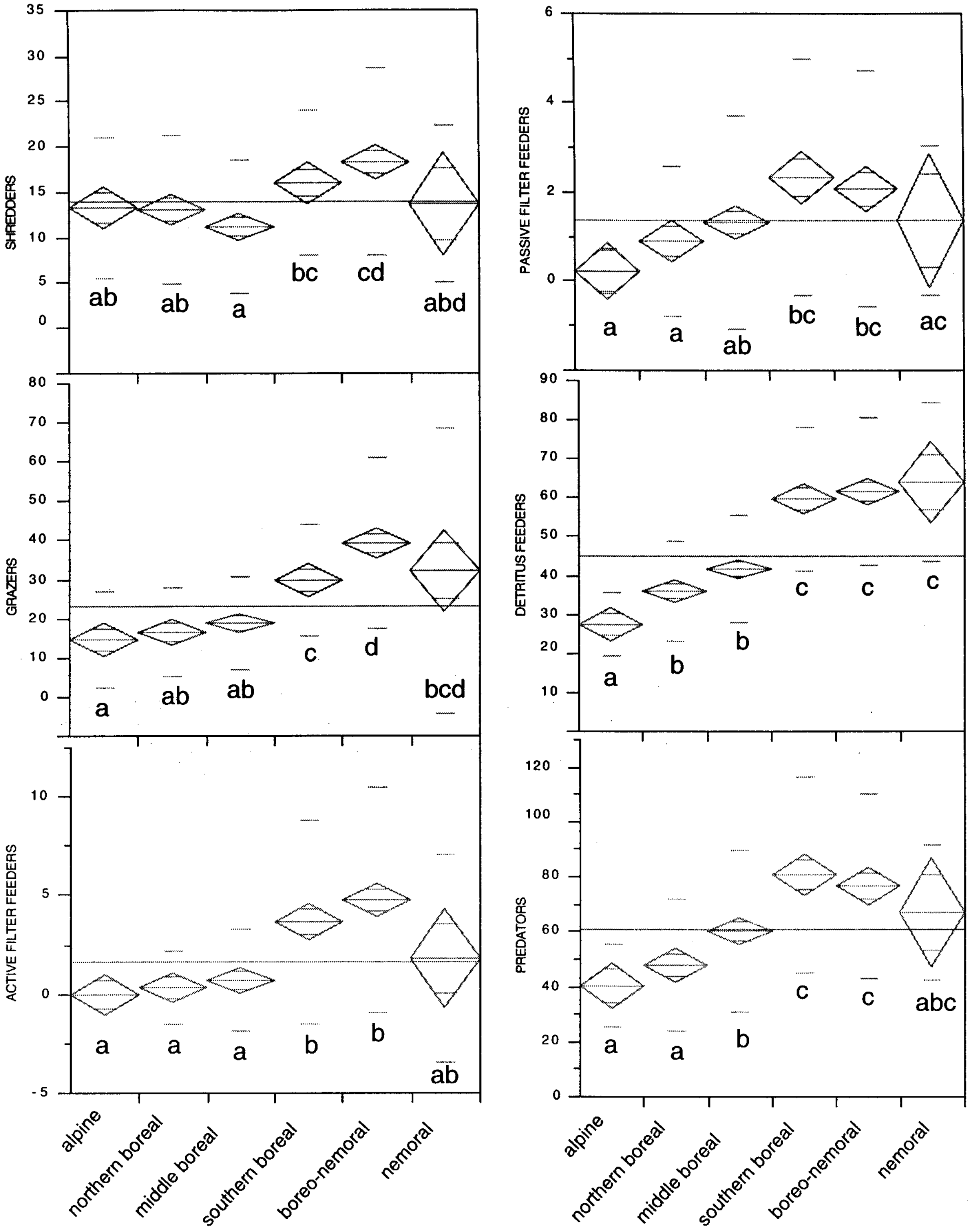

Figure 7. Mean number of functional feeding group scores in lakes within each ecoregion. Diamonds represents a 95% confidence interval and the standard deviation is shown as dashed lines above and below the diamonds. Ecoregions denoted with the same letter are not significantly different (Tukey-Kramer HSD-test).

the highest adjusted r^2-value was found for detritus feeders (54%), followed by grazers (49%) and active filter-feeders (29%).

Stream velocity solely explained the highest variance (18%) in streams (for passive filter-feeders). Stream velocity could be important also for shredders (4%) and grazers (9%), according to the regression. The substrate type could be important for the composition of functional feeding groups and similarly could the presence of forest play a major role. Geographical factors were mostly correlated with predators and active and passive filter-feeders.

