ECOLOGICAL CHARACTERIZATION OF SURFACE WATERS IN THE PROVINCE OF OVERIJSSEL (THE NETHERLANDS)

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CONTENTS

STELLINGEN

1. Een ecologische typologie is een stuk gereedschap dat ontworpen is om de werkelijkheid waaraan zij is ontleend, verantwoord te kunnen beheren.

(dit proefschrift)

2. De hoofdfactoren die de verspreiding van de benthische macrofauna van zoete wateren in Nederland bepalen, zijn stroming, zuurgraad, zoutgehalte, dimensies van het water en frequentie en duur van droogvalling. Binnen dit patroon van hoofdfactoren zijn vervolgens het gehalte aan voedingsstoffen en de habitatstructuur bepalend.

(dit proefschrift)

3. De geleidelijke verdwijning van soorten over de laatste honderd jaar uit de Nederlandse rivier- en beekstelsels gaande van monding naar bron vindt binnenkort haar trieste dieptepunt als de typische bronbewoners verdwijnen ten gevolge van het doorslaan van fosfaat in de zandgronden.

4. Het "Nutrient Spiralling Concept" (Webster et al. 1983) is in natuurlijke laaglandbeken in Nederland van ondergeschikt belang omdat het merendeel van hun voedingsstoffen niet wordt opgenomen in het systeem maar slechts wordt getransporteerd.

Webster, J.R., Gurtz, M.E., Hains, J.J., Meyer, J.L., Swank, W.T., Waide, J.B. & Wallace, J.B. 1983. Stability of stream ecosystems. In: J.R. Barnes & G.W. Minshall (eds.), Stream ecology. Plenum Press, New York: 99-136.

5. Het "River Continuum Concept" (Vannote et al. 1980) is niet bruikbaar voor toepassing in het beekbeheer in Nederland, enerzijds vanwege het uitgangspunt dat de fysische variabelen van bron tot monding binnen een riviersysteem een continue gradiënt van fysische omstandigheden bieden en anderzijds vanwege het gehanteerde schaalniveau.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37: 130-137.

6. Het routinematig onderzoeken van de waterkwaliteit komt vaak neer op het vragen naar de bekende weg.

7. Met het begrazen, bekalken en bevissen staat het moderne natuurbeheer in Nederland terecht tussen landbouw en visserij in.

8. Met de aanleg van ooibossen in de rivieruiterwaarden zal de kans op het ontstaan van lokale steekmuggenplagen sterk toenemen.

9. Het verdwijnen van een enkele ogenschijnlijk onbelangrijke soort kan een domino-effect in de hele levensgemeenschap teweegbrengen. Dit maakt het zoeken naar een no-effect-level voor toxische stoffen op ecosysteemniveau vrijwel eindeloos.

10. Many ecological concepts are limited explanations of the biological reality around us. This limitation is brought about through dimensions of space and time and through the the limitations of definitions (May 1984).

May, R.M. 1984. An overview: Real and apparant patterns in community structure. In: D.R. Strong et al. (eds.), Ecological communities. Princeton Univ. Press, Princeton : 3-18.

11. Het invoeren van bronvermelding zal beleidsstukken beter verifieerbaar maken waardoor ook de juistheid en kwaliteit zullen toenemen.

12. In tegenstelling tot wat de naam suggereert is de rol van een onderzoekbegeleidingscommissie vaak meer volgend dan begeleidend.

13. Over de ecologie van de AMOEBE (Derde Nota Waterhuishouding) is nog weinig bekend.

14. Stellingen gaan het ene oor in en het andere uit.

Piet F.M. Verdonschot
Ecological characterization of surface waters in the province of Overijssel (The Netherlands)
Wageningen, 30 mei 1990.

VOORWOORD

Toen ik in september 1980 in dienst trad van de Provinciale Waterstaat in Overijssel, had ik de keuze uit twee opvattingen van mijn functie, enerzijds vragen en problemen behandelen die op korte termijn moesten worden opgelost of anderzijds mijn aandacht richtten op de ontwikkeling van een basis voor het oplossen van vragen en problemen. Het onderwerp van dit proefschrift toont aan dat ik voor het laatste heb gekozen. De subgroep Standaardisatie van de Werkgroep Biologische Waterbeoordeling heeft een belangrijk aandeel gehad in deze keus. De discussies rond de ontwikkeling van een indeling van oppervlaktewateren liepen vooruit op het beleid en stimuleerden mij deze weg in te slaan. Een belangrijke bijdrage aan deze discussies werd onder meer geleverd door Jean Gardeniers. Sjeng, je bent steeds bij het onderzoek betrokken geweest en je was een stimulans bij de gedachtenvorming rond typologieën.

Ook al was ik in de eerste jaren bij de afdeling Waterhuishouding een vreemde eend in de bijt, toch leidden mijn, soms eigenzinnige, keuzen tot een ecologisering van de waterstaat. Mijn toenmalige collega's brachtten steeds meer het geduld op te luisteren. Alleen Jan Laseur en Elly van Mourik behoefden niet te worden overtuigd, zij steunden het onderzoek vanaf het prille begin en zorgden ervoor dat mijn onderzoekersgeest in voldoende mate op de praktijk gericht bleef.

De uitvoering van monsterprogramma's, determinaties, bewerkingen en verslaggevingen als onderdelen van dit onderzoek waren niet mogelijk geweest zonder de inzet van een groot aantal studenten, stagiairs, gewetensbezwaarden en tijdelijke medewerkers. Ieder van hen dook, soms letterlijk, in een fysisch-geografisch watertype, Gerard Willemsen in de laagveensloten, Jan Janse en Daan Monnikendam in de vaarten, Bert Oude-Egbrink en Jos Notenboom in de bronnen, Wim Heyligers en Cyril Liebrand in de vennen, Rob Gerritsen in de meren en meertjes, Gertie Schmidt en Louis ten Cate in de beekbovenlopen, Paul Latour in de kanaalbeken, Ton Ruigrok in de slootbeken, Dwight de Vries in de sloten en Steef van Hoof in de rivier en riviertjes.

In september 1984 kreeg ik een aanstelling bij het Rijksinstituut voor Natuurbeheer en verplaatste de onderzoekbasis zich naar Leersum. De samenwerking met de provincie bleef en mijn opvolger aldaar, Hans ten Cate, stimuleerde met groot enthousiasme de voortgang van het onderzoek. Vanaf mijn komst hebben de medewerkers van de afdeling Hydrobiologie steeds hun directe en indirecte bijdrage aan de voortgang van het project geleverd. Met name Bert Higler vormde een positief kritische kracht achter de wetenschappelijke fundering van de op te stellen typologie. Met de komst van Joke Schot was ik verzekerd van een meer geordende laboratoriumorganisatie en kon ik een deel van de begeleiding van tijdelijke medewerkers aan haar overdragen. De aanpak van fysisch-geografische watertypen ging door en wel door toedoen van Leon Thijssen en Ingrid Meuleman voor de middenlopen, Bert Rademakers voor de benedenlopen, Peter van Leeuwen en Gertie Schmidt voor de kanalen, Reinder Torenbeek en Gertie Schmidt voor de tijdreekspunten, Henk Ketelaars voor de droogvallende watergangen, Henk Wegman voor de randmeren, Martijn Hokken, Pierre Verbraak en Ron Huls voor de zandwinplassen, Gert-Jan Gast voor de kolken en oude

rivierarmen en Robbert de Ridder voor de poelen terwijl Jan Buijs en Hans Bakker assisteerden bij de bemonsteringstochten.

Dan bleven nog veel restanten van niet-afgemaakte deelonderzoeken en achtergebleven determinaties over die keurig werden weggewerkt door Marie-José Ruiken en Walter Mommersteeg (watermijten) en Nico Rawee (oligochaeten). Een aantal moeilijk determineerbare organismen werden door verschillende specialisten geverifieerd.

De verwerking van de gegevens was een geheel apart hoofdstuk. In de eerste jaren droegen Onno van Tongeren, Jos Notenboom en Stan Tummers in grote mate bij aan het inzicht in de mogelijkheden van automatisering en verwerkingstechnieken. De uiteindelijke verwerking was niet mogelijk geweest zonder de inzet van Joke Schot bij de in- en uitvoer van kilometers computerpapier, de gegevenscorrecties van Elbert Brethouwer en Ton van Eijden en de uiterst deskundige begeleiding door Cajo ter Braak. Cajo, zonder CANOCO had dit produkt nooit tot stand kunnen komen.

De eerste ruwe manuscripten zijn door Bert Higler van zakelijk en helder commentaar voorzien. Cajo ter Braak waakte erover dat de complexe materie van de multivariate analyse eenduidig op papier kwam. Zijn persoonlijke inzet zorgde voor een verbetering van de manuscripten die zeker niet ophield bij de statistische aspecten. Prof. dr. C.W. Stortenbeker was mijn promotor en zijn commentaren maakten mijn manuscripten toegankelijk voor anderen. Prof. dr. W.J. Wolff was mijn co-promotor en zijn kritische inbreng heeft de laatste hindernissen voor de totstandkoming van het definitieve manuscript weggenomen. Jackie Senior corrigeerde uiteindelijk mijn steenkolen engels en Arjan Griffioen maakte met veel geduld de tekeningen.

Zoals duidelijk zal zijn, hebben velen een bijdrage geleverd aan de totstandkoming van dit proefschrift. Slechts sommige direct betrokkenen heb ik met naam kunnen noemen, andere medewerkers van zowel de Provinciale Waterstaat als het Rijksinstituut voor Natuurbeheer hebben eveneens ieder op hun eigen wijze een steentje bijgedragen.

Ralf en Jeroen jullie hebben nog geen andere vader gekend dan eentje die een proefschrift probeert te schrijven. Yolande, jouw steun vormde het belangrijkste element in het welslagen van dit werk. Je leefde mee met de frustraties en successen en vroeg nooit om de tijd die voor ons was bedoeld maar aan dit werk werd besteed.

Mijn bijzondere dank gaat uit naar al degenen die dit proefschrift hebben laten worden tot wat het nu is.

SAMENVATTING

ECOLOGISCHE KARAKTERISERING VAN OPPERVLAKTEWATEREN IN OVERIJSSEL

Veel oppervlaktewateren in Nederland ondergaan een voortschrijdende nivellering van de waterkwaliteit. Om dit proces van verarming tegen te gaan is een gedifferentieerde aanpak in het waterbeheer nodig. De regionale waterbeheerders vormen een geschikt bestuursniveau om deze aanpak te realiseren. Mede daarom is de provincie Overijssel in 1981 begonnen met het project 'Ecologische karakterisering van oppervlaktewateren in Overijssel (EKOO)'.

Het doel van het EKOO-project is het ontwikkelen van een regionaal ecologisch referentiekader van oppervlaktewateren in Overijssel, dat gebaseerd is op de macrofaunasamenstelling en dat als basis dient voor de ontwikkeling van een beleid ten behoeve van het waterbeheer en het natuurbeheer. Dit referentiekader dient met name als basis voor het opstellen van waterbeoordelingsmethoden en van normstellingen in relatie met menselijke gebruiksfuncties en typen oppervlaktewateren. Met de resultaten wordt tevens beoogd meer inzicht te verkrijgen in de structuur van macrofaunagemeenschappen. Een bijkomend doel van het project is het verder ontwikkelen van de typologische benadering in het waterbeheer.

De gepresenteerde typologische benadering is een combinatie van elementen uit de zonerings- en de continuumbenadering. De zonerings- en continuumbenadering zijn beide afkomstig uit het onderzoek aan stromende wateren. Bij de zoneringsbenadering wordt het stromende water onderverdeeld in zones terwijl bij de continuumbenadering het stromende water wordt gezien als een gradient. Bij de typologische benadering worden soortencombinaties beschreven als typen. Deze typen representeren binnen bepaalde waarden van milieuomstandigheden gemeenschappen, die in elkaar overvloeien. Om verscheidene redenen kan een type slechts op regionaal niveau (een regio met onder andere vergelijkbare meteorologische, geomorfologische en hydrologische kenmerken) worden ingevuld.

De studie is opgezet als een grofschalig beschrijvend veldonderzoek waarbij de te meten parameters zoveel mogelijk zijn gekwantificeerd. De macrofaunasamenstelling (taxonsamenstelling en abundantie) is gekozen als belangrijkste parameter. Daarbij zijn op elke monsterplaats ongeveer 70 fysisch, chemisch en biologisch relevante parameters bepaald. In totaal zijn 664 monsterplaatsen, verdeeld over ongeveer twintig fysisch-geografische watertypen, bezocht. Hiermee zijn alle regionaal van belang zijnde hoofdfactoren, in verscheidene combinaties en overgangsvormen, in de studie betrokken. De fysisch-geografische watertypologie is slechts gebruikt als praktisch handvat ten behoeve van de uitvoering van het veldwerk maar speelde geen rol bij het opstellen van de ecologische typologie. De ecologische typologie is ontleend aan alle verzamelde biotische en

abiotische gegevens.

De reproduceerbaarheid van het macrofaunamonster dat genomen wordt met behulp van het standaard macrofaunanet, is nader onderzocht. Deze in Nederland veelvuldig toegepaste monsternametechniek geeft slechts een semi-kwantitatief beeld van de meer abundante soorten die aanwezig zijn in een oppervlaktewater. Ongeveer 55% van de taxa aanwezig op het moment van de monstername wordt met deze techniek verzameld. De toepassing van het standaard macrofaunanet voor regionaal typologisch onderzoek is echter gerechtvaardigd, omdat de verschillen als gevolg van bemonstering over seizoenen dan wel verschillen als gevolg van de bemonsteringstechniek zelf veel geringer zijn dan verschillen tussen de beschreven watertypen. Er kan worden geconcludeerd dat de reproduceerbaarheid van een standaard macrofaunanetmonster voldoende is voor de gekozen typologische benadering.

Allereerst zijn de gegevens afkomstig van de beschrijvingen van de twintig fysisch-geografische watertypen gecombineerd in vijf hoofdgroepen. De combinatie van biotische en abiotische gegevens is voor elk van deze vijf hoofdgroepen statistisch bewerkt. Daarna zijn alle biotische en abiotische gegevens gecombineerd en als een geheel bewerkt om een uiteindelijke ecologische typologie te kunnen opstellen. Voor dit doel zijn multivariate analysetechnieken geschikt. Verschillende multivariate analysetechnieken (clusteranalyse en canonische ordinatietechnieken) zijn toegepast om groepen monsterplaatsen te beschrijven in termen van taxonsamenstelling en gemiddelde milieuomstandigheden. De indeling in groepen monsterplaatsen op basis van multivariate analyseresultaten is in combinatie met informatie over de ecologie van de taxa handmatig bijgesteld en verfijnd. De resulterende groepen monsterplaatsen met bijbehorende macrofaunagemeenschappen worden cenotypen genoemd.

De helocrene bronnen zijn verdeeld over zes cenotypen. De belangrijkste verschillen tussen deze cenotypen kunnen worden gerelateerd aan de hydrologie (duur van droogvalling) en de zuurgraad. Daarbinnen blijken de hoeveelheid voedingsstoffen en/of de hoeveelheid organisch materiaal differentiërend te zijn. Elk cenotype bevat verschillende microhabitats. Deze microhabitats kunnen, op twee uitzonderingen na, worden gerelateerd aan de duur van droogvalling. De beide uitzonderingen zijn gerelateerd aan respectievelijk de bronkop en de bronbeek. Sommige onderzochte bronnen lijken waarschijnlijk nog sterk op de natuurlijke referentiesituatie voor helocrene bronnen. De belangrijkste bedreiging voor helocrene bronnen is de invloed van de mens op de chemische samenstelling van het grondwater. In het waterbeheer dient de aandacht dan ook allereerst hier naar uit te gaan.

De beken zijn verdeeld over elf cenotypen. De belangrijkste verschillen tussen deze cenotypen kunnen worden gerelateerd aan de dimensies, het 'beekkarakter', de duur van droogvalling en de mate van belasting met organisch materiaal. Alle beken worden in meer of mindere mate door de mens beïnvloed. Vooral de regulatie van beken heeft grote gevolgen gehad voor de beeklevensgemeenschappen. Slechts 2% van de totale lengte aan beken bezit nog een min of meer natuurlijk 'beekkarakter' en een daarbij behorende macrofaunagemeenschap. Deze 2% zijn slechts bewaard gebleven als gevolg van hun geografische ligging op steile hellingen. In het algemeen dient het waterbeheer zich te richten op het herstel van de fysische en hydrologische eigenschappen van beken.

De sloten zijn verdeeld over elf cenotypen. De belangrijkste verschillen tussen deze cenotypen kunnen worden gerelateerd aan de dimensies, de duur van droogvalling, de zuurgraad en de stroomsnelheid. Daarbinnen blijken de hoeveelheid voedingsstoffen en/of de hoeveelheid organisch materiaal differentiërend te zijn. De taxonsamenstelling van een sloot blijkt een gecombineerde weergave te zijn van het successiestadium in ruimte (vorm van het profiel) en in tijd (rijpheid). Hierdoor bestaat een overlap in de taxonsamenstelling tussen de verschillende cenotypen. Sloten zijn kunstmatige ecosystemen die vooral zijn gelegen in agrarische gebieden (dit betekent een toevoer van voedingsstoffen) en afhankelijk zijn van menselijke ingrepen (schonen, baggeren). Bij het ecologisch beheer van sloten dient men rekening te houden met de vorm van het profiel, het successiestadium en de menselijke ingrepen.

De rivieren, kanalen en randmeren zijn verdeeld over elf cenotypen. Deze cenotypen vertonen grote overeenkomsten in taxa (meestal opportunisten) en milieuomstandigheden. De grote dimensies van de stromende, lijnvormige wateren hangen samen met een groot afwateringsgebied. Grote wateren fungeren dan ook als verzamelbak van voedingsstoffen, organisch materiaal en toxicanten. Dit veroorzaakt een voortdurende stress op het ecosysteem en waarschijnlijk het verdwijnen van veel oorspronkelijke soorten. De voortdurende stress overheerst ook de werking van natuurlijke hoofdfactoren zoals stroming en dimensies. Slechts enkele taxa zijn nog karakteristiek voor een deel van een rivier of een dimensionele gradient in een kanaal.

De poelen en kleine meren zijn verdeeld over elf cenotypen. De belangrijkste verschillen tussen deze cenotypen kunnen worden gerelateerd aan de duur van droogvalling, de zuurgraad, de vorm en de hoeveelheid voedingsstoffen. Vooral de vier cenotypen waarover de stilstaande, neutrale poelen en kleine meren zijn verdeeld, vertonen onderling grote overeenkomsten in taxonsamenstelling. Deze cenotypen vertegenwoordigen een webvormig continuum waarin de dimensies (relatie tussen breedte en diepte), de voedingsstoffen en de samenstelling van de bodem (vooral het laagveen) domineren. De belangrijkste menselijke beïnvloedingen zijn wijzigingen in de hydrologie, verzuring en eutrofiëring.

Cenotypen beschreven voor de vijf hoofdgroepen van fysisch-geografische watertypen kunnen elkaar sterk overlappen. Daarom dienen alle biotische en abiotische gegevens ook in samenhang te worden bewerkt. Opnieuw is hiervoor clusteranalyse en canonische ordinatie toegepast. Na elke ordinatie zijn hiervoor de eerste twee resulterende assen gebruikt. Vervolgens zijn de herkenbare cenotypen afgesplitst en zijn de resterende data opnieuw bewerkt. Op deze wijze zijn uiteindelijk 42 cenotypen onderscheiden. Deze cenotypen zijn door middel van de ecologie van de typerende taxa en de waarden van de belangrijkste milieuvariabelen beschreven.

De onderlinge relaties tussen de cenotypen worden weergegeven in een hierarchisch dendrogram en een web van cenotypen (Figuur 11.1). Het hierarchisch dendrogram van cenotypen toont aan dat onder andere de cenotypen in midden- en benedenlopen van gereguleerde beken, kleine rivieren, sloten en enkele middelgrote, min of meer stilstaande wateren, alle met hypertrofe, mesosaprobe omstandigheden, een groot aantal overeenkomende taxa bezitten. Blijkbaar vermindert menselijke beïnvloeding (zoals regulatie van beken, lozing van afvalstoffen en intensieve agrarische activiteit in het stroomgebied) het relatieve belang van de natuurlijke hoofdfactor stroming in stromende wateren en van de natuurlijke hoofdfactoren dimensies (vorm en diepte) en bodemtype in stilstaande wateren, wat in beide gevallen eveneens leidt tot een verarming in de macrofauna.

Het web van cenotypen geeft de onderlinge positie, de overgangen tussen cenotypen (het continuum) en de belangrijkste milieugradiënten weer. De vier hoofdfactoren in deze typologie zijn 'beekkarakter', zuurgraad, duur van droogvalling en dimensies.

Om een water, zelfs subjectief, te beoordelen is het noodzakelijk dit water te vergelijken met andere wateren in verschillende omstandigheden. Voor deze beoordelingsschaal is een referentie nodig. Deze referentie hoeft geen weergave te zijn van een eindstadium in een successie of van een oorspronkelijke toestand maar dient een toestand weer te geven waarmee een richting voor verbetering wordt aangegeven. De gepresenteerde regionale ecologische typologie biedt een handvat om de mogelijke ontwikkelingsrichting naar de referentie van een water aan te geven. Voor de keuze van de oorspronkelijke referentie kan gebruik worden gemaakt van informatie verkregen uit studies aan minder beïnvloede wateren zoals natuurlijke beken, oligotrofe vennen, mesotrofe oude rivierarmen, en dergelijke.

Er worden een aantal voorbeelden gegeven van mogelijke toepassingen van de regionale ecologische typologie in het waterbeheer. Omdat de factoren in het web van cenotypen op een beschrijvende studie zijn gebaseerd, is voorzichtigheid geboden indien het web in voorspellende zin wordt gehanteerd. De typologie moet gezien worden als hulpmiddel dat samen met de juiste ecologische principes dient te worden toegepast ten behoeve van het waterbeheer. Het is een basis die gebruikt kan worden voor onder andere het monitoren en beoordelen van de waterkwaliteit, het aangeven van potenties van wateren en het opstellen van randvoorwaarden bij het beheer en de herinrichting van wateren.

SUMMARY

Nowadays many surface waters in The Netherlands tend to become ecologically uniform with the same mediocre quality. A differentiated approach to water management is necessary to stop this process of impoverishment of aquatic ecosystems. In The Netherlands the provincial authorities represent the appropriate level at which this differentiated approach to water management can be put into practice. Such an approach has been realized by the Department of Water Management of the Province of Overijssel. As a part of this approach the project 'Ecological characterization of surface waters in the province of Overijssel (EKOO)' was formulated in 1981.

The aims of the EKOO-project are to develop a regional ecological characterization of surface waters based on macrofauna composition and to reach a better understanding of the variety and the structure of the macrofauna communities present in the waters of the province of Overijssel. The project thus provides knowledge of aquatic ecosystems on a regional scale and a basis for the development of water management policies. An additional aim of this study is to develop the typological approach used in water management.

The typological approach used can be interpreted as an integration of the zonal concept and the continuum concept. Taxon combinations will be described as types. Within a limited range of environmental conditions, these types are representative of communities, but at the same time they together form a continuum. Due to hierarchical relations between major environmental variables (master factors) and evolutionary and historical factors, a type can only be described within a biogeographical region.

The study was designed as a qualitative survey but organized as much as possible along quantitative lines. Macrofauna composition (taxon composition and abundance) was chosen as a basic parameter. About 70 variables that were considered physically, chemically or biologically relevant, were measured at each sampling site. In total 664 sites were sampled, distributed over about twenty physico-geographical water types. These twenty types include all the major environmental variables relevant to this region; they overlap in abiotic features. The physico-geographical water typology was used as a practical tool for carrying out the survey, but was not used in obtaining the ecological typology. The ecological typology was derived from the collected biotic and abiotic data alone.

A study on the reproducibility of the standard macrofauna sample was carried out. The standard pond net macrofauna sampling technique used in The Netherlands appears to present only a semi-quantitative picture of the more common taxa. With this technique only about 55% of all the taxa present at a site at the moment of sampling were collected. However, when the standard pond net was used for a regional typological study it appeared that seasonal differences as well as inconsistencies due to sample technique were of little significance compared with differences between types. It was concluded that the

reproducibility of a macrofauna sample is sufficient for typological purposes.

For data analysis, the twenty physico-geographical water types were combined into five main categories. The abiotic and biotic data were processed for these five main categories. Later, all the data were processed together to obtain an ecological water typology for the province of Overijssel. Multivariate analysis techniques are appropriate in data analysis for typological purposes. Different multivariate analysis techniques (cluster analysis and canonical ordination) were used to derive and describe site groups in terms of taxon composition and mean environmental conditions. Sites intermediate between groups were manually relocated by using information from other sources (e.g. literature) about the ecology of the constituent taxa. The resulting site groups were termed cenotypes.