In contrast to streams, lake communities were more influenced by geographic position. Ecoregions showed for detritus feeders the highest individual r^2-value (36%) and this variable together with altitude seemed to be important for all functional feeding groups. Substrate type was also, like in streams, important for the composition.

Ecoregions

The composition of functional feeding groups in streams (Fig. 6) in the alpine region was significantly different from the other regions in several of the functional feeding groups (Tukey-Kramers HSD-test). Except for the alpine region functional feeding group composition did not vary among ecoregions.

For lakes, on the other hand, differences in composition of functional feeding groups occured between the middle boreal region and the southern boreal region (Fig. 7) (Tukey-Kramers HSD-test), which also coincides with the well known ecotone "*Limes Norrlandicus*" (Gustafsson and Ahlén 1996). Otherwise functional feeding groups did not differ between adjacent ecoregions, except for predators which differed between the northern and middle boreal regions. The abundance of functional feeding groups in lakes showed a tendency of increasing from north to south.

Field study

Table 12 (appendix 4) shows the number of individuals of each species or organism group found and Figure 8 shows the relative number of individuals of functional feeding groups at the six sampled sites. Only active filter-feeders showed a significant difference in composition between arable and forested land (Table 7). Comparisons of all the six sampled sites showed a significant difference in composition among every functional feeding group, except for active filter-feeders (Table 7).

The distribution among saturated, monounsaturated and polyunsaturated fatty acids within the three species groups did not show strong differences between forested and arable land (Fig. 9). According to the PCA (Fig. 10) the composition of fatty acids within *Hydropsyche* spp. and within *Asellus aquaticus* at both sites with markedly different land use were similar, but within *Gammarus pulex* the fatty acid composition showed a slight difference. The first two PCA axes for the sample species and their fatty acid content (Fig. 10) explained 72% and 19%, respectively, indicating a strong collinearity among the variables. Fatty acids, which appeared in relatively large amounts, are shown in Table 8. The most common fatty acids were 18:1ω6, 16:0, 18:2 and 12:0. At both sites *G. pulex* was high in 18:1ω6 and 16:0, and *Hydropsyche* spp. was high in 12:0 and 18:1ω6, while *A. aquaticus* was high in 18:1ω6 and 18:1ω3 in forested land, and 18:1ω6 and 16:0 in arable land. Fatty acids of bacterial origin were not possible to identify, since these fatty acids were lacking in the standard for the fatty acid analyses.

Table 7. P-values of a general linear model ANOVA using adjusted SS for testing differences in abundance of different functional feeding groups both between arable and forested land and among the six sample sites.

Functional feeding group	Between arable and forested land	Among all six sample sites
Shredders	0.487	0.001
Grazers	0.206	0.000
Active filter-feeders	0.015	0.466
Passive filter-feeders	0.523	0.000
Detritus feeders	0.882	0.000
Predators	0.671	0.001