Six cenotypes were distinguished among helocrene springs. The main differences between the cenotypes were related to hydrology (mainly duration of drought) and acidity. Furthermore, the nutrient content and/or the load of organic material differed between related cenotypes. Each cenotype contained its own microhabitat group(s). The microhabitat groups, except for two, were associated with the duration of the drought period. The other two groups were associated with the spring source and the spring stream, respectively. The natural reference situation for helocrene springs probably resembles some of the actual helocrene springs investigated. The most important human activities causing disturbance are those which cause changes in the chemical composition of the groundwater. The management of springs should be directed at this factor.

Eleven cenotypes were distinguished among the streams. The main differences between the cenotypes were related to dimensions, "stream-character", duration of drought and the load of organic material. All the streams were more or less influenced by human activities. Stream regulation, especially, has caused a dramatic change in the taxon composition. Only about 2% of the total length of streams is still more or less natural in 'stream-character' and its corresponding community. These 2% are only preserved because of their geographical position on the steepest slopes. In general, efforts at improvement of the ecological character should be directed at the physical and hydraulic conditions.

Eleven cenotypes were distinguished among the ditches. The main differences between the cenotypes were related to dimensions, duration of drought, acidity and current. Furthermore, the nutrient content and/or load of organic material differed between related cenotypes. It is illustrated that the taxon combination found in a ditch reflects a stage of succession in space (profile structure) and time (maturity). Therefore, an overlap in taxon combination between cenotypes occurred (continuum). Ditches are artificial ecosystems which mainly occur in cultivated areas (which implies eutrophication) and depend on regular human interference (cleaning, dredging). The ecological management of ditches should be based upon the relation between profile structure, succession stage and human interference.

Eleven cenotypes were distinguished among the rivers, canals and large lakes. They showed great overlap in taxa (mostly opportunists) and in environmental circumstances. Increasing dimensions of the line-shaped more or less running waters go together with an increasing drainage area. These large-sized water bodies function as collectors of nutrients, organic material and toxicants. This results in chronic stress and probably the disappearance of most taxa occurring originally. The chronic stress also overrules the natural master factors of current and dimensions. Only a few taxa are still characteristic for the reach of a river or the gradient in size of canals.

Nine cenotypes were distinguished among the ponds and small lakes. The main differences between the cenotypes were related to duration of drought, acidity, morphology and nutrient load. In particular, the four cenotypes within the group of stagnant, pH-neutral ponds/lakes showed an overlap in taxon compostion. These cenotypes represent a web-shaped continuum dominated by dimensions (relation of width to depth), nutrient load, and bottom composition (especially mesotrophic peat). The most important processess induced by men are acidification, eutrophication, and changes in the original hydrology.

Cenotypes of different main physico-geographical watertypes can be very similar. Therefore they should be combined or rearranged. This is done by processing all abiotic and biotic data together. Again, cluster analysis and canonical ordination were applied. After each ordination along two axes, the distinctive cenotypes were removed and the remaining sites were reordinated. Through this progressive removal of groups of sites, finally, 42 cenotypes were distinguished. Some notes on the ecology of the typifying taxa and the most important environmental variables were made for each cenotype.

The mutual relations between the cenotypes are shown in a hierarchical dendrogram based on biological similarity as well as in a web of cenotypes (Figure 11.1).

The hierarchical dendrogram shows, among others, that a group of cenotypes related to middle and lower reaches of regulated streams, small rivers, ditches and some of the medium-sized, more or less stagnant waters, - all hypertrophic, mesosaprobic environments -, has a fair number of the macrofauna in common. Apparantly, human activity (e.g. by regulation of streams, discharge of wastes and agricultural activity in the watershed) leads to a decreasing role of the factor current in running waters and the factors dimensions (in fact shape and depth) and bottom type in the stagnant waters and leads to an impoverishment of the macrofauna.

The web of cenotypes illustrates the mutual position of the cenotypes, the transitions between the cenotypes (the continuum) and the major environmental gradients. The four most dominant factors are 'stream-character', acidity, duration of drought, and dimensions.

To evaluate a given water body, even subjectively, it is necessary to compare it with other water bodies in different states. This scale of evaluation needs a reference water. The reference water is not necessarily an endpoint of succession nor a pristine situation, but it should at least represent a situation that can be used to indicate the desired direction of improvement. In choosing the reference communities for water management one must focus on communities present in waters where major environmental conditions are less disturbed. Such waters are the undisturbed streams, the oligotrophic moorland pools, and the mesotrophic old meanders cut off from streams.

The regional ecological typology presented (Figure 11.1) offers a tool for establishing the developmental direction from a community observed in the field towards the reference community. It is also a tool to determine the reference community for a particular water body. Because the factors in the web of cenotypes are a result of a descriptive study, the web cannot be used without caution as a predictive tool; the factors are purely indicative. The typology and associated ecological concepts are a tool to help solving water management problems. It is a basis, among others, for monitoring and assessment of waterquality, it indicates potential capacities of surface waters and it provides guidelines for management and restoration of surface waters. May it be serve to the advantage of the environment around us.

1. INTRODUCTION

1.1 Background

Until recently man has more or less taken for granted the 'self-maintaining' character of his environment. A major reason will have been that his environmental manipulations only affected local balances. Hence, in the first half of this century biologists only dealt with local or partial environmental problems. During the last decennia, however, it has become evident that not only local but also regional, national and even global balances are being affected (Odum 1971).

Environmental problems have become more and more obvious, especially in a densely populated and highly cultivated and industrialized country like The Netherlands. Around 1970, the growing awareness of the environmental problems resulted in the first steps towards improvement. In that year, the Dutch parliament passed an act which aimed at a reduction of the organic pollution of surface waters (Ministerie van Verkeer en Waterstaat 1975). Within ten years, many purification plants were improved or established all over the country. Since then, effluents and waste water are subject to water quality standards, based on oxygen and ammonium concentration and the biological oxygen demand. The organically polluted waters definitely improved in that period. On the other hand in the same period, the still undisturbed or anthropogenically only slightly disturbed aquatic ecosystems became increasingly impoverished through (secondary) eutrophication, diffuse sources of pollution, regulation of streams, acid atmospheric deposition, changes in (ground-)water level, input of water from the polluted river Rhine, etc. (e.g. Gardeniers & Tolkamp 1985, van Dam 1987, Klapwijk 1988). Most of these human influences affected not only the variables related to the load of organic material but other abiotic variables in the aquatic ecosystem as well.

Despite all the efforts to improve the water quality in the period 1970-1980, the overall water quality, and thereby the overall quality of aquatic ecosystems, remained low. Due to the increased demands made by human activities, different water types tended to resemble each other more and more. Hence, the reduction of organic pollution from point-sources did not result in the expected improvement. This was because the approach chosen only tackled a small part (the organic wastes) of the problem and the solution chosen only dealt with a technological aspect.

Furthermore, an impoverishment of more or less undisturbed ecosystems may be assumed to have taken place through the growing isolation and/or the decrease of area of these ecosystems. The area and degree of isolation of a refuge (like a nature reserve or an undisturbed pool) together allow a certain equilibrium between immigration and extinction of species. An increase of the distance between two habitats of a species results in a reduced immigration rate. A decrease of the habitat area results an increase of extinction and thus in a reduced number of species. Increasing isolation and decreasing area both cause taxa to disappear (MacArthur

& Wilson 1963, den Boer 1983).

Water quality management should not only be directed to the component H_2O and dissolved substances but to the quality of the complete aquatic environment, which on its turn is related to the conditions in the entire drainage or catchment area (Hynes 1970, Lothspeich 1980, Cummins et al. 1984). This approach is gradually becoming accepted at a national level as well as at an international level (Persoone 1979, Higler 1988). Thus in 1980, the Dutch government adjusted its policy of 1970 and stressed the importance of not only taking direct care of human health but also of protecting material and ecological interests against the effects of water pollution. "The relation between human impact and water pollution will be seen from an ecological point of view. The knowledge that surface waters are ecosystems - this means systems in which living organisms play an important part - even when these waters are man-made or disturbed, makes it possible to describe this relation in a more logical and coherent way" (translated from Ministerie van Verkeer en Waterstaat 1981).

To stop the then still continuing process of impoverishment of aquatic systems and to prevent all surface waters becoming ecologically uniform with the same average 'grey' quality, a water management policy differentiated according to the ecological properties of the water bodies, had to be put into practice. Therefore, in 1985, the national government further adjusted its policy and formulated, - from an ecological point of view -, aims which were based on the interaction between major functions for human society and water types; a differentiated water management policy. This development from the limited scope of the organic wastes approach towards one in which several functions for human society are considered together can only be achieved by means of an ecological approach (Golterman 1976). So far, these aims have not yet been put into operation. Thus, the main question now is how to translate this ecological approach into practical management.

In The Netherlands, the national government formulates the national water quality policy but provincial authorities have to put this policy into practice. The provincial authorities, therefore, represent the appropriate level at which to integrate ecological knowledge and functions for human society into a coherent water management policy. In 1981, the department of water management of the Dutch province of Overijssel started such an approach and formulated the project 'Ecological characterization of surface waters in the province of Overijssel (EKOO)'.

1.2 Aims of the study

The aims of the EKOO-project are to develop a regional ecological characterization of surface waters based on macrofauna composition and to gather a greater understanding of the variety and the structure of the macrofauna communities present in the waters of the province of Overijssel. In this way the project provides knowledge of aquatic ecosystems on a regional scale (with an emphasis on the relation between water types and the impact of human activities) and a basis for the development of policies, particularly for water management, nature management and nature conservation.

An additional aim of this study is to explain and develop the typological approach in water management and to make a contribution to its methodological basis.

1.3 Presentation of the results

The aim (Section 1.2) and the design of the study (Section 1.4) are defined first because these are important for deciding on an appropriate sampling technique (Chapter 4).

In Chapter 2 a consistent terminology and some definitions within a frame that follows from broad theoretical considerations on typology will be given. One of the most important aspects of typology or, more generally, of ecology is the community concept. The community is an arbitrary entity. Therefore, conditions and criteria should be formulated which are not influenced by the objections against the artificial recognition of communities or, more generally, of ecological entities. In Chapter 2 these conditions and criteria are formulated to make the entity 'type' functional within the aim of this study.

Chapter 3 describes the area to be studied and introduces the materials and methods used.

One of the major aspects of this study is the reproducibility of the standard pond net sample. Hence, Chapter 4 deals with aspects of presence, abundance, space and time of a standard pond net sample.

The large amount of data made it less efficient to process all the data at the same time. Therefore, a priori, physico-geographical water types were distinguished (see Section 1.4.2) and the field work was executed on each type separately. Closely related physico-geographical water types were, at a higher hierarchical typological level, combined into five main physico-geographical water types. Data processing took place for these five main water types (Table 1.1) as described in Chapters 5 to 9. These chapters have a comparable structure:

- a general introduction to the main physico-geographical water type described,
- a description of the results of multivariate analysis and the validation of these results based upon the knowledge of the ecology of the typifying taxa,
- a discussion on the ecological validity of the resulting provisional site groups and the presentation of provisional cenotypological relations between these site groups.

After the main physico-geographical water types have been analysed and translated into provisional ecological water types, Chapter 10 presents the final ecological water typology for the province of Overijssel. The relation between the water types presented will be discussed with respect to the environmental factors that cause the distinction between the different types.

Chapter 11 will indicate which environmental variables can be managed in order to influence these factors.

Table 1.1 The main physico-geographical water types in the province of Overijssel, The Netherlands.

Helocrene springs	: Helocrene springs and spring streams
Streams	: Small streams
	Upper and middle reaches of streams
	Regulated streams
	Temporary watercourses
Rivers and canals	: Lower reaches of streams
	Small rivers
	Rivers
	Regulated rivers
	Canals
	Lake IJssel
Ditches	: Ditches on clay, sand, peat and in fenland
Pools and small lakes	: Moorland pools
	Pools
	Dike ponds
	Sand-, peat- and clay-pits
	Ox-bow lakes
	Small lakes
	Ponds

1.4 Design of the study

1.4.1 Considerations and background

Warren et al. (1979) introduced 'a conceptual framework on living systems theory' and stated five conceptual and methodological rules together with this framework. These rules were taken into account in the design of this study.

Rule 1. Only the structure of a biological community can be measured, its capacity and functioning can only be represented indirectly and incompletely.

Capacity, in the sense of Warren et al. (1979), is a strictly theoretical concept. It can never be measured directly; at best it can be described as a set of structures, each determined under a different set of environmental conditions. In the view of Warren et al. the surrounding environment has two phases: an 'effective environment' composed of conditions acting immediately and directly upon the biological community at any time during its existence, and a 'generative environment' composed of sequences of conditions leading to those in the 'effective environment'. As no natural ecosystem exists in a void, the biological community exists also in a third phase. This is a surrounding 'extra-environment' composed of conditions that for theoretical reasons (e.g. the relation is not known) or methodological reasons (e.g. the variable is not measurable) have been excluded from the 'generative and effective environment' but which may ultimately be important to the persistence of the biological community. The 'potential capacity' of a biological community is the predetermination of all possible states and, therefore, of all possible structures which can evolve from the present biological community, under all possible changes in the surrounding environment. In other words, 'potential capacity' determines the forms and amounts that will permit a certain structure and thus determines the possible environments within which a certain biological community can persist. The 'realized capacity' depends on the actual surrounding environment through time. Thus, the 'realized capacity' is determined by the forms and amounts actually provided, i.e. the actual environment determines the actual biological community that persists (Figure 1.1).

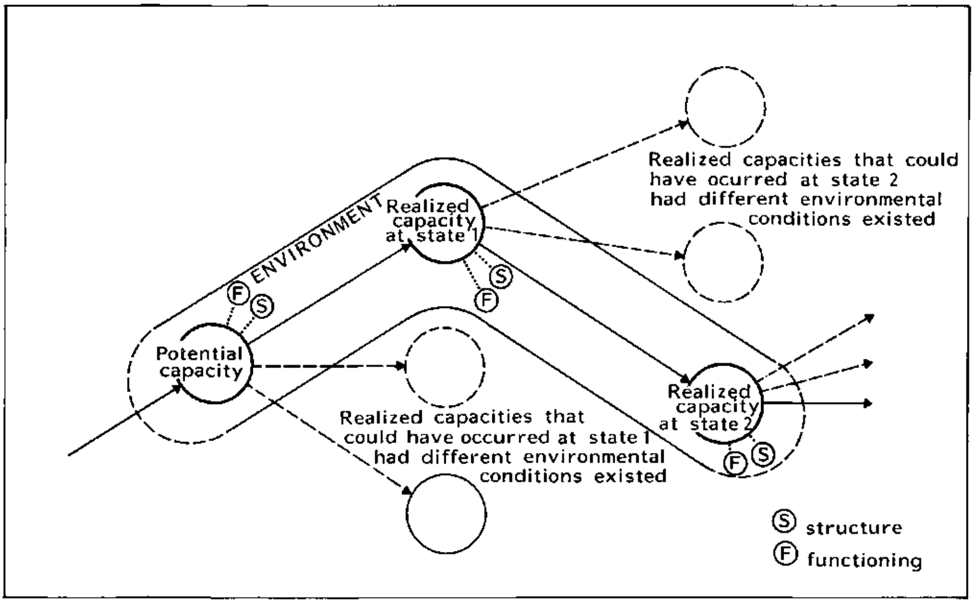

Figure 1.1 The capacity of a biological community. Each biological community possesses a potential capacity to behave in certain ways. The interaction of system capacity and the state of the environment determine the system structure realized at any moment. If the environment at any time had been different, a different sequence of capacities actually realized would have been the result (adapted from Warren et al. 1979).

Macrofauna composition (taxon composition and abundance) was chosen as the biotic structure parameter. It meets the first rule given by Warren et al. (1979), namely that only the structure of the system can be measured. Macrofauna was chosen because the many, well described and easily identifiable species are useful for the detection of changes in the external environment on the scale desired for this study. This is a consequence of the duration of their life cycles (on average 1-12 months) and the diversity of habitats they occupy (Hellawell 1978), especially because a number of representatives is more or less sessile. Furthermore, macrofauna is relatively easy to collect in the field and to process in the laboratory although the identification is time consuming. Hellawell (1978) concluded that macrofauna is likely to be the first choice when selecting a group for such a study. Macrofauna is defined as all invertebrate animals retained by a pond net with a mesh size of 0.5 mm. This mesh size boundary is used for practical reasons, since most of the sediments pass through such a net and the major part of the fauna is retained. Large representatives of meio- and microfauna groups (e.g. large nematodes, ostracods and daphnids) retained by the net were excluded from the analysis.

Rule 2. Measurements of the structure of a biological community without relevant measurements of its surrounding, level-specific environment are of little explanatory value.

An ecological characterization requires the measurement of biological parameters as well as the measurement of relevant environmental conditions to satisfy the second rule. In this study, potentially relevant variables were chosen from a set of about 135 physical, chemical and biological variables identified. Per site about seventy variables were actually measured, dependent on local circumstances (e.g. water type, site structure, presence of vegetation, etc.).

Rule 3. Explanation of the functioning of a biological community should take into account the structures and the functioning of its parts on successively lower levels of organization (e.g. taxa, populations, individuals) and cannot be based only on knowledge of its parts on the lowest level of organization.

The regional ecological characterization should be a basis for the development of water quality standards taking into account the ecological water types and the impact of important human activities. It should also be a basis for the development of a water quality assessment system. Therefore, ideally this study should aim at:

a. the characterization of macrofauna communities representative for natural, undisturbed ecological water types,
b. the characterization of macrofauna communities representative of ecological water types which are under disturbance/stress, dependent on the character and intensity of major human activities.

This division strongly depends on a subjective human evaluation and description of the natural conditions. It is artificial from an ecological point of view (each combination of environmental conditions implies a biological community which is no more or less natural than any other), but is necessary for policy purposes. The management of water requires a selection of those abiotic variables which are manageable and related to the different macrofauna communities. Therefore it is useful to separate natural and anthropogenically-induced processes.

The macrofauna communities of disturbed water types are related to the communities of natural, undisturbed ecological types. Information about the processes which influence the functioning of both these types of communities can be extracted from this relation. With this knowledge it is possible to purposefully influence the variables related to these processes. Therefore, information is needed about the ecology of the composing taxa, as the third rule states. It is then possible to relate the typifying taxa of natural and disturbed ecosystems in terms of water quality standards and to use them in an assessment system.

Rule 4. Explanatory generalizations pertaining directly to any level of organization of a biological community should contain at least one concept specific to that level and should subsume conceptual, methodological, or other sorts of indeterminacy that may exist with respect to lower levels of organization.

The choice of the typological approach, which is further explained in Chapter 2, satisfies the fourth rule. Typology is an approach useful at the community level and the presented methodology, which is based on classification and ordination techniques, uses the hypervolume model (Hutchinson 1957) as a theoretical concept. Hutchinson (1957) designates the entire set of conditions under which a species can live and reproduce as the fundamental niche (comparable to the above-mentioned potential capacity, but now for a species) and the actual set of conditions (abiotic and biotic) under which a species exists as the realized niche (comparable to realized capacity; Figure 1.2).

Rule 5. Perception and explanation of biological communities and environments are always related to its space and time dimensions and the components of the systems.

Rule five is important in stressing the relativity of collected results in space and time referring to the geographical limitations and indicating the importance, but also the limitations of, the chosen scale level. This is a general rule which probably applies to all ecological studies.

Because of practical and financial reasons the EKOO-project is limited mainly (besides the natural variation present) to aspects of organic pollution, eutrophication and stream regulation. Furthermore, the project was designed as a semi-quantitative study (Section 1.4.2) and most sampling sites were visited only once (Chapter 4).

1.4.2 The practical design

Ideally in a study like this one, detailed information should be gathered on the macrofauna and the important physical and chemical variables of each water body. But it was practically and financially impossible to investigate each water body: it was necessary to take

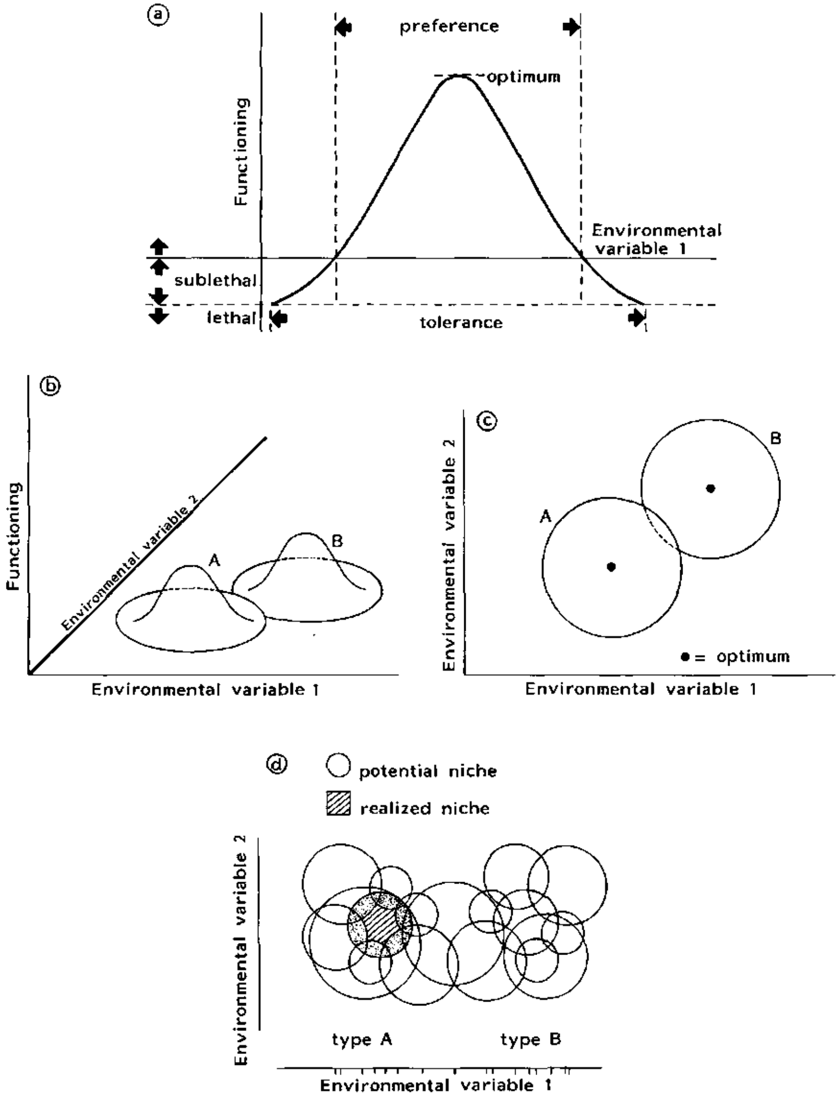

Figure 1.2 The functioning of a species with respect to environmental variables and other species. The top figure (a) illustrates the functioning of one species along one environmental gradient. Two figures showing the functioning of two communities, A and B, versus their positions along two environmental gradients, variables 1 and 2; (b) a three-dimensional figure with the functioning axis, and (c) the corresponding contour plot with the contours indicating equal functioning levels. (d) A theoretical model of the fundamental niche (dotted and cross-hatched) of a species and its realized niche (cross-hatched), which is a subset of the fundamental niche, after competition and complete competitive displacement due to six superior competitors, represented by the circles with dotted parts (adapted from Pianka 1978).

representative samples.

In general, two kinds of faunal survey can be defined; (1) quantitative surveys, and (2) qualitative surveys (Elliott 1971, Winterbourn 1985). A quantitative survey aims to estimate numbers of organisms per unit area, whereas a qualitative survey aims at discovering which species are present and trying to estimate their relative abundance. Quantitative sampling requires relatively large amounts of manpower and finance (Elliott 1971) and meets problems because of the limitations of sampling devices (Harper & Hynes 1972) and because of biological features of the organisms themselves (Resh 1979). In this study we wanted to cover a large area with many samples and a large variety of sampling sites. Because of financial restrictions, this necessitated simple field and laboratory procedures. This made a quantitative survey unfeasible, and hence a more qualitative survey was designed. To meet the desired accuracy, this qualitative survey was organized as much as possible along quantitative lines, and was thus semi-quantitative (Hellawell 1978).

As not all waters could be sampled, a reasonable number of representative samples over the area studied should be included (Elliott 1971). In random sampling, every sampling site has an equal chance of selection. But random selection of sites is difficult to achieve and can be extremely laborious (Elliott 1971). Therefore, sampling sites have been carefully selected (selective sampling). To this end the surface waters of the region studied have been divided *a priori* into about twenty physico-geographical water types (Table 1.2), based on the major environmental variables and on general ecological knowledge.

To design the sampling program for each of these physico-geographical water types, the exact locations, the major of pollution and disturbance (physical and chemical) influencing them, and the major human activities had to be established beforehand (often based on literature, information from water boards and field examination). Thereafter it was possible to select sampling sites (Figure 1.3) whereby representative sites of more or less natural and disturbed (related to the main human activities) circumstances were chosen. Then the sampling program was executed, the physical and chemical variables were analysed, the organisms were identified, and the data were prepared for interpretation (Chapter 3).

The division in physico-geographical water types does not affect the final typological outcome for the following reasons. The twenty types chosen include all the major environmental variables effective in this region and show mutually strong overlap in abiotic features. The large number of samples ensures that the effects of less obvious abiotic variables and biotic processes are also included. Furthermore, the scale of the sampling web is finer than the pursued scale of ecological types. These arguments will be verified by an elaboration of all data collected in Chapter 10. Therefore, since the chosen physico-geographical water typology is simply a practical tool to execute the survey, the resulting macrofauna community types provide the ecological typology.

Table 1.2 Characteristics of physico-geographical water types in the province of Overijssel, The Netherlands.

A. Linear shaped waters

Environmental variable/				
stream velocity	>20 cm/s	0-20 cm/s	0(5) cm/s	independent
stream direction	one-way	one-way	none/both ways	independent
bottom	sand with gravel, silt	mixed sand, silt	independent	independent
profile shape	irregular	regular	regular	(ir)regular
profile origin	natural	normalized regulated	regulated or dug	independent
dimension/				
w. 0.5-1.5 m	**SPRING(STREAM)**			
d. <25 cm	**SMALL STREAM**			
w. 1.5-10 m	**UPPER COURSE**	**REGULATED**	**DITCH**	**TEMPORARY**
d. 15-50 (100) cm	**MIDDLE COURSE**	**STREAM**		**WATER**
	LOWER COURSE			**COURSE**
w. 10-30 m	**SMALL RIVER**			
d. 1(3) m		**REGULATED RIVER**	**CANAL**	
w. >30 m	**RIVER**			
d. >1 m				

- w. = width, d. = depth
- Upper, middle and lower course are divided by dimension (respectively w. 1.5-3, 3-5, 5-10 m and d. 15-50, 15-50, 50-100 cm)
- ditches are subdivided in ditches on sand, clay, peat and in fenland
- canals are subdivided in canals and canals in fenland (w. >8 m, d. >50 cm)

B. Round or irregular shaped waters

Environmental variable/					
hydraulic regime	isolated	isolated	isolated communicating		communicating
profile origin	natural	dug	natural	dug	diking
bottom/					
sand	**MOORLAND POOL**	**SAND-PIT**			
peat	**MOORLAND POOL**	**MOORLAND POOL**			
clay		**CLAY-PIT**			
fenland				**PEAT-PIT (SMALL) LAKE**	
independent	**POND**	**POND**	**OX-BOW LAKE DIKE POND**	**POND**	**LAKE IJSSEL**

- (small) lakes are dug as peat-pits but were enlarged by wind and/or sea
- Lake IJssel (IJsselmeer) originated through diking a branch of the sea and reclamation of some polders
- if dimensions are small especially pools and ponds can be temporary
- dike ponds are formed after bursting of a dike

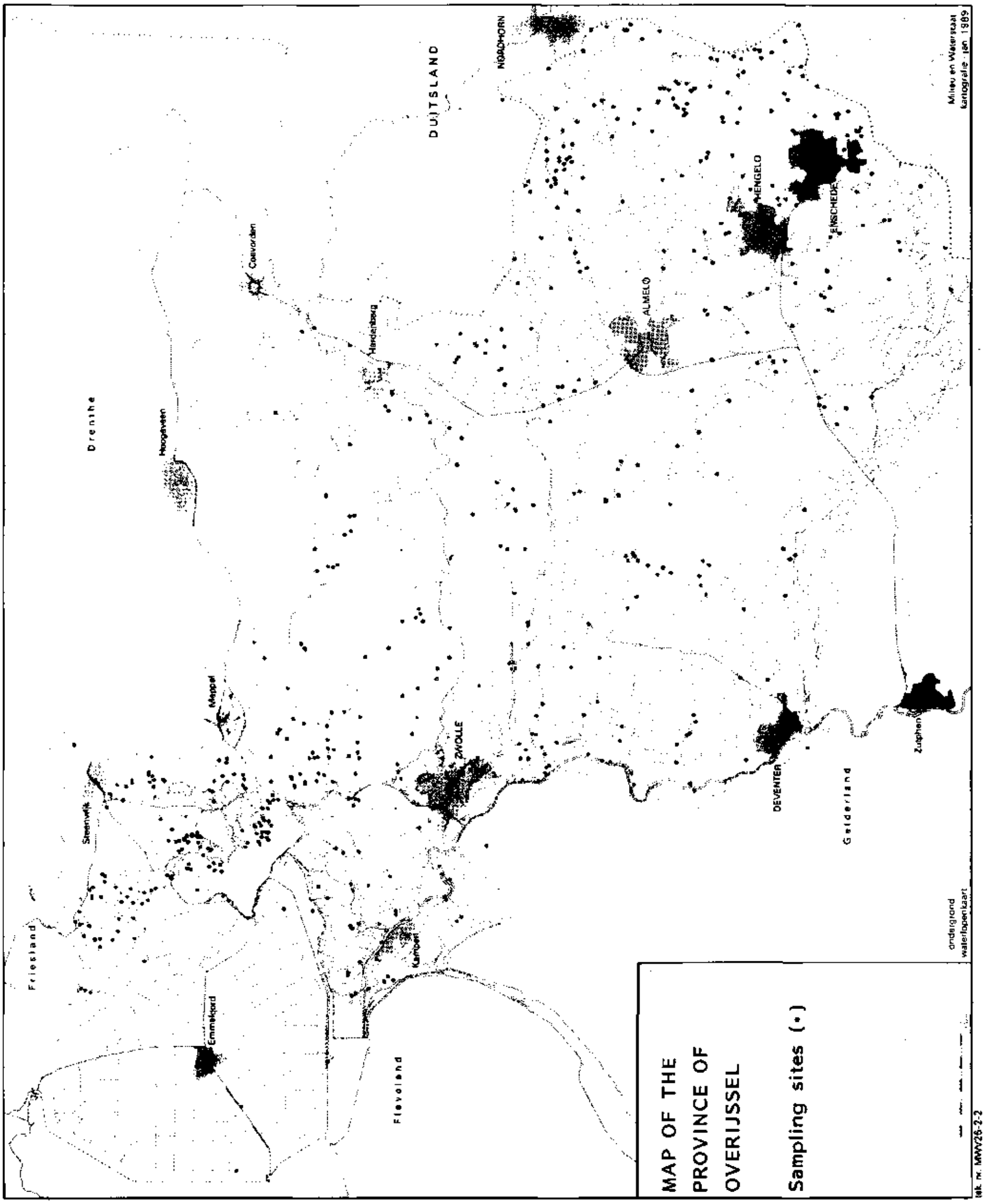

Figure 1.3 Map of the province of Overijssel (The Netherlands) with the sampling sites indicated.

2. ON THE PRINCIPLES OF TYPOLOGY

2.1 Introduction

This study tries to develop the typological approach in water management and to contribute to its methodological basis. Therefore, besides a practical plan (Section 1.4), a consistent typological concept is needed.

One of the most important concepts in ecology is that of the community (Section 2.2). Much of this concept originated in plant ecology. Here, besides the development of the community concept in general, also the development of this concept in the ecology of running and stagnant waters, respectively, (Sections 2.3 and 2.4) is briefly reviewed. The useful and often overlapping characteristics of all these developments were combined to form the basis for a general typological approach (Section 2.5). An introduction to the typological methods is given in Section 2.6. Since the typological approach is developed for water management purposes, some important aspects of the application of an ecological typology in this field are discussed in Section 2.7.

Persoone (1979) stated that there are two approaches utilized for classification systems, viz. the physico-chemical one with physical and chemical criteria, and the biological one based on autoecological or synecological data. Since the typological approach to be developed in this study should be ecological in nature, biotic and abiotic approaches are combined. An important restriction, however, is that this study mainly deals with structural and not with functional aspects.

2.2 The community concept, some general considerations

2.2.1 The classical community concept

In principle, the classical concept of a community (as an ecological entity) meets the following conditions and criterion:

Condition 1: There should be a definable environment.

Condition 2: There should be a measurable and reproducible qualitative and quantitative presence of organisms of different taxa.

Condition 3: There should be an interrelationship between environment and organisms, and between organisms mutually.

Criterion 1: There should be a method to discriminate between entities.

Ad Condition 1: Recurring combinations of species appearing under similar environmental conditions have led to the concept of community.

Thus, in 1877, Möbius described the community of an oysterbed and called it biocenosis. Ten years later Forbes (1887) identified the community as an ecological entity (a microcosm). Though Möbius' term biocenosis dealt with organisms of different species, it also included the environment: "...Gemeinschaft von Lebenden Wesen, für der durchschnittlichen ausseren Lebensverhaltnissen ..." (...community of living creatures, for the average environmental conditions...) (in Schwerdtfeger 1975). The confusion around the term 'community' is best illustrated by Newell et al. (1959) who used the terms habitat-community and organism-community. The first was defined as a natural association of organisms distinguished according to certain features of their environment, and the second as a regularly recurring combination of certain types of organisms (in Whittaker 1962). Tansley (1935), in criticizing the concept of the biotic community introduced the term 'ecosystem' for "the whole complex of organisms present in an ecological unit (the biome) together with all the effective inorganic factors of its environment". So, biocenosis as well as ecosystem imply a biotic and an abiotic component. In general, an ecological entity implies both biotic and abiotic features.

Ad Condition 2: The main reason why many authors (e.g. Illies 1955, Steffan 1965) accept the concept of community or cenosis is the (dynamic) constancy of certain species combinations in space and time. One should be careful, however, not to overemphasize this constancy because communities can be heterogeneous in both space and time, and still be called 'constant' by some authors. Beside the problem that different scales of observation result in different, but constant combinations of species, there are "natural" changes like cyclic succession and stochastic changes (Rigler 1975). Further, one should realize that seasonal changes are part of virtually any ecological entity.

The qualitative and quantitative aspects of communities can be approached in three different ways based on:

a. dominance,
b. presence/absence, and
c. abundance.

A community based on dominance is a group of sites combined on the basis of and defined by the dominance of one or more taxa. A dominant taxon may appear along a wide range of several environmental gradients; whereas subordinate taxa may be more restricted. It is even possible that two entities differ completely from each other in taxon composition except for their dominant taxon. Gersbacher (1937) used the term prevalents for the dominant taxa: "Prevalents are abundant or conspicuous animals which give aspect to the community throughout the year or the entire season, or are effective in changing the appearance of a habitat or community". This term is not adopted in our study.

In general, the advantages of the use of dominance to describe a community are that it is easily recognizable without intensive study, and that it reflects important quantitative relationships. Consequently, communities defined by dominance can be ecological units of different scales and exclusiveness. Hence, dominance is less useful for typology. Dominant taxa provide no firm basis for making objective decisions about the identity, scale and number of ecological units (Whittaker 1978, van der Maarel 1979).

The community based on presence/absence is a group of sites combined on the basis of and defined by the presence of or absence of one or more taxa. This type was already used by Lorenz (1858) for the characterization of communities. The first descriptions of communities in running water were also based on the presence or absence of species (Steinman 1907, Thienemann 1912, Lauterborn 1916-18). Presence was usually measured by the number of sites in which the taxon occurs, expressed as a percentage of the total number of sites studied. Examples are given by Lehman (1971) and Braukmann (1984).

The use of presence/absence to describe a community makes only use of qualitative data. In doing so information is lost. Therefore, the use of presence/absence is less useful for typology.

The transformation of data through weighing of abundance figures (the community description based on abundance) is important, especially in numerical treatments. Ricker (1934), in dealing with the ecological classification of Ontario streams, introduced arbitrary values (abundant, frequent, occasional and rare) denoting the occurrence per square foot. Ricker (1934) used this measure of abundance as well as the term characteristic species and/or association (without defining it) to describe his classes. Others have only used percentage classes to classify taxa within a community (Backiel 1964, Knauf 1969). Most authors distinguish about five classes of abundance and name them in a series from common to rare.

Several arguments plead for a transformation of abundance data:

- the semi-quantitative character of the sampling technique,
- the mathemathical background of the multivariate analysis techniques,
- the fact that the difference between 1 or 2 individuals being found is more significant than the difference between 101 and 102,
- the momentary character of sampling in relation to seasonal fluctuations in abundance of different taxa, and
- the different trophic levels and their differences in abundance of a macrofaunal community.

Arguments for the importance of transformation, or the special forms of differential weighing and standarization, in plant ecology are given by Noy-Meir (1973), Noy-Meir et al. (1975), van der Maarel (1979) and others. We conclude that the use of abundance to describe a community is useful for typology.

Ad Condition 3: The connection between species or "biozönotische konnexe" (Tischler 1951) is probably the most important aspect of the community. If a community is more than just a fairly coincidental aggregation of organisms, its surplus value lies in its web of interrelations. It is therefore surprising that the functional feeding group (Cummins 1973) is the only aspect of connection that has been applied to hydrobiological studies. Other aspects e.g. habitat or competition are still theoretical (Schwerdtfeger 1975).

Ad Criterion 1: The ability to discriminate between entities is strongly dependent on the criteria used to identify the entity. In classification discrete communities are defined. In the continuum concept all communities show a transitional pattern. The identification of an ecological entity as a series, in space and time (Allen & Starr 1973), of taxon combinations with corresponding environmental conditions which gradually merge into one another, integrates the concepts of classification and continuum. Recognizable taxon combinations occur but the boundaries between them have faded away. The necessity to discriminate between entities versus the reality of gradual transitions between entities is further discussed in Section 2.2.2.

The conditions and criterion mentioned above for the classical concept of ecological entities will be used to develop the typological approach.

2.2.2 Development of the community concept

As Werestschagin (in Thienemann 1925) stated at the beginning of this century "...jede Zergliederung der in der Natur herrschenden Untrennbarkeit ist künstlich, es zerteilt Dinge, die in der Natur, in der Wirklichkeit durch eine Reihe von Übergangen vereinigt sind" (...each classification of nature's indivisibility is artificial, it would divide parts which in nature, in reality are connected through a number of transitions). Although since then, many biologists must have been aware of the continuum in the surroundings they still tried to classify. Also Werestschagin distinguished entities "...um mehr Klarheit und Scharfe in die Begriffe zu bringen" (...to introduce more explicit and sharp-cut terms).

Identification and arrangement of ecological entities in general also has been defended as follows:

- -It is an intellectual challenge (Hawkes 1975).
- -It is necessary for understanding, describing and explaining the enormous diversity of the mixed species populations (du Rietz 1965).
- -It is helpful in comparing different waters worldwide (Pennak 1971).
- -It is of practical value, especially with respect to water management (van Deusen 1954, Hawkes 1975):
  - a. for utilitarian requirements (the first classification schemes were introduced by fishery biologists),
  - b. in predicting the effect of projected water management policies, and
  - c. in the assessment of water quality and pollution.

The concept of classification (Tansley 1920, Allee 1931) describes ecological entities as discontinuous parts. This is quite a static approach to ecological entities. Several hydrobiologists have stressed the disadvantages of this strict classification:

- A rigid framework creates a cage; we need freedom of thought (Macan 1961).
- Classes are arbitrary (Maitland 1966) and subjective (Armitage 1961).

Whether a community represents an artificial or a natural unit has been extensively reviewed for plant communities by Whittaker (1962). Whittaker (1962, 1978) concluded that a community is not a natural but an arbitrary unit in the sense that its definition is strongly influenced if not wholly determined by the plant ecologist's choices. Furthermore, a community has to be artificial because of the following two arguments (Ramensky 1926, Gleason 1926):

1. Species are distributed 'individualistically', each according to its own relationships to the biotic and abiotic environment; no two species are alike.
   The actual set of conditions (abiotic and biotic), under which an organism (according to its own genetic, physiological and population responses) exists, is termed its realized niche (Hutchinson 1957, Pianka 1978). Each species is supposed to occupy its own realized niche with its own fitness optimum and tolerance range (Figure 1.2). Sobolov & Utekhin (1979) called this ecological individuality. The general form for the distribution pattern of a species population along an environmental gradient is bell-shaped with a narrow or wide amplitude (Figure 2.1). The

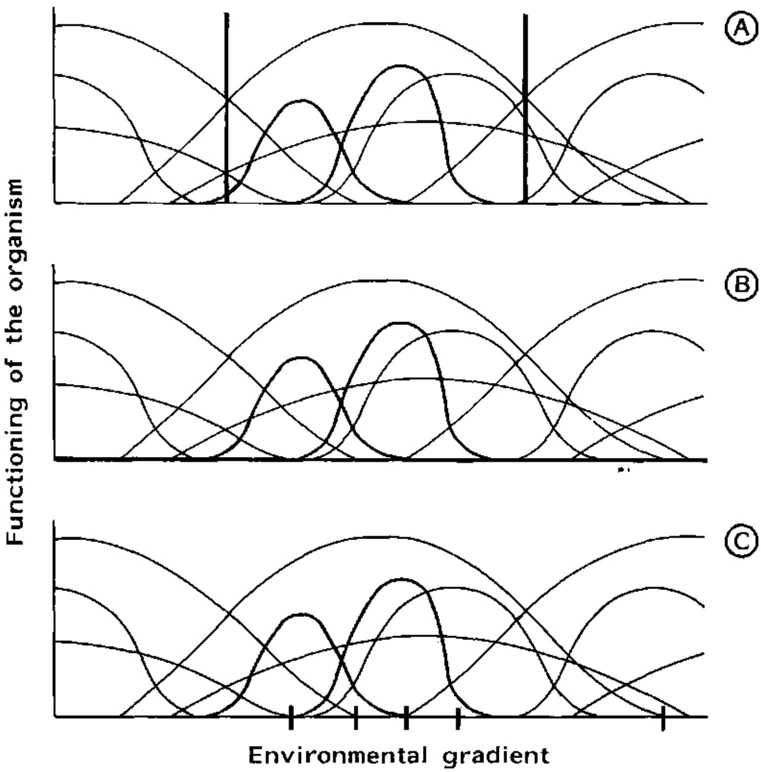

Figure 2.1 The distribution and the functioning of species along an environmental gradient according to a discrete (A), a continuum (B), and a typological (C) approach.

   centres of species populations are scattered along this gradient according to the principle of ecological or species individuality (Ramensky in Sobolev & Utekhin 1979).
2. Communities often merge into each other continuously.
   Species can be assigned to ecological groups (communities) by similarity of distribution, but the limits of such groupings are

essentially arbitrary. The logical outcome of ecological individuality is that species populations, with their scattered centres and tapering, broadly overlapping distributions along (a complex of) gradient(s), form a continuum (Whittaker 1978, Vannote et al. 1980).

These arguments have been taken into account in Section 2.5.

2.3 Developments in lotic ecology

2.3.1 Introduction

Running water ecosystems are open systems, in the sense that their continued operation depends upon a sustained input, "throughput" and output of energy, by virtue of the transport properties of running water (Fisher & Likens 1973). Due to this open character, running waters reflect the past and present structure and functioning of the catchment area (Illies 1955, Odum 1969, Lothspeich & Platts 1982).

Historically, considerable attention has been paid to spatial changes in the biotic and abiotic components along a water course (e.g. Thienemann 1912, Geijskes 1935, Huet 1949, Dittmar 1955, Verneaux 1973, Ward 1986). Numerous studies have been carried out on different benthic invertebrate groups (e.g. Hydracarina, Angelier 1952; Ephemeroptera, Macan 1957; Chironomidae, Lehmann 1971; Oligochaeta, Wachs 1967) or whole macroinvertebrate communities (e.g. Illies 1955, Maitland 1966, Chutter 1970, Wright et al. 1984). All these studies contributed major information on the distribution pattern of macrofauna along a river.

The classical concept, represented by extensive literature and reviewed by Illies & Botosaneanu (1963), Hynes (1970), Hawkes (1975) and Botosaneanu (1979), distinguishes classes or zones along a water course. Illies & Botosaneanu (1963) proposed a scheme for dividing rivers into zones (crenon, rithron, potamon) on a worldwide scale. Hynes (1970), however, critically discussed the existence of fish zones with respect to the causes of fish distribution patterns (Backiel 1964).

The concept of a water course as a continuum of communities is more recent (Armitage 1961, Vannote et al. 1980). The spatial pattern of the benthic community in interaction with its heterotrophic food resource is determined by the water flow. Organisms receive food from upstream and ingest part of it. The part that is not ingested nor used in metabolism is carried downstream and reingested by downstream organisms; thus cycling of matter does occur in streams but because of the flow the cycle becomes a spiral which is extended along the stream (Wallace et al. 1977).

Much has been published on the advantages and disadvantages of identifying stream communities. Such publications were often confused due to the absence or indistinct formulation of the goal of the study and of definitions of the concepts used. Hence, the advantages and disadvantages of both classical and continuum community concepts have been repeatedly discussed (Dudgeon 1984, Statzner & Higler 1985, Ward 1986).

This short introduction does not try to review and compare the large number of publications. It only wants to trace the historical development of the main concepts and to use this information for the development of our typological approach.

A large part of the early works on running waters (Steinmann 1907, Thienemann 1912, Lauterborn 1916-18, Behning 1928) are purely descriptive and based on two aspects of biology, namely zoogeography and ecology. Steinmann (1907) described the adaptations and habits of running water organisms. Thienemann (1912) introduced the words 'biotope' or 'biosynoecie' and biocenosis (after Möbius, 1877) in running water studies. Thus, without explicitly saying so, he introduced the first community concepts in running water ecology. He described the stream as a biotope which is composed of a number of biocenoses or communities. "So bildet im Bergbach die Organismenschar, die auf den heftig Überstromten Steinen sich aufhält, eine Lebensgemeinschaft fur sich, eine andere ist die Tierwelt der Pflanzen des Baches, eine andere siedelt im Sande und Schlamm ruhiger Buchten an. Doch ist keine dieser Biocoenosen ganz isoliert von der anderen, und wie sich Beziehungen von der tiefer gelegenen Bachstrecken bis zu den Quellrinnsalen knupfen, so sind auch z.B. die "Steinformen" und die "Pflanzenformen" des Baches durch enge und häufig recht interessante Beziehungen miteinander verbunden" (p. 8) (In streams different taxon combinations or communities occur on stones, vegetation, sand or silt. None of these communities is isolated from the other, they are related just as the communities of lower and upper reaches are related). With this description Thienemann introduced a community concept and indicated two problems, namely of scale and community boundaries. The scale problem is dealt with by introducing three levels: "Wie wir schon (S.8) erwähnten, stellt der Bergbach im ganzen einen Biotop oder eine Biosynoecie dar, und innerhalb dieses grossen Lebenskomplexes lassen sich wieder Gemeinschaften oder Biocoenosen sekundärer Art; Quellregion, Forellenbach, Aschenregion, und tertiärer Art; Steinfauna, Moosfauna, Fauna stiller Buchten unterscheiden" (p.46) (The stream as a whole represents a community within which secondary (spring, upper, middle and lower reach) and tertiary (stones, mosses, pools) communities occur). On the community boundary problem Thienemann (1912) stated: "diese Einheiten stehen nicht isoliert nebeneinander, sondern sind durch mannigfache Beziehungen verknupft" (p.46) (these entities are not isolated from each other but are related by a number of interactions). Another interesting feature in Thienemann's work is his "classification" of communities that was not based on samples taken in only one catchment area but on work by several authors in various other regions.

Many later authors have attempted, independently, to refine Thienemann's work. But most have centred their attention on only one of the three important aspects of scale (Section 2.3.2), community boundaries (Section 2.3.3), or regional approach (Section 2.3.4).

2.3.2 Scale

The problems of scale were discussed by Illies & Botosaneanu (1963) and Hawkes (1975). Illies & Botosaneanu (1963) recognized three scale levels, namely:

- classification of running waters as a whole,

- classification of running waters by zonation, and
- classification of running waters by the mosaic of biotopes.

Hawkes (1975) also arrived at a differentation in rivers, river zones, biotopes and synusia. Although Illies & Botosaneanu (1963) concluded that the three scale levels turned out to be three successive steps, neither they nor Hawkes (1975) discussed the interrelationship between these different scale levels. Other authors did recognize this mutual connection and described communities at different, sometimes hierarchical, levels (Willer 1925, Geijskes 1935, Albrecht 1953, Ditmar 1955). Most authors, in criticizing the classification of whole rivers or river zones, only accepted the community concept at its lowest level, the microhabitat (Shelford 1913, Muttkowsky 1929, Behning 1928, Gersbacher 1937, Nietzke 1937, Berg 1948, Marlier 1951, Kani 1981).