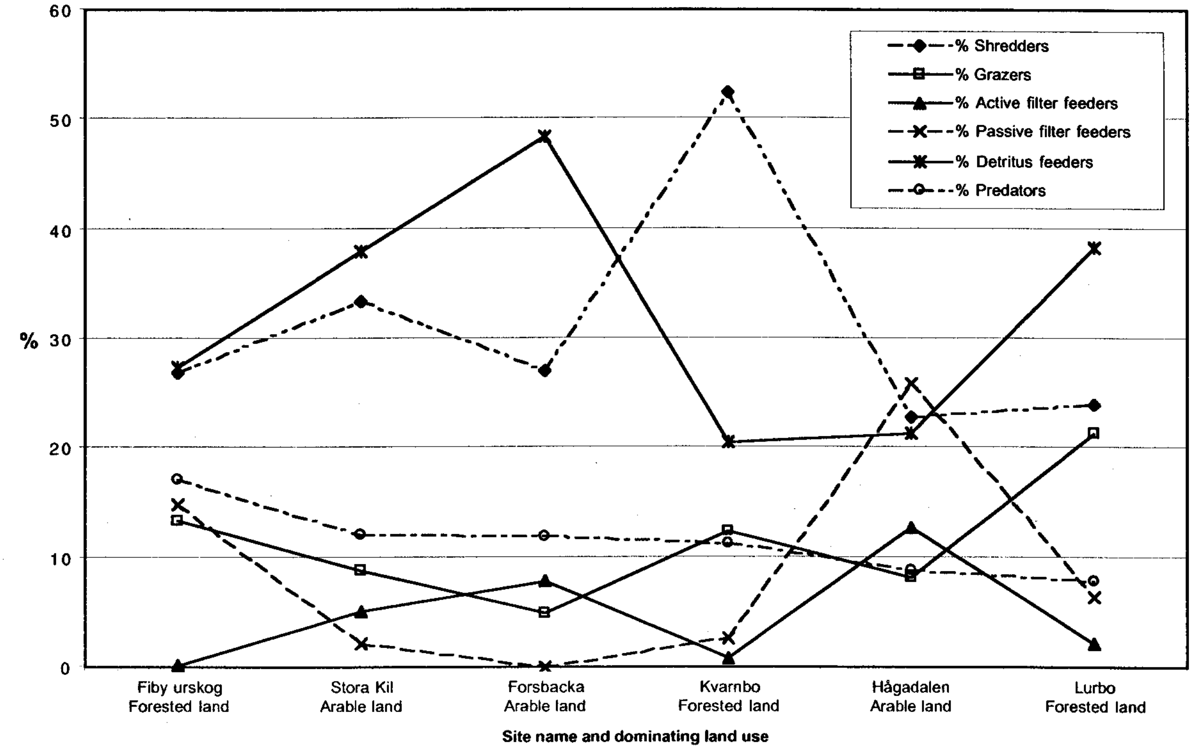

Figure 8. Relative number of individuals at different sites along *Hågaån* in % of total number at each site. The sites are arranged in the figure with upstreams to the left (Fiby urskog) and downstreams to the right (Lurbo).

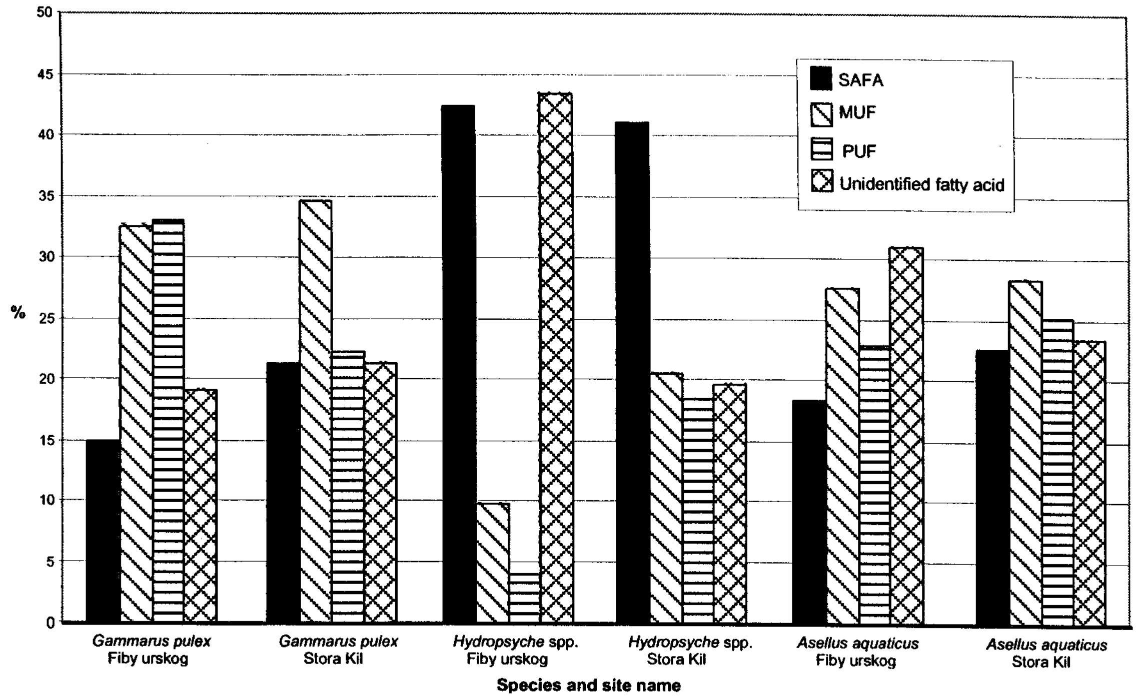

Figure 9. The distribution of saturated (SAFA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids in the three species at the two sample sites.