In a theoretical article on running water classification Steffan (1965) recognized three systems:

1. A geobiological-geographical system based on the distribution of species and communities in relation to large-scale environmental circumstances and the geological development of cenotopes. The basic unit is the biome.
2. A bio-cenological system based on the combination of species as a result of small-scale environmental circumstances and influenced by the impact and interdependence of species. The units are the biocenosis (river zones in the sense of Illies & Botosaneanu (1963)), and the chorio-, strato- and merocenosis (the habitat in horizontal direction, the habitat in vertical direction and the microhabitat, respectively).
3. A typological system based on the types of biocenoses and defined by the isobiocenoses which appear in different geobiological regions (although in climatically and edaphically similar biotopes) and which are characterized by similar combinations of species or by similar life forms.

Although the first two systems are strongly based on theoretical principles developed in plant ecology they clearly illustrate the importance of scale in aquatic (lotic) ecology. The third system is based mainly on methodological principles but it is also scale dependent. Steffan's (1965) main argument in accepting the concept of the biocenosis was "the (dynamic) constancy of species combinations in space and time". Within a certain biogeographical region each biocenosis or subdivision of it (chorio-, strato-, and merocenosis) can be characterized by those species (or semaphoronts) with an ecological range equal to the range of the biotope or subdivision (Steffan 1965). A semaphoront is an individual of a species within a certain time range (e.g. a life stage). Although this study often deals with semaphoronts, the term species will be used because it is most common practice.

In the past, it was easier to describe communities on a small-scale (microhabitats, often within one river) than on a large-scale (biomes). The advocates of the small-scale approach have already been mentioned. Probably the popularity of river zonation, a kind of middle-scale, is not due to scientific truth but to its practical value with regard to macrofaunal sampling techniques (or the scale of the macrofaunal habitats?) and aspects of water management.

Apparently scale is important in describing ecosystems. It appears that systems can be described on any scale and all scales are interconnected.

From this literature review it can be concluded that to describe ecological entities, one should choose a method which is scale-independent but one should outline, within the research objectives, on what scale a description is made.

2.3.3 Community boundaries

In the first half of this century there existed a strong belief in the concept of discrete communities. Although Thienemann (1912) had already recognized the problems regarding the community boundaries, some years later he still worked with this concept (Thienemann 1918). The concept of the community as an "organism" (Clements 1916, Allee et al. 1949, Tansley 1920) with various degrees of discreteness for its boundaries stands opposed to the concept of the community as an aspect of a continuum (Gleason 1926, Curtis & McIntosh 1951, Whittaker 1952).

In running water ecology the concept of discrete communities (especially zonation) was dominant for a long time. At least one reason was the great number of publications based on monographic studies of only one river or river-catchment (Lauterborn 1916-18, Behning 1928, Berg 1948, Illies 1952), and specialist studies based on only one or a few macrofaunal taxonomic groups (Voigt 1904, Boycott 1936, Nielsen 1942, Fittkau 1953). Indeed, it is easier to classify units of species aggregations within only one river or river-stretch than on a larger scale. Such a classification directly reflects the situation observed but has a restricted applicability.

Several other studies restricted to one river or catchment area have stressed that communities can only be described as large and small mosaic units which do not usually map directly into longitudinal gradients (Behning 1928, Hynes 1941, Berg 1948, Marlier 1951, Sowa 1965, Higler 1977). However, with our typological aim it is of little value to describe in detail each square centimeter.

Also a number of recent macrofauna studies in running waters were restricted to only one or a few taxonomical groups. Hynes (1970) reported on factors limiting the distribution of individual species. Each taxonomically related group of species and often each species reacts differently to these factors. Macan (1961) questioned whether a division of a river based on the ephemeropteran fauna was the same as those based on other groups. Zwick (1974) showed that this was not true for the river Fulda. Wachs (1967) found that the oligochaetes did not show any pattern of zonation in the river Fulda but that they were merely distributed in relation to differences in substrate.

Both taxonomical and regional/local monographic ecological studies led to many local zonations and classifications. But in the second half of this century more and more doubts arose (Funk & Campbell 1953, Macan 1961, Maitland 1966, Malicky 1978). "Because different factors are responsible for the longitudinal distribution of different taxa and because these factors, although partly interdependent, do change independently along the length of a river, the change in composition of the benthic biocoenosis would tend to show a transitional rather than a zonational pattern (Hawkes 1975)." Or as Schwoerbel (1961) pointed out "the wide variety of animals and conditions found in rivers suggests that no scheme of zonation will ever be found".

Armitage (1961) noted that "the community boundaries are subjectively chosen by the observer", although his data neither supported the concept of discrete communities nor, as he stated, "the continuum concept". Hynes (1961) found that "over some stretches, although no change is observed in the species present, their relative abundance changes along the length of the river thus reflecting a change in the ecological structure of the community". Gibon & Statzner (1985) found that there was no longitudinal zonation but a zone of faunistic transition in the Bandana river, a river without a well-defined source and a gentle slope. Also in estuaries sharp boundaries lack. Wolff (1973) concluded that 'undoubtly, in an ideal estuary with a perfect smooth salinity gradient the number of species would decrease and increase in a very regular manner' and that divisions in this gradient 'in all cases may be found at sharp discontinuities in the gradients of environmental factors'.

We conclude that until now no author has been able to prove the existence of sharp boundaries between ecological entities other than those due to abrupt environmental changes. We already concluded from a theoretical point of view that ecological entities merge into each other. Therefore, ecological entities can only be described by their centroids (optima in performance) not by their boundaries.

2.3.4 Region

From the discussion about scale (Section 2.3.2) it was already concluded that the use of a medium scale (the region) had practical advantages, especially for water management. Also problems around community boundaries could only be solved by restricting community descriptions to smaller scales (Section 2.3.3). There are other arguments to restrict typology to a regional scale.

The two most important factors separating natural ecosystems are climate and geology (lithology and morphology) (Lotspeich 1980). For example, Thienemann (1950), Illies (1955) and Hynes (1970) stressed the importance of the geographical factor. A third, historical factor important in the distribution of aquatic species in Europe is the Ice Ages (Illies 1966b). In combining these factors Illies (1966) divided Europe into 25 zoogeographical regions. Each region can be characterized by its own macrofaunal species composition. This is also true for the vegetation within the catchment areas (Schmithüsen 1968). The arguments which hold for these large regions also are valid on a smaller scale. For example, weather characteristics and geomorphology of our study area differ from those in other parts of The Netherlands.

2.3.5 Concepts in lotic ecology

The first concepts were introduced by Thienemann in 1912 (see Section 2.3.3) and refined in the following decennia. The river zonation concept published by Illies in 1955 presented a further refinement of Thienemann's ideas. After this article the number of publications on zonation increased markedly.

In recent years some other important concepts have been developed. The "nutrient spiralling concept" (Webster, in Wallace et al. 1977) suggests that the dynamics of benthic communities can be viewed as spirals of community interaction with the food resource. This concept was integrated in the "river continuum concept" (Vannote et al. 1980), which states that stream communities can be viewed as continua consisting of mosaics of population aggregations responding to the gradient of physical factors formed by the drainage network. Thus energy input and organic matter transport, storage and use by macroinvertebrates is regulated largely by fluvial/geomorphological processes. Petersen (1979) concluded that although the total process as a water mass flows downstream may be unidirectional in the continuum sense, the changes in community structure will depend not only on what a stream receives from the upstream section but also on its local surroundings (the catchment area) and the degree to which the community present is able to exploit the total input.

Statzner & Higler (1985) criticized the river continuum concept and suggested that communities respond to the physical characteristics of flow ('stream hydraulics') and that these characteristics often change rather abruptly. Where these changes occur species aggregations overlap and some species are found solely at the overlap. In general, when population continua are interrupted by abrupt environmental changes, species from neighbouring communities can pass the environmental boundary, producing a transitional zone, a marginal deviation (Sobolev & Utekhin 1979), an ecotone (Park 1948), or an edge effect (Whittaker 1953, Odum 1971). Whether these border zones are inhabited by their own characteristic species still remains a question.

In general, it can be concluded that classification and continuum are not contrary but supplementary concepts. Consensus on this issue of classes versus continuum can be reached by combining the pragmatic part of classification and the recognition of abstract conceptions with the realism of the multidimensional model in the continuum approach, i.e. the lack of boundaries.

2.4 Developments in lentic ecology

Forbes (1887) introduced the view of a lake as a microcosm, a unit which functions independent from its outer environment. This view strongly influenced the lake typologies published in the first half of this century (e.g. Thienemann 1918, Naumann 1919, Berg 1938). Lakes were classified on the basis of trophic status, amount of humic material, morphometry, oxygen content, sediment composition and successional stage ('maturity'). The early typologists realized the complexity of nature and considered a type as an abstract conception of an ideal state brought into a workable form (Naumann 1919, Thienemann 1925), i.e. they recognized the continua between the classes. Thienemann (1955) defined a type as an original image which cannot be found in nature but which each time is individually adapted from this image and which has its own spatial and temporal characteristics. Since the lake typology does not represent a classification of individual lakes, it is not a matter of right or wrong but of practical, scientific use (Thienemann 1955).

Later, the classification of lakes appeared to become less a tool and more a goal in itself. New categories and subdivisions of the original types were introduced (e.g. Lundbeck 1936, Jarneveld 1953, Brundin 1956) and classes became increasingly rigid.

However, more detailed studies on, for example, oligochaetes (Brinkhurst 1964), chironomids and molluscs revealed mosaics of local environments within a lake. These studies showed that lakes are not uniform and unchanging (constant) environments, but are made up of complex combinations of variables (Wiederholm 1980) such as morphometry (Johnson & Brinkhurst 1971), substrate (Northcote 1952), presence of predators (Brinkhurst 1965), organic matter content (Lellak 1965) and oxygen (Berg 1938). This approach of subdivision within a lake as well as the classification of lakes as a whole, suffers from the absence of both unifying criteria (often there is no agreement between the various typologies) and a clear definition of boundaries (Macan 1970). Brinkhurst (1974), in his review on the benthos of lakes, concluded "Perhaps we must recognise that lakes exist in a number of continuous serial arrays around some generalised average state, and that the whole range can be visualised as a multidimensional shape with many pointed rays diverging from a central core. The core lakes may be regarded as the harmonic series, and extending from these are groups of lakes in which one criterion or another begins to dominate its ecology".

This continuum, already stressed by the early typologists, is also stressed by more recent workers (Margalef 1958, Legendre et al. 1980, Zimmerman et al. 1983).

It is interesting to note the parallel development of lentic ecology with lotic ecology on the issue of classification versus continuum.

2.5 Type as an ecological entity

Before type is defined as an ecological entity some remarks are made on the role of abiotic versus biotic conditions in shaping a species community and about the differences between an animal and a plant community.

Types can be seen as assemblages of populations structured by the constraints of their abiotic environment and by biotic interactions. Such a type is the result of long-term evolutionary processes, biogeographical processes and adaptation. According to this view the types do not consist of coincidentally-occurring taxa but are structured through ecological processes. This view does not indicate the extent to which biotic or abiotic factors contribute to the structure. So, what is the role and importance of the biotic and abiotic interactions which determine the structure of a type? Both Thienemann (1925) and Naumann (1932) introduced typologies of water bodies based upon the idea that taxon distributions are controlled by abiotic factors. Macan (1961) argued, however, that most freshwater species have rather broad tolerance ranges and, therefore, the major abiotic factors are only decisive at the extremes of a range. Biotic interactions, especially competition and predation, seem to be far more important. Hart (1983) stated that competition indeed can play a critical role in determining patterns in a stream but 'there are still a number of questions to be solved'. However, Thiery (1982) concluded that the magnitude and periodicity of environmental variation, not just the mean values of a particular habitat, determine the community structure. Recently Wiens (1984) suggested that natural communities should be viewed as being arranged along a gradient from non-equilibrium to equilibrium. The major difference along this gradient is the range in environmental variation, which is dependent on the scale of space and time. Wiens (1984) further asked 'do process explanations (e.g. competition) apply equally well to distribution patterns of species and populations, as well as to individuals?'. According to him, patterns of species distribution are based on biogeographic and evolutionary processes and species do not interact competitively as units, only individuals do. So he feels that it is very unlikely that communities have biological interactions, if communities exist at all.

We conclude that the species themselves are subject to the environmental conditions present but that the biotic interactions can shape the species assemblages.

The main object of this study is the aquatic macrofauna. There exist fundamental differences between a virtually static (motionless) plant community with a relatively uniform structure and function of the individuals and the mobile (freedom of movement) animal community with a diverse structure and function of the individuals (Szelenyi 1955, Karaman 1964). Animals change their habitat during their life-cycle, so a habitat-type defined in terms of species assemblages shows seasonal changes. Animals can avoid suboptimal environmental conditions or even leave them, but on the other hand through their movement they can be caught outside their optimal environment. Animals change their habits and functioning during their life-cycle. Hence, animals can belong to different communities during their life-span. For example, the larva of a chironomid lives in the water, the adult in the air. This means that not the species but the semaphoront is the basic unit in animal ecology (Hennig 1950). A faunal community contains more taxa and life-forms with more interrelations than a plant community. These considerations must be taken into account in describing a faunal ecological entity.

In defining type as an ecological entity it is necessary to meet all conditions and criteria that resulted from the discussion around community concept, scale, community boundary and region in the foregoing sections.

Based on theoretical considerations Steffan (1965) introduced the typological approach, strongly inspired by methodological arguments. It is based on the zonal concept though taxon combinations are not well-defined communities but types which are, within a certain range of variation and under certain environmental conditions, representative of zones and grade into one another. His 'type' can be used for any ecological entity because it meets most of the objections against the artificial recognition of ecological entities.

A type is generally defined as the primitive form that one or more phenomena have in common. Examples of variables chosen to describe these phenomena are chloride (Venice System 1959), nutrients (Naumann 1932), macro-ions (Piper 1944; van Wirdum 1981), and hydraulics (Higler & Mol 1985). An ecological type is defined as the primitive form that one or more ecological phenomena have in common. So, an ecological type should be based on the conditions and criteria which define an ecological entity. These conditions and one criterion were already formulated in the classical community concept and are dealt with in Section 2.2. Based on the foregoing discussions the criterion given in the classical community concept (Section 2.2) should be extended:

There should be a method to discriminate between types (on the basis of environmental variables and the presence and/or abundance of organisms) whereby a clear boundary between the types is not required but only a recognizable centroid, and whereby each type may show a limited internal variation.

A clear boundary between types is not required according to Tüxen (1955), who interpretated phytosociological classification through the ideal concept of types, recognized in an empirical way from 'correlation concentrates', i.e. groups of correlated characters. That aspect which is evident and characteristic of a type is always its centroid (nucleus), not its periphery; types are not rigid compartments but foci in a field of variation (Westhoff & van der Maarel 1978).

The conditions and criterion given above and in Section 2.2 which have to be satisfied to describe an ecological type are independent of scale. But due to hierarchical relations between master factors and the evolutionary factor a type can only be effective within a biogeographical region and its actual description is therefore always scale-dependent (Section 2.3.4). A type can have a local, regional or global occurrence but it must always include the biotic and abiotic components.

Terms should be available to define the respective scale of an ecological type. For such a scale-dependent description the terms mero-, strato-, chorio- and biotype (Tischler 1949, Steffan 1965; Section 2.3.2) can be used. Each term is often indicated by the ending "-cenosis" for the biotic component and "-tope" for the abiotic one. In a typological approach the ending "-type" is recommended. In this study the ecological type, as defined above, will be used at the scale of a stream zone, an isolated pool, a section of a ditch, etc. Therefore, the ecological types distinguished should be called biotypes. A biotype is that structural part of an ecological entity (for example: a stream zone, an isolated pool) inhabited by a syntaxonomically differentiated community and physiographically recognizable. Examples are the river zones (Illies 1955, Huet 1949, Muller 1955, Schmitz 1957), the first-order biocenosis (Dittmar 1955), and the lake-types of Nauman (1932). As the word biotype was already defined for taxonomical purposes (among others Heslop-Harrison 1964) for this study the term cenotype will be used.

2.6 Typology methods

This section deals with the problem how to extract a typology from a data set. We used multivariate analysis techniques (Whittaker 1978, Gauch 1982, ter Braak 1987) for this. These techniques should be used when the main objectives are (Gauch 1982, Jongman et al. 1987):

- ordering of sites on the basis of species composition, either in classes or in a restricted-dimensional space, such that sites with comparable species composition aggregate and sites with different species composition separate;
- selection of environmental variables that can account for, or even explain, the ordering of the sites and, thus also the distribution of the species on which the ordering is based.

Ordination of data illustrates site and species relations in a low-dimensional space. The results are represented in a diagram, usually two-dimensional, in which similar sites or species or both are near each other and dissimilar entities are far apart (Gauch 1982). Cluster analysis involves grouping similar sites or species together in clusters. In ordination and clustering the biotic data are elaborated first. The results are then related to environmental variables. This is a two-step approach named indirect gradient analysis. By contrast, in direct gradient analysis, biotic data are described directly as a function of the environmental variables. The following table shows the different techniques:

Indirect gradient analysis	Direct gradient analysis
Classification	Regression
Ordination	Constrained ordination

Gauch (1982), Jongman et al. (1987) and others have dealt with the advantages and disadvantages of these techniques. Both classification and ordination are indirect methods which appear to be less effective in describing the relation between abiotic and biotic parameters than the direct method of regression analysis. But regression is less appropriate for typological purposes (Verdonschot 1987). Regression and ordination have been integrated into one technique called constrained or canonical ordination. In constrained ordination, the similarity of sites is not only based upon the occurrence of taxa and their abundance, but also on how these taxa are related to the environmental data. Both classification by clustering techniques and canonical ordination are useful for typological purposes. This is because it appears advantage to base similarities not only upon the occurrence of a taxon and its abundance, but also on the environmental description. The criterion given for the ecological type (Section 2.5) consists of two parts. Firstly, the possibility to discriminate between types (on the basis of environmental variables and the presence and/or abundance of organisms). This can be achieved by the use of clustering techniques. Secondly, the recognition of types within ordination whereby only a recognizable centroid but not a clear boundary between types is required, and whereby each type may show a limited internal variation. This can be achieved by the use of canonical ordination.

Different techniques are used because each has its own characteristics and eligible options, and therefore its own type of results. The results of these techniques are compared mutually and with existing information about autecology and/or synecology of the collected taxa, and/or about waters under comparable environmental conditions, to define the resulting types (Section 3.4.3).

In this study, types are recognized by their macrofaunal composition. Of all the characteristics (e.g. a diversity index, a saprobic index, the overall oxygen consumption) the full taxon composition of types is considered to be the best expression of the relations between the types and between them and the environment. Among those taxa some respond more sensitive to a given environmental condition than others (this is scale dependent). For practical purposes those taxa are selected whose ecological relation with the environment make them the most effective indicators at that geographical scale. The selection criterion is the typological weight that is defined in Section 3.4.3 and that is calculated for each taxon. Taxa which differentiate between types have a high typological weight and are indicated as typifying taxa. Typifying taxa can be completely confined to, prefer or have an optimum (expressed in presence and/or abundance) in a type. Typifying taxa will tend to be optimally present in the centroid of a type and decline outwards. Besides these taxa, also indifferent taxa (taxa without any preference for a type) and coincidental taxa (with an optimum outside the respective type) are defined and indicated. The coincidental taxa can be accidental intruders from neighbouring types or relicts from preceding conditions.

In general, the diagnostic value of taxa is geographically limited. Westhof & van der Maarel (1978) stated:

- Taxa present different ecological amplitudes or habitat relations in different parts of their distribution areas due to the heterogeneity in climate and geology.
- The distribution range of the taxon and the type can differ.

2.7 Typology and water management

In water management one mostly tries to influence the abiotic variables. Hereby, the distinction between natural and disturbance related variables is important. Water quality assessment asks for a qualification or even quantification of the relation between disturbance induced by human activity and the response of communities. In Section 1.4.1, the distinction between natural, undisturbed water types (reference-types) and disturbed water types (disturbance-types) is indicated. From an ecological point of view, the division is artificial. But some additional remarks will be made below, whether or not to distinguish between reference- and disturbance-types for practical water management purposes.

The following line of thinking is accepted in ecology and applied in management. Under natural, undisturbed (pristine) conditions a community will be in an equilibrial stage. This stage is seen as the optimally structured and balanced stage (after an initial developing stage in which primary succession takes place) of the community and is used as the reference-type. The degree of change of this community under the impact of a disturbance will depend upon its stability in relation to the degree and type of environmental disturbance. The length of the recovery process (secondary succession) towards the equilibrial stage, depends on the degree of change and the type of community.

The definition of the reference-type is derived from the concepts of succession and equilibrium, and stability. Succession is defined as a directional change towards maturity in the flora and/or fauna of an area over a moderate period of time during which period environmental conditions remain relatively constant. The reverse of succession is called retrogression (Sheehan 1984) which, for example, can be caused by human activity.

The recovery of a community after severe stress starts with a colonization phase. The colonization community consists of, more often highly resistant, opportunists (r-strategists). Later biotic interactions are re-established by specialists (K-strategists). It is important to realize that a community can recover to a different configuration; its path and resulting configuration are not always predetermined. Continuous stress (chronic harshness) of the environment will keep the community in a colonization stage. Stability can be defined as the constancy of the species composition of a community. It is demonstrated by its ability to recover from disturbances to which it is subjected (Webster et al. 1983). A number of concepts have been developed so far to describe the aspects of stability (e.g. inertia, elasticity, amplitude, hysteresis, malleability and persistence (Holling 1973, Orians 1975, Sheehan 1984)).

The definition of the disturbance-type is derived from the concepts of stress and disturbance. In general, the response of a community to a change in the abiotic environment (e.g. through input of a toxic pollutant) will be reflected in an alteration of its structure. Extremes in the environment (e.g. a very low pH, a long period of drought) and changes in the environment caused by external factors induce environmental stress upon an organism. In general, the response of an organism on environmental stress induced by human activity is similar to that caused by natural forms of stress (Thiery 1982, Sheehan 1984). Environmental stress is characterized by an infrequency of occurrence in space and/or time, and/or by the degree of deviation from the normal pattern. Pickett et al. (1989) refined the definitions of environmental stress and disturbance. He defined environmental stress as a change in the interaction maintaining a structure, caused directly or indirectly by an external factor, and disturbance as the direct impact of an external factor on an ecological entity within a structure. In practice, within one ecosystem both stress and disturbance may act at the same time on different scales, and be mutually interrelated.

Not only the ecological concepts themselves but also their applications to management raise questions. For example, artificial waters (e.g. due to man-made excavations or regulation of streams) illustrate the difficulties in applying ecological concepts. Already their existence is a consequence of human activity. Another example which illustrates the difficulties in applying the concept of succession is found in stagnant waters. Stagnant waters do not have a dynamic equilibrial state. The endpoint of succession in these waters is the terrestrial stage. Therefore, another concept should be used. The reference situation of most stagnant waters should be described in terms of ranges of environmental conditions which provide desired taxon assemblages. This can be associated with a certain level of maturity of the aquatic stage. On the other hand, flowing waters are systems dominated by the master factor current, which causes a degree of continuous instability. An endpoint of succession of flowing waters can be seen as the reference situation although their equilibrium is dynamic, especially on a smaller scale.

It can be concluded that the knowledge embodied by the concepts of community, environmental stress, succession, stability and equilibrium can be used towards a better understanding of the biological reality around us and can contribute to an ecologically responsible water management.

3. STUDY AREA, MATERIALS AND METHODS

3.1 Study area

There is a natural arrangement which generally directs ecological processes, proceeding from the abiotic to the biotic part. The major factors in the abiotic part set the background for the ecology of all organisms living in it (Pianka 1978). The main abiotic factors are described for the study area. Climate (Section 3.1.1) is the ultimate determinant of hydrology and the temperature conditions. The hydrology (Section 3.1.3) further depends on the geological processes which form the soil and the morphology of the landscape (Section 3.1.2). These relations of dominance between major environmental components and ecological processes are influenced by human activities (Table 3.1; Section 3.1.4).

3.1.1 Climate

Precipitation and temperature data from meteorological stations of the KNMI (Royal Dutch Metereological Office) were used to describe the climate of the province of Overijssel. The maximum value of the average precipitation per month occurs in August (90 mm), the minimum in March (50 mm). The maximum value of the average evaporation per month occurred, in 1984 for example, in July (96 mm) and the minimum in December (2 mm). Over the period 1980-1985, the mean annual precipitation was 770 mm and the mean evaporation 619 mm. The differences in precipitation between the various stations within the province are 100 mm on average. Precipitation directly influences the hydraulics of streams, especially those fed by rainwater.