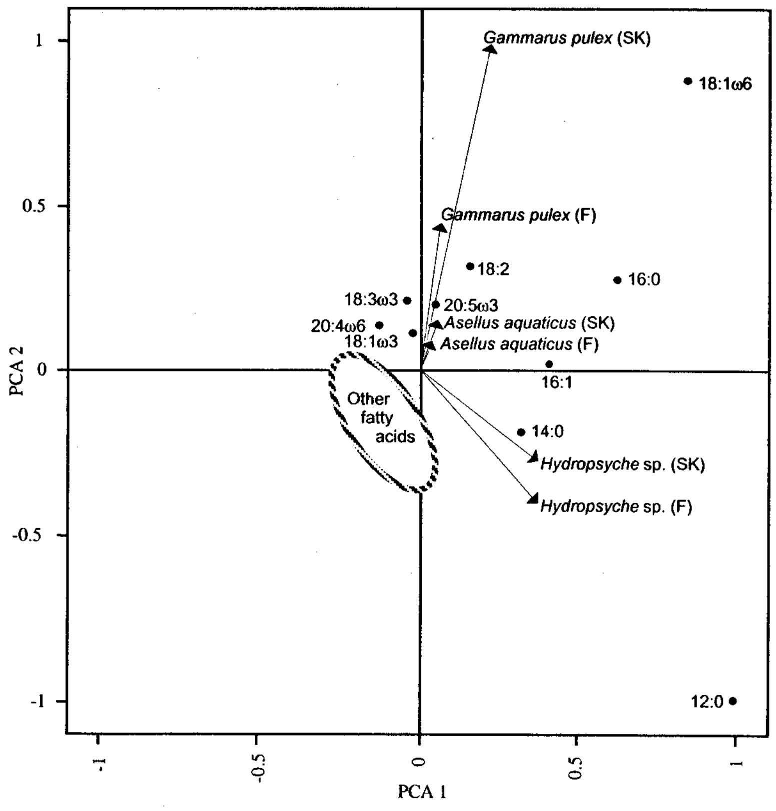

Figure 10. PCA ordination of fatty acids and three species groups along the first two principal component axes. F = Fiby urskog; SK = Stora Kil.

Table 8. Fatty acid composition of *Gammarus pulex*, *Hydropsyche* spp. and *Asellus aquaticus* at two sites in Hågaån, given as a percent of total fatty acid weight.

Fatty acid	Stora Kil (Arable land)			Fiby urskog (Forested land)		
	Gammarus pulex	*Hydropsyche* spp.	*Asellus aquaticus*	*Gammarus pulex*	*Hydropsyche* spp.	*Asellus aquaticus*
12:0	1.0	19.7	3.4	0.2	18.5	3.5
14:0	4.7	7.0	2.2	1.4	8.5	2.0
14:1	0.6	0.3	1.2	0.2	0.4	0.3
15:0	0.9	0.4	0.0	0.7	0.5	0.4
16:0	12.9	9.7	9.6	10.0	11.1	7.8
16:1	7.9	7.4	6.2	4.8	9.3	7.3
17:0	0.5	0.8	0.7	0.6	0.8	0.7
18:0	1.3	2.8	4.5	1.6	2.1	2.8
18:1ω6	21.3	12.6	13.5	23.1	10.4	9.1
18:1ω3	4.0	2.3	6.3	3.3	2.4	10.1
18:2	7.6	4.6	8.3	10.2	3.6	4.7
18:3ω6	0.3	0.3	0.0	0.4	0.2	0.4
18:3ω3	4.8	2.9	2.3	8.1	0.0	1.9
20:0	0.0	0.3	0.9	0.2	0.2	0.5
20:1	0.9	0.2	1.2	0.9	0.2	0.8
20:2	1.0	0.2	0.5	1.4	0.1	0.2
20:3ω6	0.2	0.1	0.5	0.2	0.1	0.0
20:4ω6	2.8	1.6	5.3	4.0	0.0	7.0
20:5ω3 (EPA)	5.0	6.2	6.6	6.1	7.2	6.9
22:0	0.3	0.3	1.5	0.3	0.0	0.8
22:6ω3 (DHA)	1.1	0.3	1.6	1.6	0.0	1.9
Other fatty acids	20.9	20.0	23.7	20.7	24.4	30.9

Discussion

Local scale environmental factors explained the largest part of variability among functional feeding groups in both lakes and streams. Regional scale environmental factors were, on the other hand, more important in lakes than streams, but geographical factors were also important. In PCA ordination of the functional feeding groups a north-south gradient was evident (Fig. 2 and 3). In both lakes and streams, for example, passive filter-feeders were more common in the northern parts of the country and active filter-feeders and predators were more common in the southern parts of the country. This was expected, since passive filter-feeders are more common in faster flowing water, while active filter-feeders are less dependent on current velocity. Fast flowing water is more common in the north, and slow flowing water is more common in the south.

Harding et al. (1997) studied the composition of functional feeding groups in New Zealand streams and showed that little discrimination was possible using functional feeding groups among ecoregions. For all functional feeding groups in the present study, the abundance of macroinvertebrates in streams was, in accordance with Harding et al. (1997), more or less constant among ecoregions (Fig. 6), but in lakes, a tendency of increasing mean abundances from north to south could be seen (Fig. 7). One explanation for this could be that lakes are relatively stable environments with well developed macroinvertebrate community structure controlled by biotic factors (e.g. competition, predation), while streams are less stable environments with strongly fluctuating abiotic conditions for the macroinvertebrates (e.g. stream velocity, substrate type). Magnuson and Kratz (1999) emphasized, however, the importance of considering lake and stream systems as an "*interacting network of heterogeneous patches related by a complex of processes and where differences in connectivity matter, and where location and scale matter*".

For lakes there was a clear and highly significant difference in abundance between the middle and southern boreal regions. This trend was not noted for streams. In this area a major ecotone, referred to as the *Limes norrlandicus*, is situated which is characterized by the southern distribution of the Swedish taiga and the northern distribution of oak and many other plants and animals (Gustafsson and Ahlén 1996). This likely indicates that geographical position plays an important role for the functional feeding group composition. According to the partial RDA analyses done here, the influence of regional factors (including geographical factors and ecoregion) seemed to play an insignificant role in accounting for the variation in functional feeding group community structure. In contrast, local scale factors explained most of the variation. Similarly, stepwise multiple regression and PCA also showed that habitat factors were important for explaining the variation in functional feeding group composition. For example, both substrate and vegetation seemed to be important descriptors of habitat types, and this may indicate the importance of leaf litter (e.g. Casas 1997).

Substrate and vegetation often differ with land use. The field study was done to test if the composition of functional feeding groups differed with land use. According to the stepwise multiple regression (Tables 5 and 6) and the PCA (Fig. 2 and 3), land use in the catchment area and in the riparian zone seemed to influence the functional composition of the macroinvertebrate community. Stepwise multiple regression showed that forested land seemed to be more important than arable land. This is possibly due to the often large amounts of substrate in the forests, which is important for some macroinvertebrates (Casas 1997). However, significantly differences between arable and forested land were not detected among the functional feeding groups in the present field study, except for active filter-feeders, which were more common at arable sites. Not finding a differences may, however, be an artifact of the stream selected for this field study, as even the sites classified as "forested" were nested within a landscape that is predominantly classified as arable.

According to Barlow (1966) and Hanson et al. (1983), the composition of fatty acids in insect tissues should differ with diet. The findings of this study support this conjecture. The fatty acid composition within both *Asellus aquaticus* and *Hydropsyche* spp. was similar at both sites (Fig. 10). *Gammarus pulex*, however, differed in fatty acid composition between the two sites. These findings indicate that the feeding behaviours of both *Asellus aquaticus* and *Hydropsyche* spp. are less dependent on site characteristics, whereas *G. pulex* seems to be more opportunistic in its dietary intake. For example, *Gammarus pulex* maybe change from acting as a shredder when surrounding land use is forested land to a detritus feeder when surrounding land use is arable land.

Moog's classification of macroinvertebrates into different functional feeding groups (Moog 1995) is one of several modifications of a classification used since 1973 (Cummins 1973). There are always uncertainties with classifications like this. Many species select for example a wide range of items as food resource and some of the organisms shift their diet during their ontogeny (Moog 1995). According to Rounick and Winterbourn (1983), the number of trophic transfers between bacterial production and a macroinvertebrate consumer can be one or many, leading to significant consequences for energy dissipation, and this may vary between water column and benthic habitats. Vannote et al. (1980) explained with the "River Continuum Concept" how the relative abundance of functional feeding groups changes from headwaters to river mouths. The river continuum hypothesis suggests that macroinvertebrates change downstream in response to changes in food supply (Vannote et al. 1980). In the present study the streams were relatively small and hence the river continuum concept is not entirely applicable. The concept was developed primarily for rivers where the variation of stream width is greater, which makes the concept less useful for conclusions in studies like this. In lakes, the richness and composition of fish communities is supported by differences in geomorphology of the landscape (Magnuson et al. 1998). Magnuson et al. (1998) emphasized that it is easier to predict richness and assembly of fishes in lakes connected via streams that differ along environmental gradients. A similar conclusion for macroinvertebrates is in the present paper not impossible.