The mean annual air temperature is 9.6 ^{o}C, with a minimum of the mean monthly temperature in January of 0.9 ^{o}C and a maximum in July of 17.8 ^{o}C. Water temperatures fluctuate normally between zero and 21 ^{o}C.

3.1.2 Geology, soil and morphology

Figure 3.1 shows that the larger part of the area of the province is covered with Pleistocene deposits. Only in the eastern part some Tertiary deposits are found; in the western part some Holocene deposits occur. The Tertiary deposits are mainly glauconitic clay and sand. These Tertiary deposits and their younger fluvial cover were pressed upwards (during the Saalian glaciation), forming ice-pushed ridges (Figure 3.2). As the ice passed some of these ridges in a later stage, it deposited boulder-clay. After the disappearance of the land-ice, fluvioglacial sands were widely deposited. Around streams peat was formed. In the Holocene, sedimentation by streams continued and peat formation increased, especially where stagnation of discharge took place (Pannekoek 1956).

The soils and morphology are shown in Figures 3.1 and 3.3. The natural chemical composition of the surface waters is directly related to the nature of the soil. The glauconitic clay is rich in calcium

Table 3.1 Relations of dominance in surface waters in the province of Overijssel, The Netherlands.

History ↘

	Ecological processes →	*Major environmental factor*	← *Human activities*
	Climatic variation (long-term variation)	Climate (e.g. precipitation, temperature, wind, light)	Atmospheric pollution (e.g. influence on temperature, precipitation)
⇓↑	Changes in the balance of matter through erosion/deposition, mineralisation/accumulation	Geology (bottom; e.g. sand, clay, peat)	Removal/addition of matter (e.g. digging waters, extraction of peat, infillin
⇓↑	Erosion/deposition by wind and water (e.g. meandering, bank erosion)	Morphology (longitudinal, transverse profile)	Changes in profile (e.g. dredging, canalisation, regulation)
⇓↑	Changes in water level due to variation in precipitation, evaporation and infiltration	Hydrology (water quantity	Water level fluctuations due to winning, drainage, infiltration
⇓↑	Changes in minerals due to erosion, vegetation	Chemistry (water quality)	Eutrophication (e.g. agricultural runoff, effluents toxic discharges)
⇓↑	Vegetational processes	Plants	Management (mechanical, chemical, biological clean ing; shading)
⇓↑	Faunal activity	Animals	Management (fisheries)

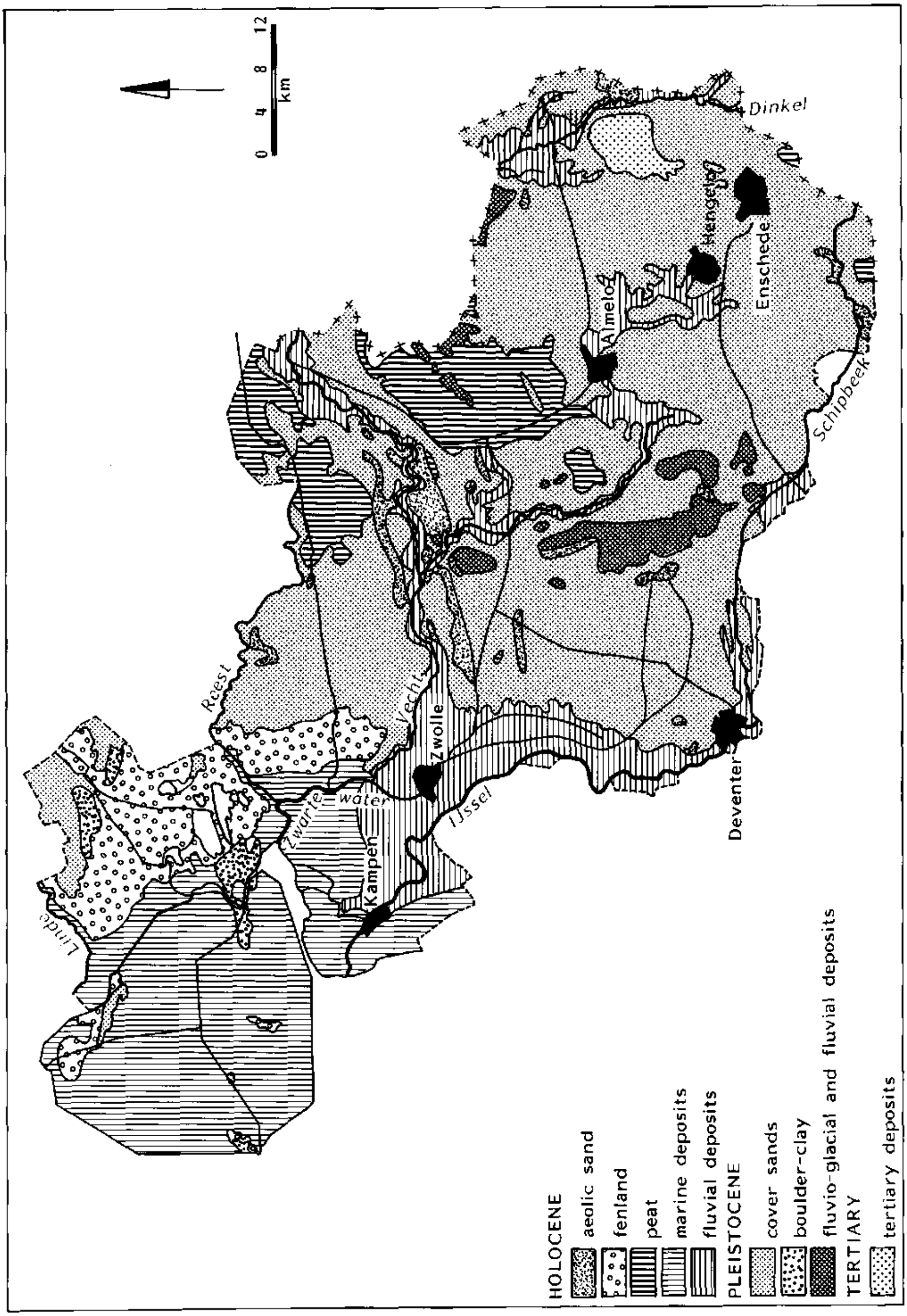

Figure 3.1 Simplified map of the geology and surface deposits of the province of Overijssel, The Netherlands.

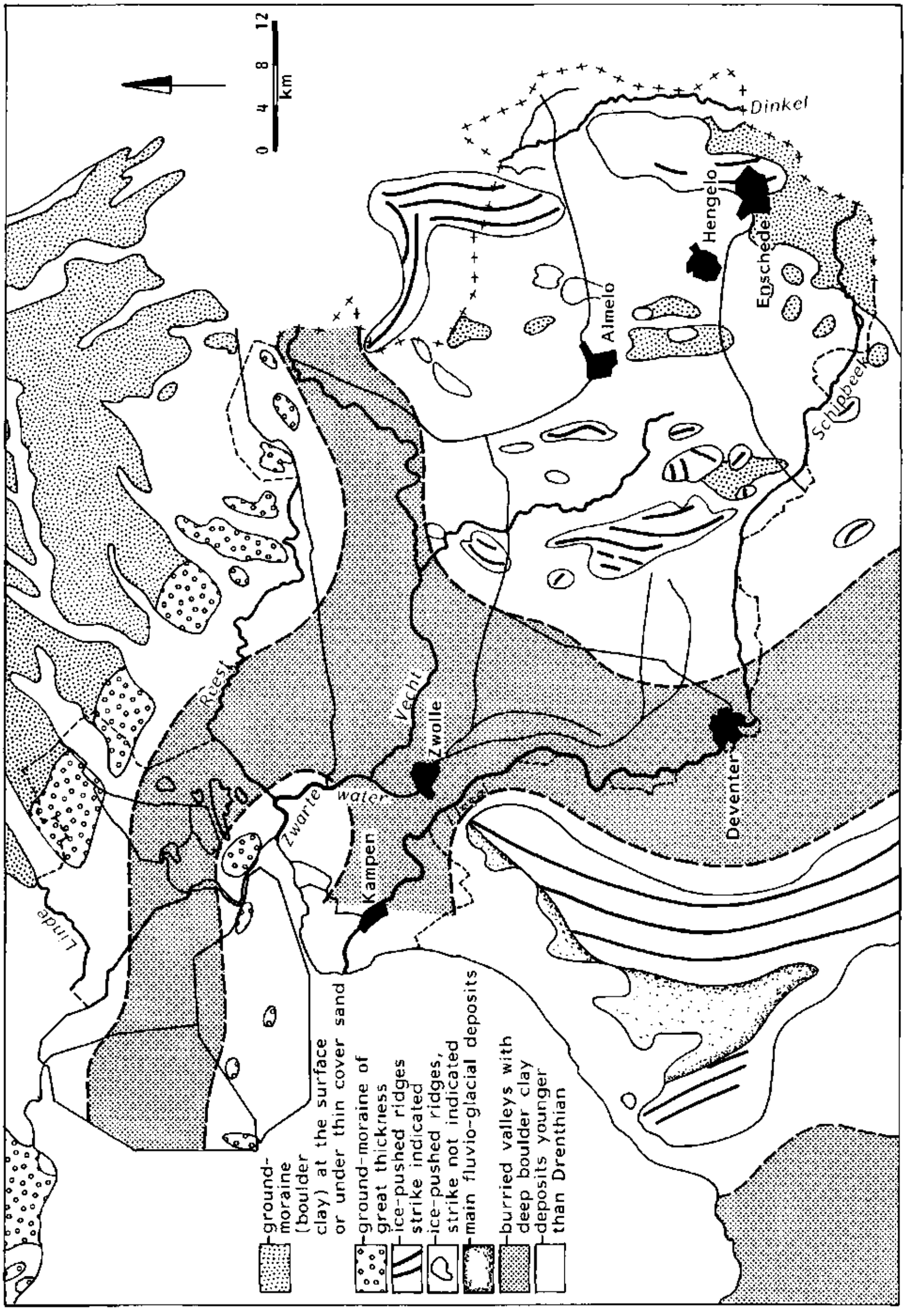

Figure 3.2 Map of the Pleistocene deposits in the province of Overijssel (The Netherlands) with boulder clay and ice-pushed ridges indicated (Pannekoek 1956).

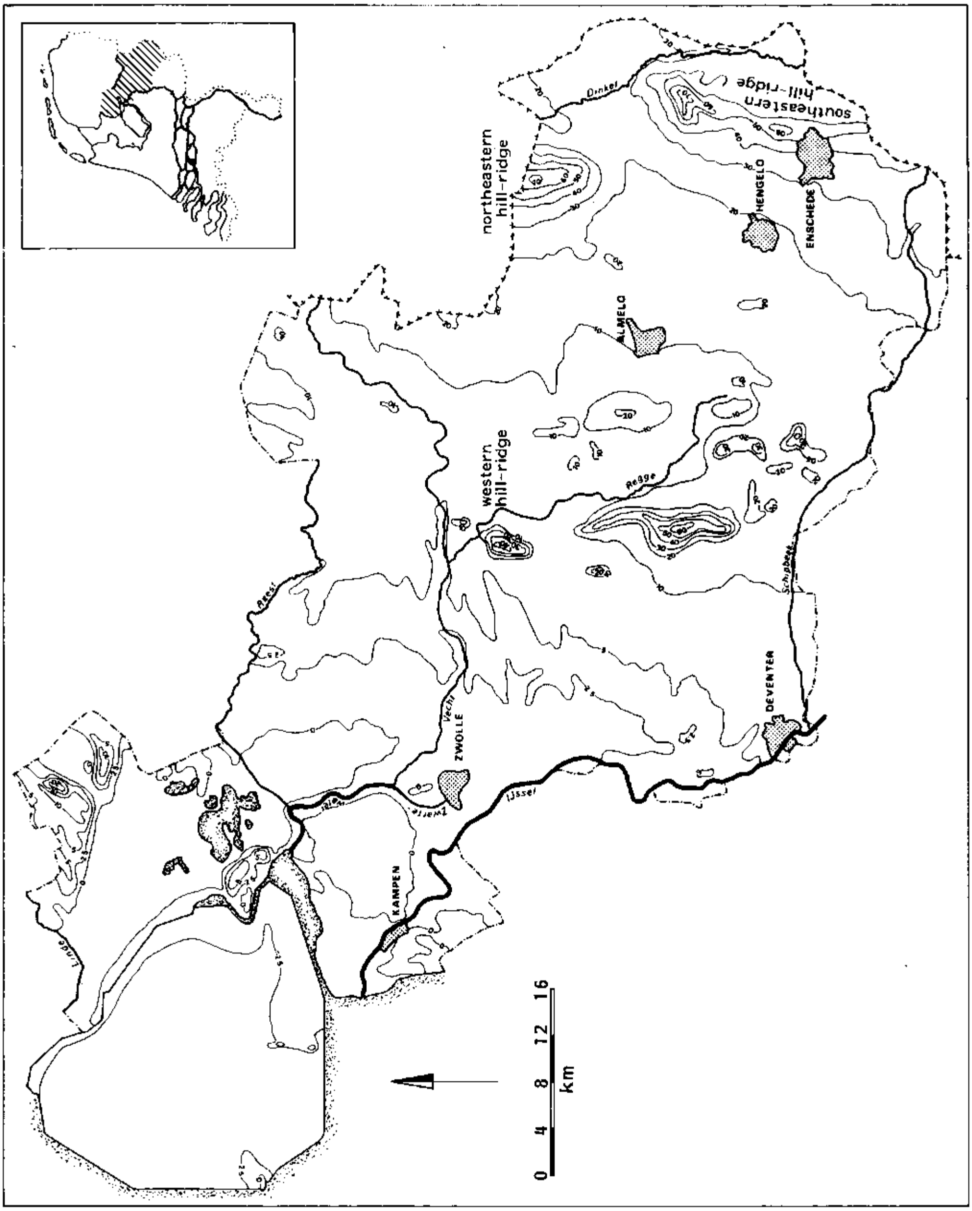

Figure 3.3 Map of the province of Overijssel (The Netherlands) with altitude contour lines indicated.

but the boulder-clay is calcium poor. In general, streams which are in contact with clay contain more minerals than those on the fluvioglacial sands.

The province is intersected by three sandy hill-ridges (elevation up to 85 m), running north-south, on which most streams arise (Figure 3.3). The western hill-ridge is entirely sandy, but both eastern hill-ridges contain clay layers with a low permeability resulting in a perched groundwater table (see Section 4.1). Sometimes this apparent groundwater discharges in helocrene springs. Most streams, however, are fed directly by rainwater and therefore lack a well-defined source. The areas between the hill-ridges are sandy with a slightly rolling relief. Where water discharge stagnates, oligotrophic moorland pools or bogs are formed.

The river IJssel deposited mineral-rich clay along its course. Marine clay is only found at the mouth of this river and in the 'Noordoostpolder'. The 'Noordoostpolder' was reclaimed in 1942 from a part of Lake IJssel (this lake (IJsselmeer) was formerly an inlet of the sea which was cut off by a dike in 1932).

Peat-soils formed in the northeastern part of the province are very poor in minerals (oligotrophic) although most of them are cultivated now. The pattern of canals and ditches results from intensive peat extraction.

The northwestern part of the province consists of a large area of undrained fen, situated in a broad valley which is intersected by a finely meshed pattern of ditches, canals, peat pits and lakes. This structure of the landscape is the result of human activities. Especially peat extraction, which was started in the Middle Ages, has shaped the landscape.

3.1.3 Hydrology

The natural hydrology of the province of Overijssel consists of a discharge of rainwater from the southeast towards the northwest, parallel to the elevation of the landscape. The discharge of surface waters is shown in Figure 3.4 in more detail. Man has strongly influenced this discharge pattern by digging ditches and canals, regulating streams and changing catchment areas. The present catchment areas are shown in Figure 3.5.

The polders at the mouth of the river IJssel and the 'Noordoostpolder' have a completely artificial hydrological regime. Directed water intake and pumped drainage provide a constant polder water level.

Groundwater level and discharge closely follow the elevation pattern and interact with the main streams (Figures 3.6 and 3.7).

3.1.4 Human impact

The system of streams, rivers and canals in the province of Overijssel has been continuously changed. Especially over the last hundred years man's influence has become more and more apparent. In the 14-17th centuries canals were dug to improve drainage, for navigation, and for peat digging. Rivers were connected to expand the navigation routes. This process was intensified in the following centuries and is still going on today. A major change was due to the construction of the

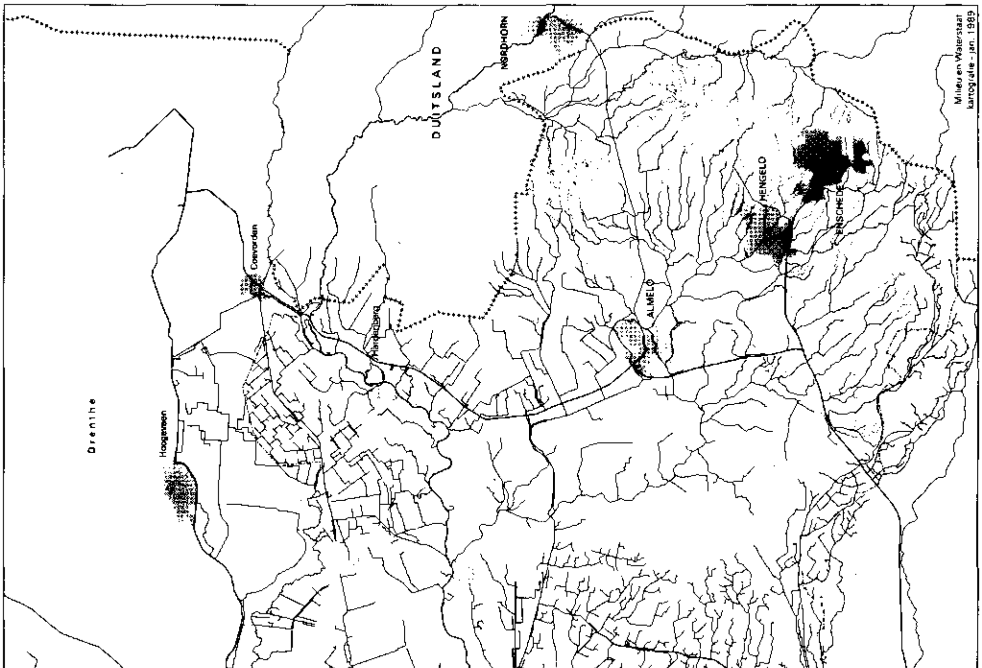

Figure 3.4 The main discharge patterns of surface water in the province of Overijssel, The Netherlands.

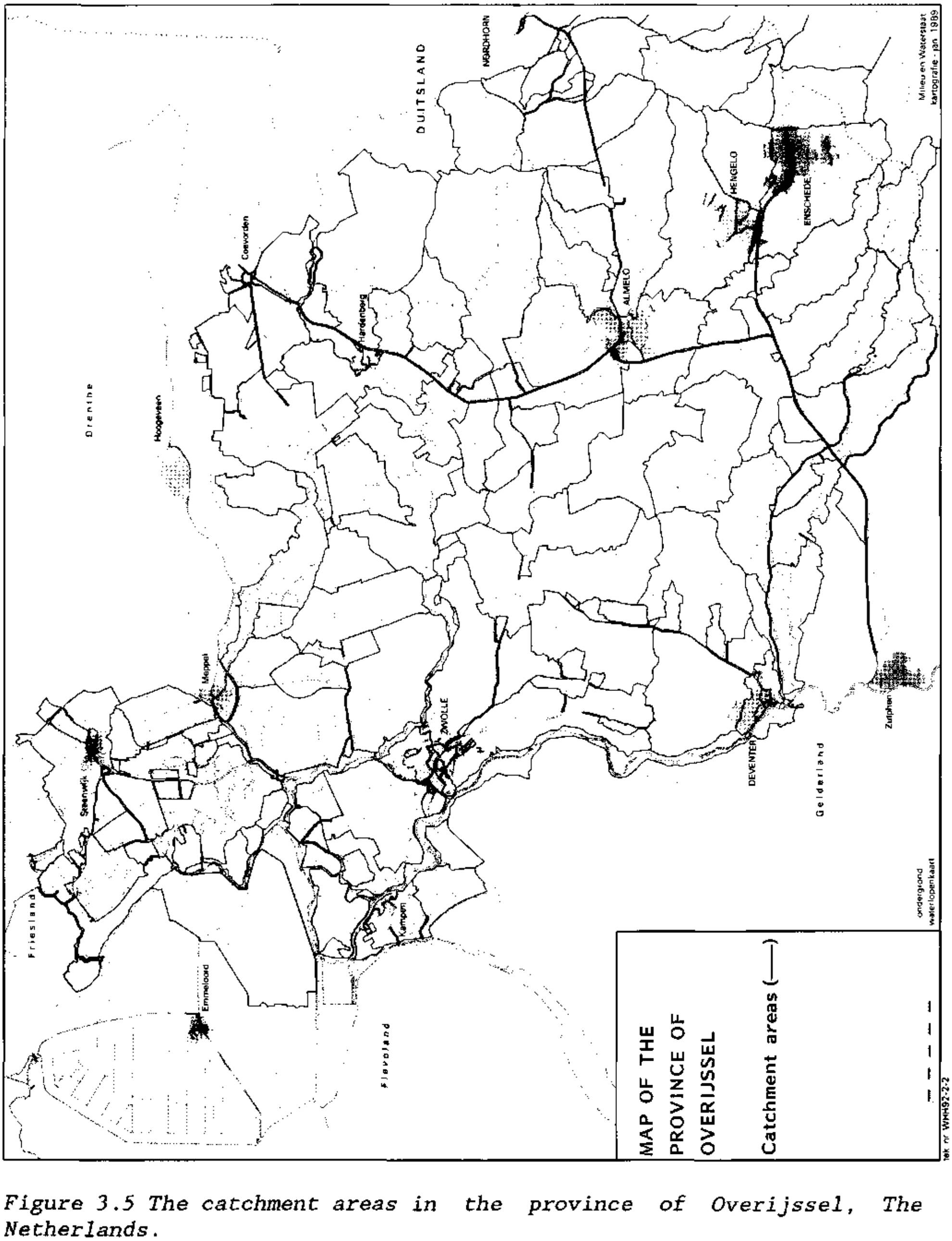

Figure 3.5 The catchment areas in the province of Overijssel, The Netherlands.

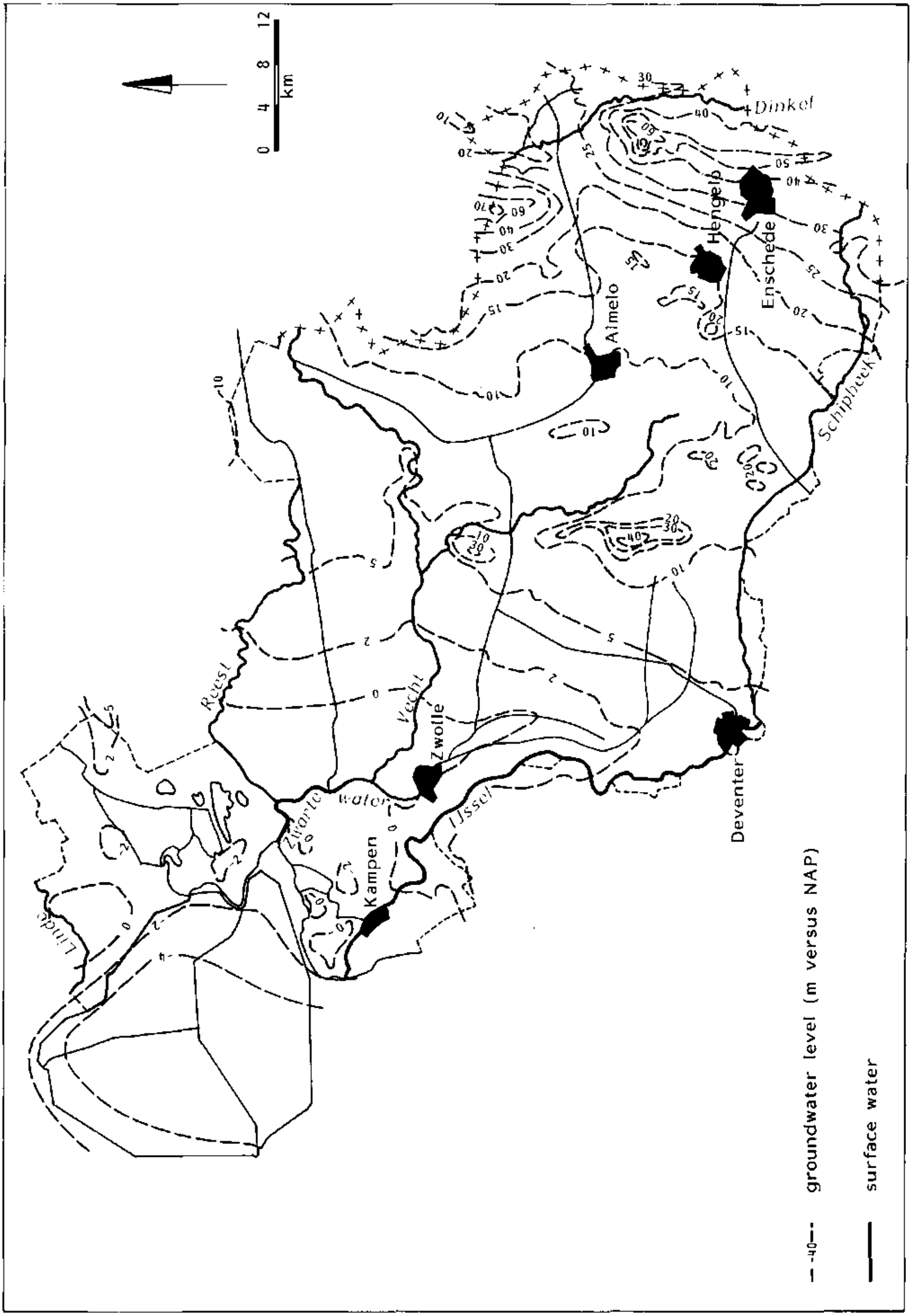

Figure 3.6 Map of the province of Overijssel (The Netherlands) with groundwater levels indicated (Bruinsma 1982).