The statistical methods used, both indirect (PCA) and direct (RDA) gradient analyses, complemented each other well. However, regardless of the technique used (ordination or regression) only a small portion of the total variance was accounted for, despite the large number of environmental variables used in the analyses. The finding that more variance was accounted for when analyses are run on community composition (Johnson and Sandin pers. comm) indicates that a certain amount of information is lost when macroinvertebrates are classified by feeding behaviour. These analyses performed here showed that local factors were important for both lake and stream communities. Hence, for future studies it would be of interest to concentrate more on the effect of substrate type on functional feeding group composition and adjacent land use.

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Appendix 1

Table 9. The procedure of partitioning variation in functional feeding groups (FFG) of macroinvertebrates in Swedish streams explained by three sets of environmental variables, regional (Reg), catchment (Cat) and local (Loc) by partial redundancy analysis (RDA).

Run	Responder	Environmental variable	Covariable	Eigenvalue
Total effect: Reg & Cat & Loc				
	FFG	Reg & Cat & Loc	No	0.397
Partial effect, combination 1: Reg and Cat & Loc				
1	FFG	Reg	Cat & Loc	0.027
2	FFG	Cat & Loc	No	0.369
3	FFG	Cat & Loc	Reg	0.277
4	FFG	Reg	No	0.120
Joint effect: Reg ↔ Cat & Loc = 0.120-0.027 ≈ 0.369-0.277 = 0.092				
Partial effect, combination 2: Cat and Reg & Loc				
1	FFG	Cat	Reg & Loc	0.035
2	FFG	Reg & Loc	No	0.361
3	FFG	Reg & Loc	Cat	0.274
4	FFG	Cat	No	0.122
Joint effect: Cat ↔ Reg & Loc = 0.361-0.274 = 0.122-0.035 = 0.087				
Partial effect, combination 3: Loc and Reg & Cat				
1	FFG	Loc	Reg & Cat	0.236
2	FFG	Reg & Cat	No	0.161
3	FFG	Reg & Cat	Loc	0.099
4	FFG	Loc	No	0.297
Joint effect: Loc ↔ Reg & Cat = 0.161-0.099 ≈ 0.297-0.236 = 0.061				

$$\begin{aligned}
&\text{Joint effect of Reg and (Cat and Loc)} = A + B + D = 0.092\\
&\text{Joint effect of Cat and (Reg and Loc)} = A + C + D = 0.087 \qquad (1)\\
&\text{Joint effect of Loc and (Reg and Cat)} = B + C + D = 0.061
\end{aligned}$$

$$\begin{aligned}
&\text{Pure Reg + Pure Cat + joint effect of Reg and Cat} = 0.027 + 0.035 + A = 0.099\\
&\text{Pure Reg + Pure Loc + joint effect of Reg and Loc} = 0.027 + 0.236 + B = 0.274 \quad (2)\\
&\text{Pure Loc + Pure Cat + joint effect of Loc and Cat} = 0.236 + 0.035 + C = 0.277
\end{aligned}$$

By solving equations (1) and (2), we obtain

$$\begin{aligned}
&\text{Joint effect of Reg and Cat} = A = 0.037\\
&\text{Joint effect of Reg and Loc} = B = 0.011\\
&\text{Joint effect of Cat and Loc} = C = 0.006
\end{aligned}$$

and

$$\begin{aligned}
&\text{Joint effect of Reg, Cat and Loc} = D\\
&= 0.092 - 0.037 - 0.011 = 0.044\\
&= 0.087 - 0.037 - 0.006 = 0.044\\
&= 0.061 - 0.011 - 0.006 = 0.044
\end{aligned}$$

Finally the total variation was partitioned into

$$\text{Total explained variance} = \overbrace{0.044}^{\substack{\text{Joint variation}\\ \text{Reg, Cat and Loc}}} + \underbrace{0.037 + 0.011 + 0.006}_{\substack{\text{Partial joint variation}\\ \text{Reg and Cat}\\ \text{Reg and Loc}\\ \text{Loc and Cat}}} + \overbrace{0.027 + 0.035 + 0.236}^{\substack{\text{Unique variation}\\ \text{Reg, Cat, Loc}}} = 0.396$$

Appendix 2

Table 10. The procedure of partitioning variation in functional feeding groups (FFG) of macroinvertebrates in Swedish lakes explained by three sets of environmental variables, regional (Reg), catchment (Cat) and local (Loc) by partial redundancy analysis (RDA).