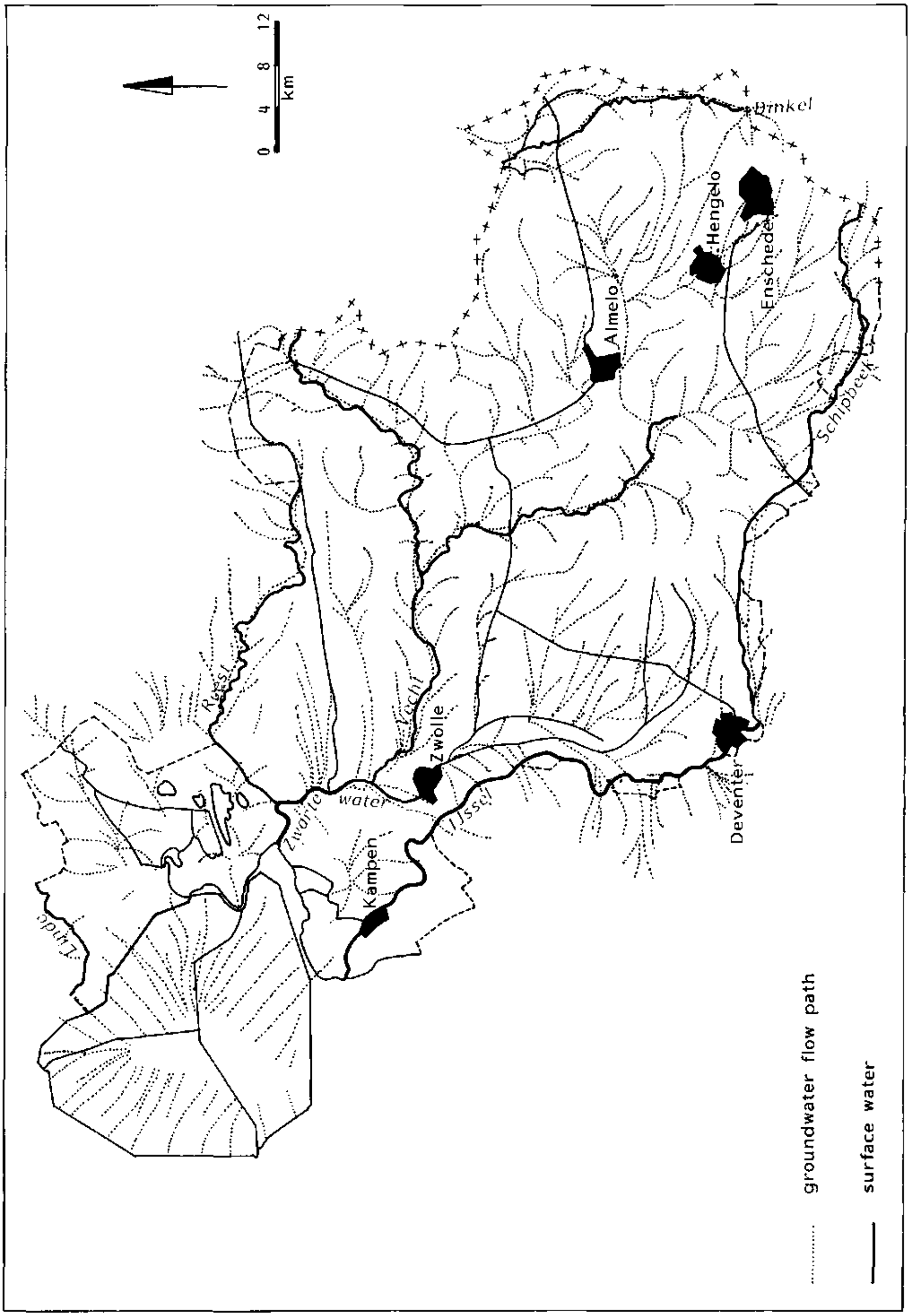

Figure 3.7 The main discharge patterns of groundwater in the province of Overijssel, The Netherlands (Bruinsma 1982).

Afsluitdijk, a dike across the sea-inlet of the Zuiderzee, which formed lake IJssel. After the reclamation of the 'Noordoostpolder' the groundwater flow, which until then had fed the peat area in the northwestern part of the province, changed direction towards the polder. The seepage area of the northwest became an infiltration area.

During the last century, in general, streams and rivers have changed in three chronological phases:

1a. Around 1900 the major bends were removed which resulted in an increase of fall (and current velocity). This reduced the number of summer floods. Some weirs were constructed to prevent summer-drought

2a. Between 1930-50 more weirs were constructed, transverse profiles were enlarged, more bends were cut out and branches of streams and rivers were diverted.

3a. In the 1960s the actual channel forms were made permanent; the banks were strengthened by stones and groynes, dikes were enlarged whereby riparian vegetation was removed, weirs or sluices were improved, and with weirs and pumping-engines much of the river system was extensively diverted.

These major alterations of streams and rivers induced the following changes in habitats:

1b. The increase of fall leads to an increase of current velocity and coarse substrates, resulting in more diverse habitats. Prevention of summer-drought is positive for the macrofauna assemblages.

2b. Weirs lead to a reduced current and the total combination of physical alterations leads to a more constant seasonal flow, both resulting in siltation. The interstices become filled up and a more homogeneous substrate evolves, a process more generally described by Ward & Stanford (1979). The bank and bed become more stable, and the current and temperature regime become more uniform, generally resulting in a change from a small-river character to large-stream or river character with the corresponding macrofauna assemblages. The macrofauna often comprises a more lentic, collector-dominated species assemblage, with bottom feeders and planktivorous taxa (Cummins 1979).

3b. The processes described under 2. become definite and widespread. Removal of the riparian vegetation strongly alters the functional relations (as described in general by Cummins et al. (1984)) present in the system and bed fixation markedly impoverishes the diversity of habitats.

Apart from physical changes, the macrofauna have suffered severely from an increase of pollution stress during the last century. Both physical and chemical changes have resulted in the extinction of a number of rheophilic species (Mol 1986b).

The natural state is no longer present in the streams and rivers of the province of Overijssel. However, studies of the actual biota can improve our knowledge of running waters which is necessary to predict the consequences of our present management of water quality and quantity.

Besides all hydrological changes brought about by human activities, some other important figures will be given to illustrate man's impact on the quality of the environment in this province. The total population density is about 270 inhabitants per km^2. About 50 % lives in the major municipalities with more than 30,000 inhabitants. Most of the province is used for agriculture (Table 3.2).

Table 3.2 The total area and land use in the province of Overijssel, The Netherlands.

Area (km^2) = 3925

Land use (%)

urban	woods	nature reserve	recreation	water	agriculture	others
8.4	8.8	3.3	1.3	2.9	74.8	0.7

Agricultural activity implies a continuous but diffuse source of contaminants for the surface waters. It also promotes a transport into the environment of especially nitrogen (959 kg/ha), phosphorous (326 kg/ha), potassium (713 kg/ha) and pesticides. Another non-point source of contaminants is precipitation (Table 3.3).

Table 3.3 Contaminants present in precipitation (calculated with an average of 2.3 mm precipitation/day) in The Netherlands.

Precipitation	pH*	Cl	SO4	F	NO3	NH4	PO4	Zn
($mg/m^2/day$)	4.4	6.7	12.9	0.11	6.9	3.7	0.01	0.07

* natural unpolluted pH = 5.6

The main point sources of contamination discharge mostly waste water on surface waters to a total of 715,000 inhabitant equivalences (1 inhabitant equivalence = 125 litre water with BOD (biodegradable organic matter) 54 g, Kjehldahl-N 10 g, and total-P 4 g).

3.2 Macrofauna sampling and sample processing

In total 664 sampling sites were sampled. Most sites (609) were only visited once and some sites (55) were visited twice. The sampling dates were spread over the four seasons as well as over several years (1981-1986) (for further information see Sections 5.2.1, 6.2.1, 7.2.1, 8.2.1 and 9.2.1).

Before samples were taken, 25-50 m stretches of linear waters and along the banks of large lakes, or the total circumferences of small lakes and ponds were searched for the partitions of various habitats. This search resulted in a schematic picture of the major habitats present, e.g. stands of macrophytes, leaf packets, bare sandy bottoms etc. At each sampling site it was attempted to compose the sample by combining subsamples which were taken in proportion to the various habitats present as estimated from the schematic picture. So, the total sample represented the observed environment. This careful presampling procedure is necessary for obtaining a reliable sample.

A bottom subsample was obtained by placing the pond net (mesh size 500 µm, frame height 200 mm, and frame width 300 mm) on the bottom and, facing upstream in running waters, sampling the substratum (sometimes including some of the standing lower parts of the vegetation) direct in front. The pond net was pushed, with short quick movements, through the upper centimetres of the substratum and then swept back immediately above the sampled area. Subsamples from bank, emergent, floating and/or submerged vegetation were obtained by sweeping the pond net several times through that part of the vegetation. At each sampling site all the major habitats were sampled in this way. A traject of about 0.5-1 m was sampled in every major habitat, so the total combined sample comprised at least about 5 m (or 1.2 m^2 of vegetation and 0.3 m^2 of bottom subsample). In small water bodies, the sample could not be composed of both a vegetation and a bottom subsample, so only one combined sample was taken. In the deeper parts (depths of more than 1 to 2 m) of large waters an Ekman-Birge sampler was used, with which five grab samples were taken at each site. In deep waters the grabs substitute one 0.5 m pond net bottom subsample.

In helocrene springs the pond net could not be used and here the micro-macrofauna shovel was used (Tolkamp 1980). This shovel is 10 cm wide and 15 cm long and subsamples were taken to a sediment depth of 3 cm, which permits sampling of small-scale mosaic substrate patterns.

All samples were washed in a bucket, taken to the laboratory and stored in a refrigerator (at 6 ^{o}C) while they were aerated. In the next few days the sample was carefully processed in the laboratory while most of the animals were still alive, by sieving the sample over three sieves (4.0, 1.0, and 0.2 mm mesh sizes) and placing the sample in white, flat-bottomed trays from which the animals were sorted by eye. If a taxon was present in large numbers, a representative part (large and small individuals) was removed and the remaining part was estimated.

The collected individuals were conserved in ethanol (70%) except for oligochaetes and watermites which were conserved in formalin (4%) and Koenike-fluid, respectively.

Organisms were identified by using the keys listed by Tolkamp (1984). Most macrofauna organisms, except for some dipteran families, could be identified to genus or species level. Closely-related taxa which could not be distinguished consistently are presented as a 'group'. Because identification was carried out by several people, a substantial control procedure was part of the identification process to ensure accuracy and consistency in identification. In cases of doubt, specialists were consulted. A reference collection of all the taxa is kept at the Research Institute for Nature Management.

An eight-letter code was developed for all macrofauna taxa occurring in The Netherlands (Verdonschot & Torenbeek 1988), which facilitated the transfer of the macrofauna data to the computer. Physical and chemical variables were also coded for this purpose.

3.3 Abiotic sampling and sample processing

A data sheet was used to note a number of abiotic (and some biotic) variables directly in the field. Some of those variables were measured directly (width, depth, surface area, temperature, transparancy etc.) or classified (substrate, colour etc.). Field recorders were used to measure oxygen, electrical conductivity, current velocity and pH. A number of chemical variables were analysed at the moment of sampling from all water surface samples. The water samples were fixed immediately in the field by adding $HgCl_2$ (Mackereth et al. 1978) and were later frozen (Harmsen et al. 1981). Analyses were conducted by generally following the prescriptions of the Dutch Normalization Institute.

3.4 Data processing

3.4.1 Preprocessing of the data

The conclusions presented in Chapter 4 led to the following techniques being used in this study. A flow scheme of the data analysis is given in Figure 3.8.

The performance of most multivariate analysis techniques is best when taxa have response surfaces of a simple form (linear or unimodal) with respect to environmental gradients. This condition is best met at species level. Due to taxonomical shortcomings individuals could sometimes only be identified to generic or higher levels. Higher taxonomical units often have response curves with a wider amplitude. Whether or not a taxon is included in the analysis is based on careful individual weighing. This weighing is based on ecological knowledge and the frequency of occurrence of the taxon. Furthermore, a taxon cannot belong to more than one taxonomical unit. Because of its aims this study was restricted to the macro-invertebrates (e.g. fishes and amphibians were excluded) (Verdonschot 1983).

Data transformation is an important step in ecological ordination (Noy-Meir 1973, Noy-Meir et al. 1975, van der Maarel 1979). Due to the semi-quantitative character of the sampling technique, the mathematical background of the multivariate techniques and the fact that the difference between 1 and 2 individuals found is more significant than the difference between 101 and 102, the taxa abundances need to be transformed when using quantitative data. The higher ranges of abundance lead to an overweighting of abundant species due to the effect of dominance (Section 2.2.1). Therefore,

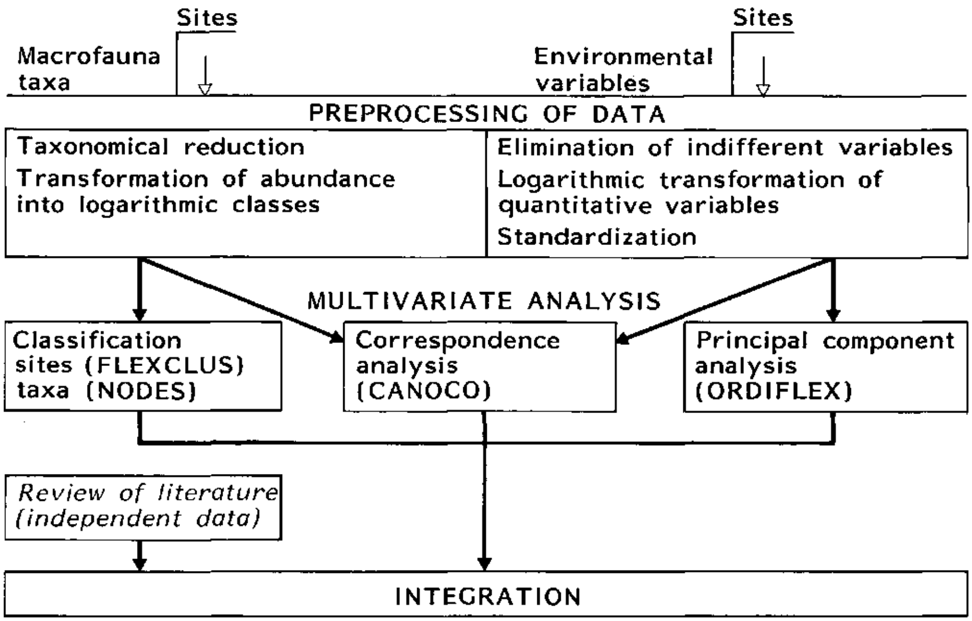

Figure 3.8 Scheme of data processing.

the data were transformed into the following logarithmic abundance classes, as indicated by Preston (1962):

Number of individuals	Log class
1	1
3	2
7	3
15	4
31	5
63	6
127	7
255	8
511	9
1023	10
2047	11
4095	12 etc.

To avoid overemphasis of the role of single samples with a highly divergent taxon composition (so-called 'outliers'), the option of 'downweighting of rare species' (Hill 1979) is invoked in each run of the multivariate techniques used.

Quantitative environmental variables, except pH, were transformed into logarithms because of skewed distributions. The other variables such as 'substrate type', 'permanence', 'shadow' and 'season', are nominal and were dealt with by defining so called dummy variables. A dummy variable takes the value of one when it concerns the observed state of the variable and the value zero otherwise.

3.4.2 Multivariate analysis techniques

Cluster analysis

Sites were clustered by means of the program FLEXCLUS (van Tongeren 1986). The clustering strategy of FLEXCLUS can be summarized as follows. The strategy is based on an initial, non-hierarchical clustering, following the algorithm of Sørensen for a site-by-site matrix based on the similarity ratio. In this initial clustering, sites are fused according to single linkage but a fusion is skipped when two sites with a lower resemblance to each other than a specified threshold would become members of the same cluster. The value of the threshold depended on the number of sites clustered and the cluster homogeneity. The *homogeneity of a cluster is defined as the average* resemblance (based on the similarity ratio) of the sites of this cluster to its centroid. The initial clustering is optimalised by relocative centroid sorting. Large and/or heterogeneous clusters are divided, small and/or comparable clusters (with a high resemblance) are fused, and then sites are relocated. In relocation each site is compared to each cluster (as it was before relocation of any site) and, if necessary, moved to the cluster to which its resemblance is highest. Before a site is compared to its own cluster, the respective site is removed from that cluster and the new cluster centroid is computed.

Ordination

The data are ordinated by detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA), using the program CANOCO (ter Braak 1986, 1987). Both DCA and DCCA are ordination (reciprocal averaging) techniques. DCCA is an extension of DCA, in which the ordination axes are chosen as linear combinations of the environmental variables. DCCA is an integration of regression and ordination (Jongman et al. 1987, ter Braak 1987) and shows the response of taxa or groups of taxa to environmental variables. Detrending by fourth-order polynomials is used. DCCA leads to an ordination diagram in which taxa, sites and environmental variables (arrows) can be represented. An example is given in Figure 3.9. The arrow of an environmental variable points approximately in the direction of steepest increase of that variable across the ordination diagram and the rate of change in that direction is equal to the length of the arrow. This means that the value of an important environmental variable in a site (or site group) is visualized by its perpendicular projection on the environmental arrow or its imaginary extension (in both directions). Note that this relation is optimized for species, not for sites. Within the diagram the sites (or site groups) and environmental arrows should be seen as a relative projection upon each other. Note that sites with a taxon composition of only common taxa lie in the centre of the diagram. These common taxa have their optima in the centre or are independent of the axes. Sites with a poor and aberrant taxon composition often lie near the periphery of the diagram. When the taxon composition is due to a specific environmental situation it is considered typifying otherwise it is due to chance. Although sites were classified into site groups, the distribution pattern of the individual taxa is not discontinuous. Therefore, in the ordination diagram each site group is represented by

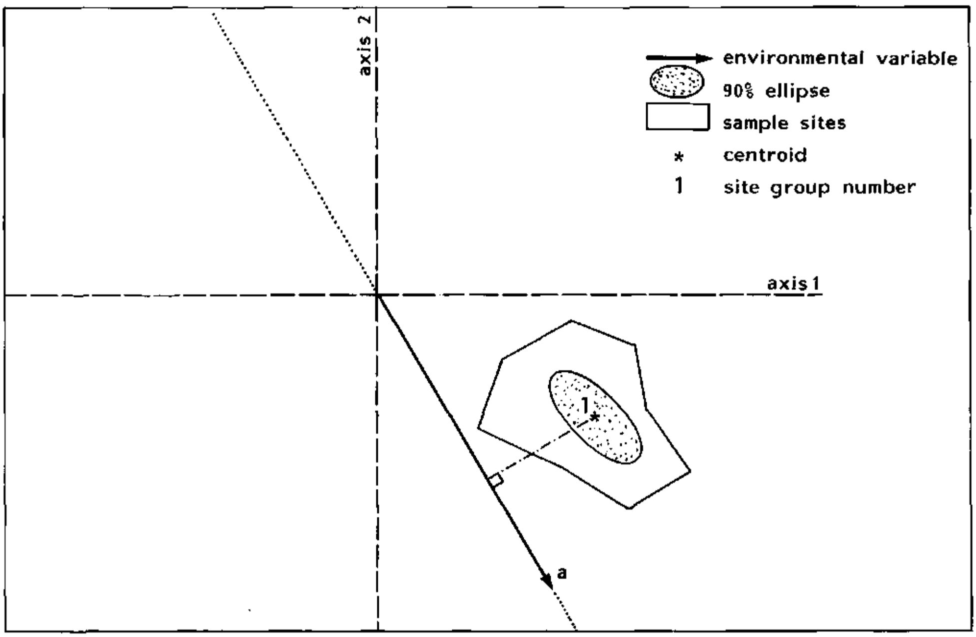

Figure 3.9 Artificial ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically) with the centroid (asterisk) and the 90 % confidence ellipse (dotted) of the mean of site scores of site group 1. The contour line describes the total variation of site scores. One environmental variable, a, is shown (arrow). The arrow of an environmental variable points approximately in the direction of the steepest increase of that variable across the diagram and the rate of change in that direction is equal to the length of the arrow. So, the value of variable a in site group 1 can be seen by projecting the centroid of group 1 perpendicular to the arrow (as shown) or its imaginary extension (as shown) in both directions.

a centroid (*) which is surrounded by a 90 % confidence region of the mean of site scores. Contour lines in the diagram indicate the total variation of all site scores within the data set. The diagram best shows how taxa composition varies with the environment and represents the main structure of the data set.

One other parameter is of interest within ordination. The eigenvalue lies between zero and one and can be considered as a measure of between-site variability (beta diversity). The eigenvalue is near zero in a homogeneous table and equals one when the table separates into two completely disjunct parts. The eigenvalues of the individual axes are regarded as a measure of their relative importance within one analysis.

The environmental variables were also ordinated separately by principal component analysis (PCA) with the program ORDIFLEX (Gauch 1977). Before applying this program the environmental variables were adjusted to zero mean and unit variance. From the resulting biplot (ter Braak 1983) interrelations can be seen when variables are grouped. The diagram is a visualization of the correlation matrix and shows the most obvious relations between environmental variables. PCA also reveals a diagram of site scores. As in DCCA, the relation between a variable and a site or site group can be seen by drawing an imaginary arrow from the centre of the diagram in the direction of a variable (Figure 3.10).

3.4.3 Application of multivariate analysis

Both the results of clustering (FLEXCLUS) and DCCA (CANOCO) were used to establish the site groups. The results of the clustering were used as a starting point. Firstly, the homogeneity of a cluster was examined, not by looking at the calculated homogeneity value but by comparing the taxon composition and environmental parameters of each site within the respective cluster. Clusters were sometimes divided or fused and/or sites were assigned to other clusters or set apart. Secondly, the clusters were projected on to the DCCA ordination diagrams of the first four axes. Sites which caused an overlap of clusters within a diagram were further examined by comparing their taxon composition and environmental condition with the overall taxon composition and environmental condition of each of the overlapping clusters. Next, the overlapping sites were either assigned to the most similar cluster or set apart. The resulting clusters were called site groups.

Ordering of taxa was done by the new NODES program. The site groups were used as input. In NODES the typifying weight of a taxon is calculated per site group by combining the formulae of constancy, fidelity and concentration of abundance (Boesch 1977; Verdonschot 1984). Constancy is defined as the number of occurrences of a taxon in a site group divided by the number of sites of that site group. Fidelity is the degree to which a taxon prefers a site group; fidelity is defined as the ratio of the relative frequency of a taxon in a site group and its overall relative frequency. Quantitative aspects are expressed by the 'concentration of abundance', defined by the average abundance of a taxon in a site group divided by its average abundance overall. Constancy, fidelity and concentration of abundance

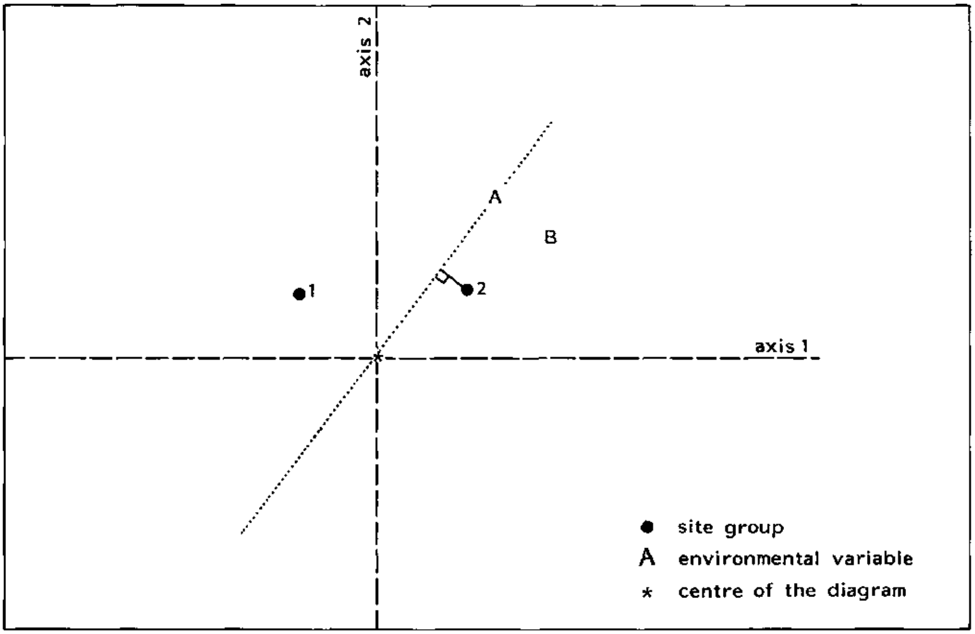

Figure 3.10 Artificial ordination (PCA) diagram for axes 1 (horizontally) and 2 (vertically) with centroids of the site groups 1 and 2, and two environmental variables (A, B) indicated. The relation between the variables A and B can be seen from their mutual distance, if it is small (as in this case) the value of the variables follow a comparable pattern. The relation between a variable and a site group can be seen by drawing an imaginary line through the centre of the diagram and a variable (as is done for variable A) and projecting the site group (in this case group 2) perpendicular to this line (as shown). The line points approximately in the direction of the steepest increase of the variable across the diagram from the centre towards the variable or its extension. So the value of variable A in site group 2 can be seen by projecting the centroid of group 2 perpendicular on to the arrow (as shown) or its imaginary extension (as shown) in both directions. The value of variable A in group 1 will be lower than in group 2.

are combined to assign a typifying weight to a taxon per site group according to the limits given in Table 3.4. Taxa can be ordered in a taxon-site group matrix according to their typifying weight. Small site groups, often composed of aberrant sampling sites (outliers), can be excluded from the process of weighting. Rare taxa (with a low frequency) can be moved to the 'tail' of the table.

The ordering of site groups was based on the graphical projection of these groups in the DCCA ordination diagram, largely following their ordering along the first axis.

Table 3.4 Typifying weights used in the program NODES. A specific typifying weight is assigned to a site when constancy, fidelity, and concentration of abundance are all three more than the indicated value.

Constancy	Fidelity	Concentration of abundance	Typifying Weight	Typifying character
0.50	3	5	12	High
0.40	4	4	11	High
0.25	5	5	10	High
0.50	2	4	9	Medium
0.40	3	3	8	Medium
0.25	4	4	7	Medium
0.50	1	3	6	Low
0.40	2	2	5	Low
0.25	3	3	4	Low
0.50	1	1	3	Indifferent
0.25	1	1	2	Indifferent
0.00	-	-	1	Coincidal

For the resulting site groups the mean and standard deviation of each environmental variable was calculated.

In the DCCA ordination diagram only the more important environmental variables are shown. The program is limited to 72 variables each run, so to select these variables DCCA was run several times, with partly different sets of variables. Those variables with a high correlation with one (or more) of the axes were selected. However, of all environmental variables some will always be more or less strongly interrelated. Therefore, the PCA ordination diagram is given as well. From the diagram the relations between the important variables selected by DCCA and the other variables can be seen, as well as the mutual relations between all the variables measured and the site groups.

A basic assumption underlying the use of association analyses is that grouping the taxa together implies that they may have similar environmental requirements (Learner et al. 1983). Knowledge about the ecology of taxa with at least a higher typifying weight supports the

ecological validity of the presented site groups. But detailed descriptions of the physico-chemical habitat of most taxa are not available and information is often restricted to rough indications like 'littoral zone of lakes', 'slowly flowing reaches' or 'brooks'.

Each taxon has its own individual tolerance to different environmental variables, so in most ecological studies such a taxon is not the object of the study but only a part of it. More detailed studies and monographs of one taxon are scarce. Besides, a taxon experiences not only the abiotic environment but also the biotic one. Biotic interactions can significantly alter community composition (Hart 1983) but this will not be discussed further in this study.

Nevertheless, existing ecological knowledge is used to adjust the site groups. Thus, the characterization of each site group implies a description of the ordination results, the averages of differentiating environmental variables, and knowledge of the ecology of the typifying taxa. A site group is defined as a collection of sites; a cenotype is defined as an ecological entity (Section 2.5). After a site group has been adjusted and/or verified by the ecologist it acquires the status of cenotype.

4. REPRODUCIBILITY OF A MACROFAUNA SAMPLE

4.1 Introduction

How representative and reproducible is the macrofauna collected in one standard pond net sample in space and in time for typological purposes? In particular, what is the effect of spatial, seasonal and yearly differences in the macrofauna on the typology? This question should be answered because, in general, in this study every site was only visited once and sampling dates were spread over the four seasons as well as over several years.

This study required a macrofauna survey over a large area. So a simple technique was needed to discover most of the species present and to estimate their relative abundance.

The advantages of simple sampling techniques are that they do not require an elaborate apparatus, that they usually catch a high proportion of the total number of species present at each station, and that they often provide fairly comparable figures, especially when the biotope and collector are the same for all samples (Elliott 1971). The second and third advantages are qualitative but should be quantified for this study. Therefore, this section will give special attention to the chosen sampling technique (the standard pond net) and frequency (one sample per site) and their limitations.

The simple standard pond net was chosen for this because it is often used in survey work (Winterbourn 1985) and in water quality surveys in The Netherlands. Hammen, Claassen & Verdonschot (1984) standardized sampling with a standard pond net (mesh size 0.5 mm, frame height 200 mm and frame width 300 mm) for the Dutch situation. However, only a few studies have dealt with the quality of the standard pond net sample. Beltman (1984) and Pinkster & Goris (1985) have studied some aspects of the reproducibility of the standard pond net sample as used in this study. Beltman (1984) concluded that, when all major habitats were sampled in proportion to their occurrence, the total sample over a stretch of 5 m (an area of 1.2 m^2 of vegetation and 0.3 m^2 of bottom) was appropriate for typifying a whole ditch. Pinkster & Goris (1985) concluded that, when sampling once a year, hardly ever more than 50% of the yearly total number of taxa were found and usually this percentage was much lower.

Needham & Usinger (1956) sampled a relatively uniform riffle and found that to estimate population densities as to total numbers, according to their criteria 73 samples would be required. Mackey et al. (1984) concluded that six sampling occasions in alternate months trough 1 year, each with four replicate pond net samples taken at two sites in each distinctive environmental zone along a river, yielded an adequate sampling programme. To process such a number of samples would be far beyond the limits of costs, personnel and/or time of most institutions.

Therefore, the question is how reproducible the observed abundances are in one single standard pond net sample.

4.2 Material and methods

A series of replicate samples was taken at one selected site. The selected site will be referred to as the replicate site. The site is situated in a regulated stream which is moderately polluted. It can be considered representative for about 80% of all linear waters present in the Pleistocene (eastern) part of the province of Overijssel. The stream is situated in an agricultural landscape; it is characterized by a regular longitudinal and transverse profile; it is permanent, located on a sandy bottom and it is mechanically cleaned. The stream is up to 6 m wide, reaches a depth of 80 cm and it has a current speed of 0-5 cm/s.

Samples were taken according to the following procedure. Ten replicate samples were taken at the same time, for which a homogeneous stretch of the stream was divided into ten parts each 10 m long. Each part was sampled according to the standard procedure by using a standard pond net (Chapter 3). The first sample was taken in the most downstream part, for the following continuously upstream. This

Table 4.1 Environmental variables of the replicate site in different months. Abbreviations are explained in Table 10.5.

	December	April	July	September
T	6.0	8.5	16.0	13.0
PH	7.2	8.3	7.9	7.8
EC	569	520	460	470
O2	8.1	7.6	7.5	7.0
O2%	65	65	76	66
NH4	0.5	0.4	0.1	0.2
NO3	1.8	2.0	1.5	1.8
O-P	0.01	0.01	0.05	0.01
T-P	0.11	0.15	0.09	0.10
CL	24	43	42	39
SO4	66	75	59	58
FE	0.86	2.8	1.0	2.8
NA	14	23	21	21
K	2.0	3.2	6.0	2.5
MG	10.0	8.5	8.5	8.3
CA	31	94	98	108
TRANSPAR	50	45	80	45
S-T	3	4	17	22
%-A	0	0	30	1
%-F	1	0	5	1
%-S	40	5	70	30
%-E	1	0	5	1
%-B	1	1	1	1
%-T	40	5	95	30

procedure was repeated once per season (December 1984 and April, July and September 1985). In total 286 taxa were collected at the replicate site within the forty samples taken. Some physical and chemical parameters are given in Table 4.1.

For each taxon the index of precision (IOP) was calculated to study the reproducibility of abundance. The index of precision is chosen to overcome the problem of differences in abundance of taxa (due to natural variation during a life cycle and/or variation caused by the sampling technique) when looking at standard deviation (sd) or arithmetic mean (x) separately. The index of precision is the ratio of standard error and arithmetic mean:

$$IOP = 100 * (\text{standard error}/\text{arithmetic mean}) = 100 * (sd/(x * \sqrt{n}))$$

The index of precision indicates the error percentage in the estimate of the population mean. An error percentage of zero implies that all samples are identical. Since absence obfuscates the outcome of the index, only the samples in which a taxon was present were taken into account. The precision of the value of the abundance of a taxon can only be indicated for the moment it was collected. For taxa collected only once, the standard deviation and the index are indeterminate.

4.3 Reproducibility of presence

Table 4.2 shows the average percentage of taxa caught by a single

Table 4.2 Percentage of taxa caught on average in a standard pond net sample in dependence of the sampling date. (a) Percentage out of all the taxa collected at the replicate site. (b) Percentage out of the taxa present in 90% of the samples collected at the replicate site. (c) Percentage out of the taxa present in 75% of the samples collected at the replicate site.

	Percentage of		
	all taxa (a)	more common taxa (b)	common taxa (c)
Month (date)			
December (031284)	54	61	68
April (150485)	55	63	67
July (080785)	51	65	68
September (160985)	64	77	84

sample in relation to sampling dates. September appears to be the

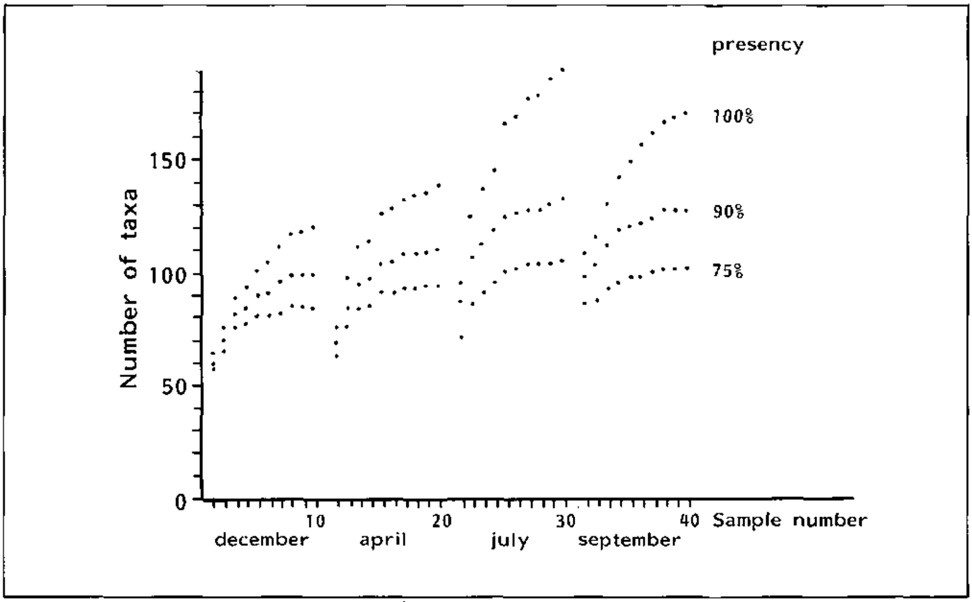

Figure 4.1 The cumulative number of taxa present at the replicate site over the samples taken per sampling date for, respectively, all taxa (a presence of 100%), the more common taxa (a presence of 90%), and the common taxa (a presence of 75%).

best month to take a sample: it contained on average 64% of all taxa and 84% of the common taxa (as defined in Table 4.2).

Sampling over a larger stretch at the same date increased the number of taxa caught (Figure 4.1). Compared to a single sample, the ten samples taken at the same date approximately doubled the number of taxa caught.

4.4 Reproducibility of abundance

In Figures 4.2 and 4.3 the index of precision (IOP) of a taxon is plotted against its frequency. For observed abundances the index fluctuates between 60% and 200% (Figure 4.2). This means that if a taxon is collected in a standard pond net sample, its abundance estimate is not precise. To make the distribution of observed values less skew, the abundances are transformed to a logarithmic scale (see Section 3.4.1). The index for transformed abundances fluctuates around 45% (Figure 4.3). Hence, this log transformation has been performed before processing the data.

Elliott (1971) reported 20% (on the original scale) as a

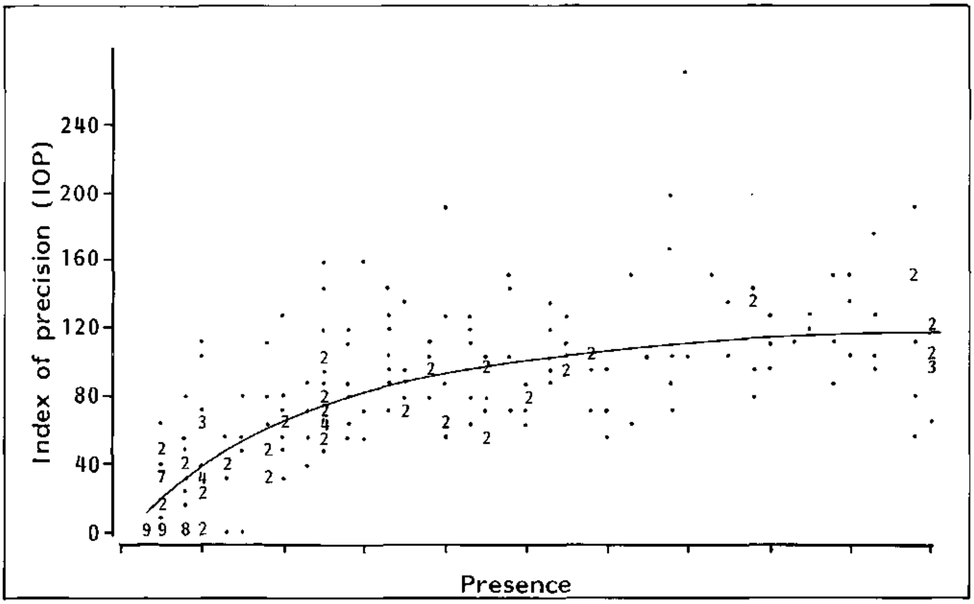

Figure 4.2 The relation between the presence of the taxa and the index of precision (IOP) calculated for observed abundances.

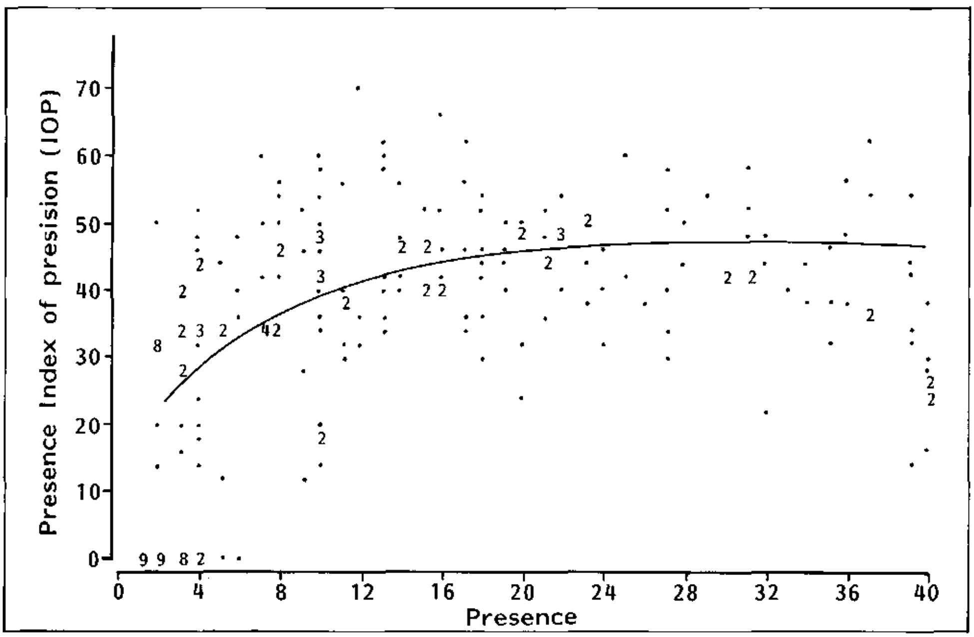

Figure 4.3 The relation between the presence of the taxa and the index of precision (IOP) calculated for transformed abundances.

reasonable error in homogeneous bottom samples. The standard pond net samples were not taken from a homogeneous substratum but from several microhabitats. Therefore, an index error of 45% is considered acceptable since the conditions were more heterogeneous (patchy).

4.5 Reproducibility in typology

One standard pond net sample collects only a part of the total macrofauna present and it is affected by season. It is therefore necessary to study the consistency of the forty replicate samples within the typological framework of this study. This consistency was tested with detrended correspondence analysis (DCA) (Hill 1979). If two sites have a comparable species composition they will be close to each other in the DCA ordination diagram.

Figure 4.4 shows the ordination diagram of DCA applied to the data

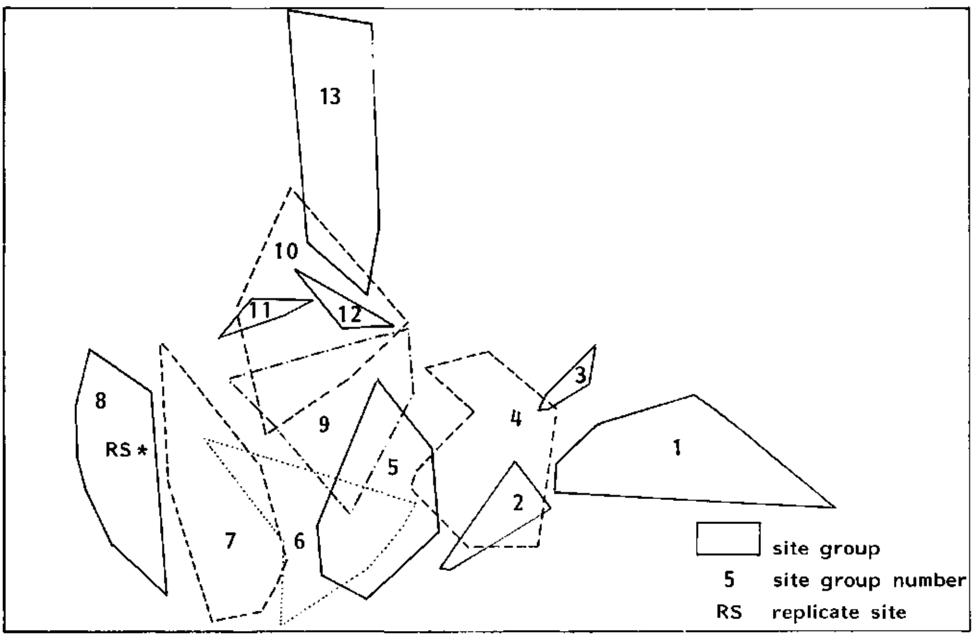

Figure 4.4 Ordination (DCA) diagram for axes 1 (horizontally) and 2 (vertically) with the site groups (contour lines) and one sample taken at the replicate site (RS) indicated.

set of streams. The replicate site belongs to this data set and is represented by a single sample (the first December sample), labeled RS. This sample belongs to site group 8; the cenotype 'permanent, lower reaches of regulated streams'. This data set is further described and analysed in Chapter 7. Next, all replicate samples were added to the ordination diagram as 'passive samples'. This is easy as

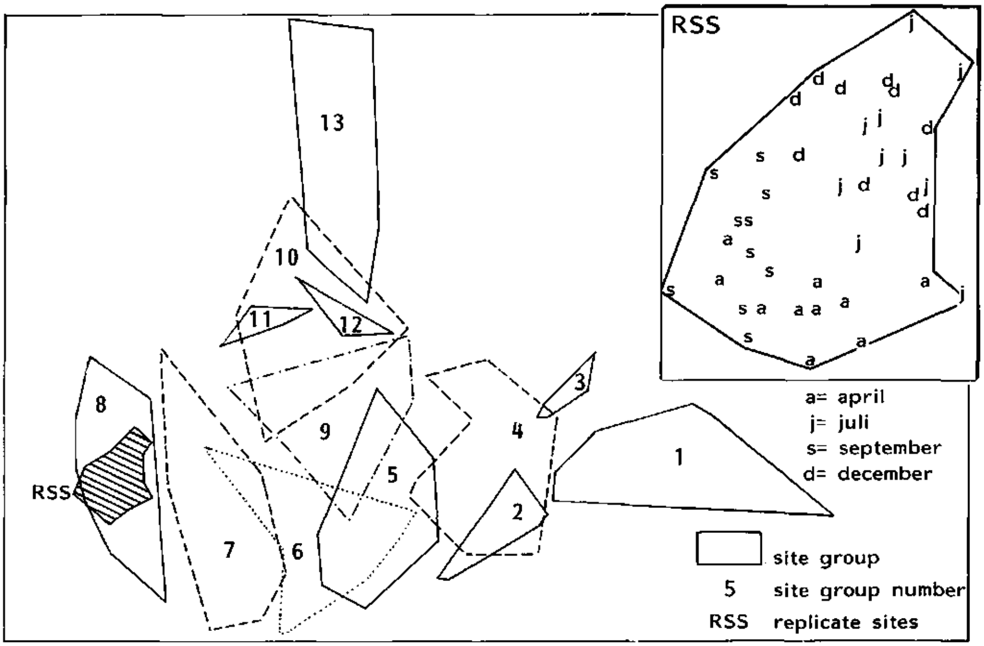

Figure 4.5 Ordination (DCA) diagram for axes 1 (horizontally) and 2 (vertically) with the site groups (contour lines) and all samples taken at the replicate site (RSS) indicated.

a site point lies in the centroid of the species points of species that occur at that site (ter Braak 1987). All the added samples (except one) lie in the hatched region within site group 8 (Figure 4.5). This indicates that, despite the seasonal differences present within the forty replicate samples, the differences are small in comparison with the differences between different site groups of streams. The inset of Figure 4.5 illustrates the seasonal differences between the forty replicate site samples. According to the first axis there is a difference between samples taken in April versus September and July versus December, while according to the second axis there is a difference between samples taken in April versus December and July versus September.