Run	Responder	Environmental variable	Covariable	Eigenvalue
Total effect: Reg & Cat & Loc				
	FFG	Reg & Cat & Loc	No	0.439
Partial effect, combination 1: Reg and Cat & Loc				
1	FFG	Reg	Cat & Loc	0.012
2	FFG	Cat & Loc	No	0.428
3	FFG	Cat & Loc	Reg	0.224
4	FFG	Reg	No	0.216
Joint effect: Reg ↔ Cat & Loc = 0.216-0.012 = 0.428-0.224 = 0.204				
Partial effect, combination 2: Cat and Reg & Loc				
1	FFG	Cat	Reg & Loc	0.020
2	FFG	Reg & Loc	No	0.419
3	FFG	Reg & Loc	Cat	0.242
4	FFG	Cat	No	0.198
Joint effect: Cat ↔ Reg & Loc = 0.419-0.242 ≈ 0.198-0.020 = 0.178				
Partial effect, combination 3: Loc and Reg & Cat				
1	FFG	Loc	Reg & Cat	0.191
2	FFG	Reg & Cat	No	0.249
3	FFG	Reg & Cat	Loc	0.044
4	FFG	Loc	No	0.396
Joint effect: Loc ↔ Reg & Cat = 0.396-0.191 = 0.249-0.044 = 0.205				

Joint effect of Reg and (Cat and Loc) = A + B + D = 0.204
Joint effect of Cat and (Reg and Loc) = A+ C + D = 0.178 (1)
Joint effect of Loc and (Reg and Cat) = B + C + D = 0.204

Pure Reg + Pure Cat + joint effect of Reg and Cat = 0.012 + 0.020 + A = 0.044
Pure Reg + Pure Loc + joint effect of Reg and Loc = 0.012 + 0.191 + B = 0.242 (2)
Pure Loc + Pure Cat + joint effect of Loc and Cat = 0.191 + 0.020 + C = 0.224

By solving equations (1) and (2), we obtain

Joint effect of Reg and Cat = A = 0.012
Joint effect of Reg and Loc = B = 0.039
Joint effect of Cat and Loc = C= 0.013

and

Joint effect of Reg, Cat and Loc = D
= 0.204 – 0.012 – 0.039 = 0.153
= 0.178 – 0.012 – 0.013 = 0.153
≈ 0.205 – 0.039 – 0.013 = 0.153

Finally the total variation was partitioned into

$$\text{Total explained variance} = \overbrace{0.153}^{\substack{\text{Joint variation}\\ \text{Reg, Cat and Loc}}} + \underbrace{0.012 + 0.039 + 0.013}_{\substack{\text{Partial joint variation}\\ \text{Reg and Cat}\\ \text{Reg and Loc}\\ \text{Loc and Cat}}} + \overbrace{0.012 + 0.020 + 0.191}^{\substack{\text{Unique variation}\\ \text{Reg, Cat, Loc}}} = 0.440$$

Appendix 3

Table 11. Parameters in the stream and lake data sets used in statistical analysis.

Geographic scale	*Unit*
Altitude	m a. s. l.
Latitude	
Longitude	

Ecoregion scale	*Unit*
Ecoregion	classified 1-6

Catchment scale	*Unit*
Forest	classified 0-3^A
Arable land	classified 0-3^A
Mire	classified 0-3^A
Grazing ground	classified 0-3^A
Bedrock or shallow soil	classified 0-3^A
Alpine coniferous forest	classified 0-3^A
Alpine	classified 0-3^A
Urban	classified 0-3^A
Freshwater	classified 0-3^A
Roads and railroads^S	classified 0-3^A
Power-lines^S	classified 0-3^A
Enclosed area^S	classified 0-3^A
Catchment area	km^2

Riparian scale	*Unit*
Coniferous forest	classified 0-3^A
Deciduous forest	classified 0-3^A
Mixed forest	classified 0-3^A
Clearcut	classified 0-3^A
Heath	classified 0-3^A
Arable land	classified 0-3^A
Wetland	classified 0-3^A
Alpine	classified 0-3^A
Urban	classified 0-3^A
Other use of land	classified 0-3^A

Ecosystem scale	*Unit*
Ca	meq·L^{-1}
Mg	meq·L^{-1}
Na	meq·L^{-1}
K	meq·L^{-1}
SO_4	meq·L^{-1}
Cl	meq·L^{-1}
F	mg·L^{-1}
Si	mg·L^{-1}
Al^L	µg·L^{-1}
Fe^L	µg·L^{-1}
Mn^L	µg·L^{-1}
Cu^L	µg·L^{-1}
As^L	µg·L^{-1}
NH_4-N	µg·L^{-1}
NO_2+NO_3-N	µg·L^{-1}
Total N	µg·L^{-1}
Total P	µg·L^{-1}
Total organic carbon (TOC)	mg·L^{-1}
pH	
Water color	Abs (420 nm)
Conductivity	mS·m^{-1}
Exceedence of critical load	meq·m^{-2}·yr^{-1}

Habitat scale	*Unit*
Block (>200 mm)	classified 0-3^A
Cobble (60-200 mm)	classified 0-3^A
Pebble (20-60 mm)	classified 0-3^A
Gravel (2-20 mm)	classified 0-3^A
Sand (0.02-2 mm)	classified 0-3^A
Silt (<0.02 mm)	classified 0-3^A
Fine detritus	classified 0-3^A
Coarse detritus	classified 0-3^A
Emergent plants	classified 0-3^A
Floating leaved plants	classified 0-3^A
Isoetids	classified 0-3^A
Broad leaved submergent plants	classified 0-3^A
Fine leaved submergent plant	classified 0-3^A
Fontinalis	classified 0-3^A
Other mosses (not *Fontinalis*)	classified 0-3^A
Filamentous algae	classified 0-3^A
Total vegetation coverage	classified 0-3^A
Stream velocity^S	classified 0-3^B
Depth^S	m
Width^S	m
Inclination^S	m·km^{-1}
Lake area^L	km^2
Shading^L	classified 0-3^C

A = classified as percent coverage (0 = <5%, 1 = 5-25, 2 = 25-75%, 3 = >75%);
B = classified (0 = 0 m·s^{-1}, 1 = 0-0.2 m·s^{-1}, 2 = 0.2-0.7 m·s^{-1}, 3 = >0.7 m·s^{-1});
C = classified as percent sample area influenced by shading from trees and bushes (0 = <5%, 1 = 5-25%, 2 = 25-75%, 3 = >75%);
L = measured only in lakes;
S = measured only in streams

Appendix 4

Table 12. Number of individuals of each species or organism group found at the six sample sites in Hågaån.

	Number of individuals						
Species or organism group:	Fiby urskog	Stora Kil	Forsbacka	Kvarnbo	Hågadalen	Lurbo	**Sum**
Acroloxus lacustris	0	0	0	0	5	0	**10**
Anisus contortus	10	0	0	0	0	0	**20**
Asellus aquaticus	352	56	7	61	20	227	**1219**
Athripsodes albifrons	0	0	0	0	0	1	**1**
Baetis spp.	23	1	0	0	0	0	**48**
Ceratopogonidae	0	19	1	0	2	4	**48**
Chironomidae	156	323	35	1	43	4	**1120**
Corixidae	0	1	0	0	0	0	**2**
Elmis aenea	0	0	0	0	0	95	**95**
Ephemera vulgata	0	8	0	0	0	0	**16**
Gammarus pulex	544	1034	264	670	155	168	**5502**
Gastropoda, other	0	0	0	0	0	1	**1**
Glossiphonia complanata	1	8	7	0	1	0	**34**
Helobdella stagnalis	1	0	0	0	0	0	**2**
Hemerodrominae	0	0	0	3	0	4	**10**
Heptagenia fuscogrisia	25	10	0	0	0	3	**73**
Herpobdella octoculata	0	4	30	2	1	6	**80**
Hydracarina spp.	1	1	0	0	0	0	**4**
Hydropsyche spp.	110	68	1	24	27	100	**560**
Leptophlebia spp.	32	0	0	2	3	289	**363**
Limnius volckmari	0	0	0	2	1	153	**159**
Lymnea palustris	0	0	0	0	0	3	**3**
Nematoda	1	0	0	5	0	0	**12**
Neumora cinerea	1	0	0	1	0	11	**15**
Oligochaeta	17	205	193	1	12	78	**934**
Phryganea grandis	3	8	0	0	0	0	**22**
Physa fontinalis	0	55	0	0	2	0	**114**
Polycentropus flavomaculatus	0	0	0	0	0	2	**2**
Rhyacophila spp.	48	1	0	5	1	26	**136**
Sialis lutaria	1	1	0	0	1	0	**6**
Simulidae	179	9	0	3	126	34	**668**
Sisyra spp.	1	0	0	0	0	0	**2**
Somatochlora metallica	0	2	0	0	0	0	**4**
Sphaeriidae	3	89	51	6	67	21	**453**
Tanypodinae	180	48	1	2	8	8	**486**
Tipulidae	1	2	0	0	0	1	**7**
Turbellaria	0	0	0	0	0	2	**2**
Sum	1693	2042	641	794	542	1262	**12686**