4.6 Reproducibility in time

The field work of the EKOO-project was carried out over a period of five years from 1981-1986. Besides seasonal differences small climatological variations can also affect the results (Rasmussen 1985). To give an example of the fluctuations within a sampling site over a period of five years, some results of monitoring macrofauna at some stations within the watershed of the Water Board 'Regge & Dinkel'

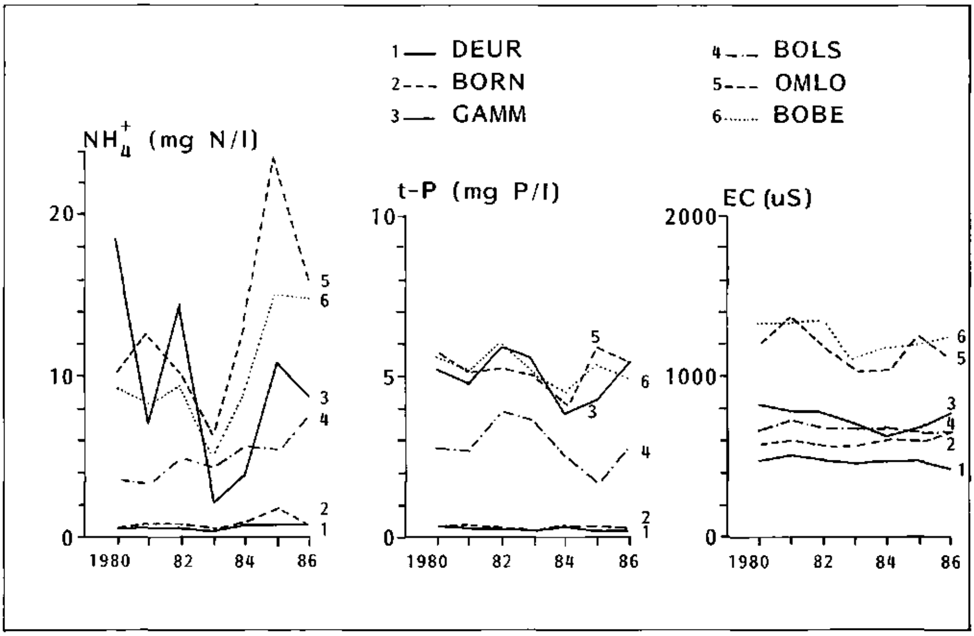

Figure 4.6 Physical and chemical parameters of some regulated streams within the catchment area of the water authority "Regge & Dinkel" over the years 1980-1986 (stream codes: DEUR='Deurninger beek', BORN='Bornerbroekse waterleiding, GAMM='Gammelker beek', BOLS='Bolscher beek', OMLO='Omloopleiding', BOBE='Bornse beek').

were processed. The stations chosen agree with sites sampled in the EKOO-project. It concerns regulated streams which can be compared to the replicate site except for their degree of pollution. The stations show a reasonable constancy in abiotic features over the studied time period. Figure 4.6 shows the pollution status in terms of electric conductivity, ammonium and total phosphate concentration of these stations over the last five years. Three different pollutional groups can be recognized. The stations in the Deurninger beek (DEUR) and the Bornerbroekse waterleiding (BORN) are not polluted, the Gammelker beek (GAMM) and Bolscher beek (BOLS) are moderate polluted and the Omloopleiding (OMLO) and the Bornse beek (BOBE) are strongely polluted. The macrofauna was collected each season in the first two years and in spring and autumn of the following three years. So, each station is described by fourteen samples.

If species composition is constant over the five-year period, the samples taken at one station should be projected close to each other and be separated from samples taken at other stations within the DCA ordination diagram. The DCA-diagram of the macrofauna collected by the waterboard at the six stations over the five years period is given (Figure 4.7). Besides some slight overlap of samples of different stations within the same pollutional group, the three pollutional

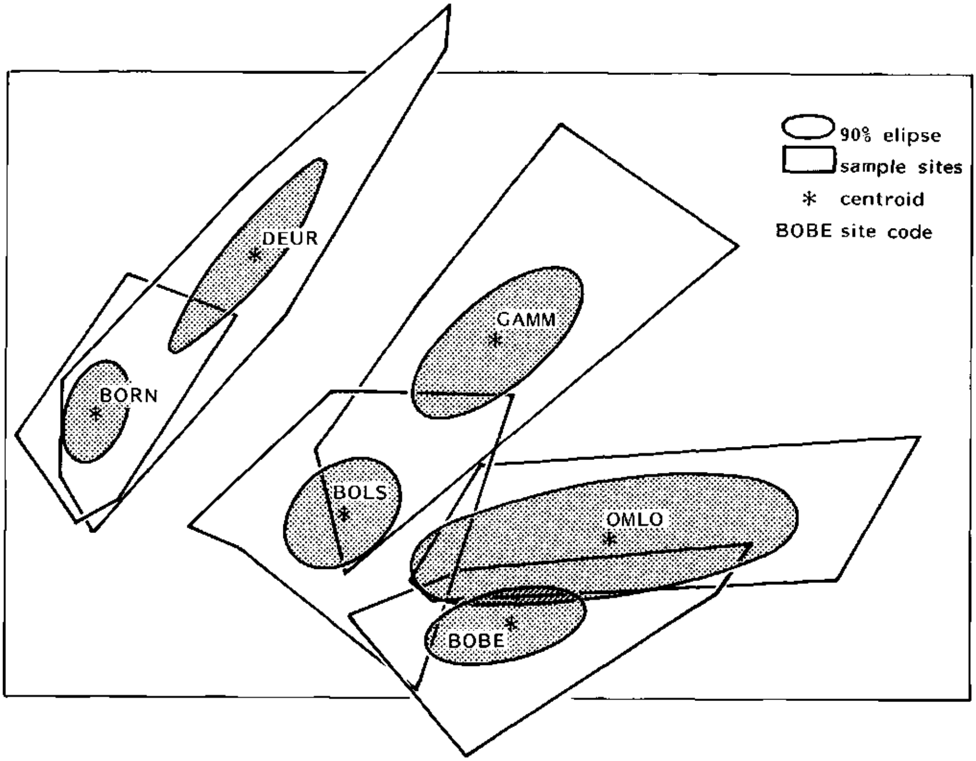

Figure 4.7 Ordination (DCA) diagram for axes 1 (horizontally) and 2 (vertically) with the regulated streams (contour lines) and the 90% confidence ellipse of the mean of site scores per regulated stream indicated (stream codes are explained in Figure 4.6).

groups remain clearly separated and recognizable over the five years period. So there is a marked constancy in time of species composition at the studied stations. These three groups (a pollution gradient) can be seen going from the lower right corner to the upper left corner. Each station shows a slight expansion from the upper right corner to the lower left corner which is probably due to a trend with time from 1981 to 1986 respectively (not shown in the figure). As all stations show this trend it can be explained by the improvement of sample processing and especially identification. Furthermore, the different confidence ellipses remain clearly separated, indicating that differences between stations are more important than differences in time.

4.7 Conclusions

Macrofauna sampling by the standard pond net as used in The Netherlands is a technique which presents only a semi-quantitative picture of the more common taxa. On average, only about 55% of all taxa present at the moment of sampling, are collected. If only one standard pond net sample can be taken it should preferably be taken in September. Furthermore, observed abundances should be transformed to a logarithmic scale when processing data according to the indicated procedure. So, one standard pond net sample collects only part of the total number of taxa present and their abundances are quite inaccurate.

If the standard pond net is used for a typological study seasonal differences, as shown for the replicate site, as well as inconsistencies due to the sampling technique are of little significance compared to differences between types. This is supported by two additional facts. Firstly, some of the sites were sampled twice (in different seasons) or sites were situated close together in the same water. Nearly all of these sites were finally grouped within one site group. Secondly, each of the site groups is a combination of several sites and thus the conclusions do not depend on one but on several observations.

5. MACROFAUNAL COMMUNITY TYPES IN HELOCRENE SPRINGS

5.1 Introduction

Springs occur where groundwater aquifers discharge at the surface. According to their morphology, area and volume of flow, springs are divided into four categories described as rheocrene, limnocrene (Bornhauser 1912), helocrene (Steinmann 1907), and arkocrene (Tolkamp 1983) springs. In the province of Overijssel mainly helocrene springs are found. A helocrene spring is formed when a small volume of groundwater discharges more or less constantly over a relatively large, slightly sloping area. This area (called a spring source) becomes marshy with patches of vegetation on beds of organic material which are water saturated and from which small spring streams arise. This results in a mosaic of substrates, each providing a habitat for several faunal groups (Thienemann 1912, Illies 1952, Thorup 1966, Thorup & Lindegaard 1977). The most important of these groups are (Figure 5.1):

- I - groundwater fauna
- II - spring fauna
- III - running water (lotic) fauna
- IV - hygropetric fauna (fauna living in a thin water film)
- V - stagnant water (lentic) fauna
- VI - ubiquitous freshwater fauna
- VII - terrestrial fauna (semi-aquatic fauna).

In the province of Overijssel, helocrene springs occur high on the slopes of the three hill-ridges. The western hill-ridge (Chapter 1, Figure 3.3) is sandy and the carrying capacity of the groundwater aquifer is low. This small quantity of groundwater discharges in small seepage areas of temporary character. Both of the eastern hill-ridges contain clay layers with a low permeability (Figure 5.1) resulting in a perched groundwater table. This apparent groundwater discharges in helocrene springs situated at heights between 55-70 m on the hill-ridges. Many of them are overgrown by Alnus glutinosa and Salix sp. The organic beds are frequently covered with plants like Chrysosplenium oppositifolium, Ranunculus repens, Stellaria alsine and Cardamine amara.

5.2 Results

5.2.1 Data collection

Macrofaunal and environmental data were collected (see Section 3.3) from 23 sites, sampled in the winter of 1981/82. Each sampling site was visited once. For 12 sites all the samples (approximately five samples taken by the micro-macrofauna shovel (Section 3.2) in the spring source and five taken in the same way in the spring stream per

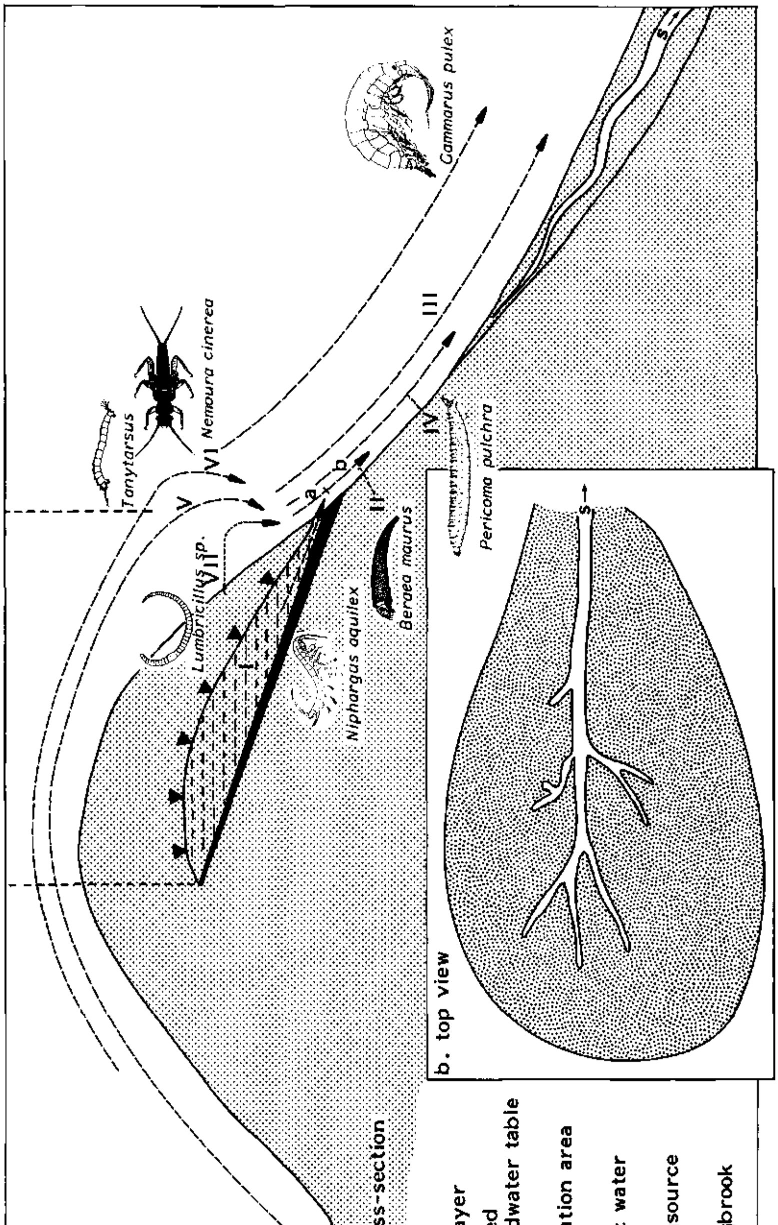

Figure 5.1 A general illustration of the macrofauna inhabiting a helocrene spring in relation to the hydrology of this spring.

site) were stored separately (microhabitat samples). By combining the data from the five samples taken from the spring source and spring stream, respectively, each site could also be characterized by the resulting two habitat samples. For the remaining 11 sites, two combined samples (each composed of approximately five samples taken by the micro-macrofauna shovel) were taken from the spring source and the spring stream, respectively (indicated as habitat samples), except for one site where only one combined sample could be taken. This yielded four data sets: two macrofaunal sets, one comprising 109 microhabitat samples (comprising leave packets, bare sand, iron deposits, gravel etc.) and the other 45 habitat samples (comprising spring source and spring stream, respectively), and two sets of environmental variables, one comprising 10 variables of the microhabitat and the other 50 variables of the habitat.

5.2.2 Preprocessing of the data

All macrofaunal data collected (a total of 155 taxa) were included in the analysis. Further information on the preprocessing procedures is given in Section 3.4.1.

5.2.3 Multivariate analysis

Clustering (program FLEXCLUS) and ordination (program CANOCO) of the macrofauna and environmental data of habitat and microhabitat resulted in the description of six habitat and nine microhabitat groups, respectively. For these groups information on the autecology of typifying and indifferent taxa (program NODES) is given in Table 5.1. Taxa with a low frequency of occurrence (accidentals) have been omitted. Numbers of sites and arithmetical means and standard deviations of the environmental variables per site group are given in Table 5.2.

Among all the environmental variables measured, certain groups of variables are more or less interrelated. Principal component analysis (program ORDIFLEX) shows those groups (Figure 5.2). For example, there is a clear contrast between the variable spring stream on the right side of the figure with related variables such as current velocity, depth, width, shadow and coarse detritus versus the variable spring source. The spring source is related to vegetation cover, thickness of the silt layer, silt and permanence. Because the chemical variables are the same (only one water sample was taken per spring), they do not influence this division. However, the position of the eutrophication parameters at the top of the figure versus that of sulphate at the bottom is interesting. Projection of sites (not represented) reveals a relation between habitat group 1 (see below) and the eutrophication parameters, and between habitat group 6 (see below) and sulphate. The other sites are more or less scattered around the centre, although groups 3 and 5 can be seen as transition groups between groups 1 and 6.

The results of ordination of taxa and environmental variables (DCCA; program CANOCO) are given in Figures 5.3 and 5.4, where the habitat groups (Figure 5.3) and microhabitat groups (Figure 5.4) are

Table 5.1 Autecology of typifying and indifferent taxa.

	GROUP	HABITAT	MICRO HABITAT	HABITAT GROUP TYPIF.	HABITAT GROUP INDIF.	MICRO-HABITAT GROUP TYPIF.	MICRO-HABITAT GROUP INDIF.	REMARK
Microtendipes gr. chloris	VI	i	is	1		D		
Sericostoma personatum	III	s,u	im,bc	1		D		
Chironomus gr. thummi	VI	i	io	2		G		p
Limnephilus bipunctatus	VI	i	bc	2		F		t
Limnephilus cf. coenosus	VI	i,s	bc	2				
Limnephilus sparsus	VI	i	bc	2				t
Peloscolex ferox	VI	i	io	2		F		
Polycelis tenuis	VI	i	us	2				
Conchapelopia sp.	III	i	bc	2	3		C	
Elephantomyia sp.	VII	i	is	2				
Limnodrilus udekemianus	VI	i	io	2		F		p
Lumbriculus variegatus	VI	i	in	2		F	G	a,t
Nemoura cinerea	VI,III	i	bc	2,4		A,C	F	t
Tubificidae (with hairs)	-	-	-	2		F		
Tubifex tubifex	VI	i	io	2		F		p
Eiseniella tetraedra	VI	i	io	2		F	E,F	s
Chaetocladius gr. piger	II,III	s,u	bc	3				
Dixa dilatata	IV	s,m	bc,um	3		E		
Hemerodromia sp.	II	s,m	wv	3		E		
Pericoma sp.	IV	s	um	3				
Sperchon squamosus	III	s,u	wv	3			E,C	
Telmatoscopus sp.	III	s,m	us	3			E	
Zavrelimyia sp.	VI	i	is	3		C		
Parametriocnemus stylatus	III	m	wv	3				
Agabus sp. 1.	VI	i	us	4	2,3		C,E,G	
Tipula sp.	VII	i	is	4	5	A		
Chironomus gr. plumosus	VI	i	io	4,6				p
Corynoneura cf. lobata	III	u	bc	4,5		A	B	
Hydroporus nigra	VI	i	wv	4	5			t
Tipula fulva	VII	i	is	4	2,5,6			
Anacaena globulus	VI	b	us	6				t
Bidessus sp. 1.	VI	i	bc,wv	6	2	G		
Helophorus grandis	V	i	bc	6				a
Hydroporus memnonius	VI	i	bc	6				t
Limnoniidae	VII	i	is	6			E	
Tipula maxima	VII	i	is	6			E,F	
Limnophyes sp.	VI	i	is	6	3			s,a
Orthocladiinae	-	-	-			E		
Elodes minuta 1.	III	s,u	bc		1,3	D	E	
Gammarus pulex	IV	s,u	bc		1	D	E	
Stenophylax sp.	III	s,u	bc		1,3		C,F	

Ptychoptera sp.	VI	i	io	1			
Dicranota sp.	III	r	is	1,3	C	E	
Pisidiidae	-	i	is	2,3	E,F		
Ceratopogonidae	-	i	is	2,3		E,F,G,H	t
Pedicia sp.	II	s	bc,wv	2,3		E,F	
Brillia modesta	II,IV	s	um	3	E		
Limnophila sp.	VII	i	is	3		E,H	s
Macropelopia sp.	III	s,u	is	3,4	E	C	
Micropsectra sp.	II,III	r	io	3	E		
Plectrocnemia conspersa	III	s,u	us	3,5	C	B	
Beraea maurus	II,IV	s	bc	3	E		
Krenopelopia sp.	II	s	us	3	E		
Enchytraeidae	VII	i	is	5	I	E,F	s
Nemurella picteti	III	s,u	bc	5		E,B	
Polypedilum breviantennatum	III	s,m	us	1			
Radix peregra	VI	i	us	1			
Thaumasoptera sp.	IV	s,m	us	1			
Asellus aquaticus	V	i	us	2,3	C		
Diptera	-	-	-	2,3	F		
Scirtes sp. 1.	VI	i	us,bc	2	G		
Chironomus gr. annularius	VI	i	io	2			
Psectrotanypus varius	VI	i	io	2			
Adelphomyia sp.	VII	i	io	3	E		
Dixa maculata	III,IV	s,u	bc,um	3	E		
Dicranomyia sp.	IV	s,m	us	3			
Ochtebius sp. 1.	III	i	bc,us	3			
Ormosia sp.	VI	i	us	3		E	
Prodiamesa olivacea	III	i	io	3			
Psychoda sp.	III	s,m	us	3			
Muscidae	-	-	-	4,5			
Tanytarsus sp.	V	i	us	4,6	C		
Sialis fuliginosa	II	s,u	is	5			
Glossiphonia complanata	VI	i	us			D	
Proasellus meridianus	VI	i	us		C		

Legend:

GROUP	HABITAT	MICROHABITAT
I = groudwater	s = spring	bc = between coarse material
II = spring	u = upper-reach	us = upon sediment
III = lotic	m = middle-reach	um = upon mineral sediment
IV = hygropetric	i = indifferent	is = in sediment
V = lentic	b = bank	im = in mineral sediment
VI = ubiquitous	r = running water	io = in organic sediment
VII = terrestrial		wv = between dense vegetation and mosses

(MICRO)HABITAT GROUP
(figures and characters are explained in the text)
TYPIF. = typifying taxon
INDIF. = indifferent taxon

REMARK
s = semi-aquatic
a = acidophilous
t = temporary
p = polysaprobic

Table 5.2 Helocrene springs; number of sites, means, and standard deviations of the quantitative environmental variables and percentages of the nominal environmental variables per site group. Abbreviations and dimensions or units are explained in Table 10.5.

Quantitative environmental variables

Habitat group	1	2	3	4	5	6
Number of sites	13	6	14	3	4	3
T	4.7	2.9	4.5	4.3	3.5	3.7
sd	1.7	3.0	1.3	1.2	0.6	0.6
PH	7.0	6.0	6.3	4.4	4.9	4.2
sd	0.2	0.8	0.4	0.3	0.3	0.2
EC	261	207	240	327	175	120
sd	91	49	60	101	6	0
O2	8.2	7.0	7.2	9.0	8.7	18.
sd	3.7	2.8	2.5	9.0	8.7	18.
O2%	67	51	56	69	65	135
sd	28	28	20	25	31	32
kj-N	1.3	2.0	0.8	0.7	0.7	0.8
sd	0.6	0.5	0.4	.04	0.4	.02
NH4	.24	.24	.09	.08	.19	.13
sd	.16	.15	.10	.09	.01	.05
NO2	.04	.03	.02	.01	.00	.02
sd	.04	.03	.02	.00	.00	.01
NO3	10.	9.0	14.	26.	11.	6.5
sd	8.0	8.4	8.7	15.	5.3	2.1
O-P	.21	.11	.11	.01	.05	.04
sd	.10	.12	.07	.01	.01	.02
T-P	.22	.13	.14	.04	.06	.07
sd	.09	.10	.06	.00	.02	.02
CL	36	26	28	22	25	14
sd	19	7	10	10	1	3
SO4	10	30	28	31	36	33
sd	17	24	19	4	12	6
FE	.06	.75	.04	.40	.30	.00
sd	.10	.91	.07	.35	.35	.00
NA	30	14	22	10	11	5
sd	18	6	19	5	1	1
K	13	12	14	11	10	4
sd	6	8	8	6	2	0
MG	7	9	9	7	7	3
sd	1	4	3	3	2	0.1
CA	43	42	51	56	41	12
sd	18	21	18	36	7	2
BOD	18.	23.	9.3	8.0	7.0	10.
sd	12.	16.	7.0	0.0	0.0	1.7
COD	1.0	1.3	0.9	0.7	0.6	0.5
sd	.43	.10	.29	.17	.00	.00
TOC	7.4	9.0	3.6	1.7	1.0	1.3

sd	8.6	9.6	4.3	.58	.00	.29
W	.47	.39	.74	.34	.21	.38
sd	.49	.63	1.1	.41	.23	.12
D	.07	.06	.14	.09	.06	.10
sd	.08	.08	.18	.10	.07	.09
S	.15	.02	.11	.14	.10	.07
sd	.18	.02	.11	.15	.11	.05
FALL	73	70	74	83	63	83
sd	32	46	38	29	25	29
SOURDIST	.07	.03	.00	.00	.00	.00
sd	.17	.08	.00	.00	.00	.00
S-T	11	18	19	13	25	12
sd	17	15	21	23	30	16
%-S	0	0	3	0	0	0
sd	0	0	11	0	0	0
%-B	13	41	24	18	34	27
sd	26	37	30	28	36	46
%-T	13	41	27	18	34	27
sd	26	37	33	28	36	46
%MM-B	6	23	10	23	8	33
sd	10	21	20	25	15	58
%MM-E	0	0	4	0	0	0
sd	0	0	12	0	0	0
%MM-S	0	0	1	0	0	0
sd	0	0	5	0	0	0
%MMSILT	9	23	15	7	0	0
sd	15	23	22	12	0	0
%MMSAND	26	17	21	3	15	7
sd	16	24	23	6	19	12
%MMGRAVE	11	0	4	0	0	0
sd	14	0	12	0	0	0
%MMDETR	48	37	44	67	78	60
sd	22	36	22	15	17	53

Nominal environmental variables

Habitat group	1	2	3	4	5	6
SPRINGSOURCE	39	83	43	33	50	67
SPRINGSTREAM	62	17	50	67	50	33
TEMPOR	0	83	29	33	0	33
STCMDLPE	31	33	36	33	50	67
STSAND	69	33	50	33	25	33
STCDLE	69	33	57	33	50	33
STFDPE	15	0	7	67	0	33
STSILT	8	50	21	0	25	0
SHADOW	92	67	86	67	100	67
SURFOR	62	67	86	67	100	67
SURGRA	15	50	14	0	0	0
SURWOB	23	0	0	0	0	0
SURHEA	0	0	0	33	0	0

Nominal environmental variables

Microhabitat group	A	B	C	D	E	F	G	H	I
Number of sites	6	12	10	24	23	13	7	2	8
leaves	33	58	50	13	48	23	14	0	0
leaves/sand	17	8	20	25	13	0	0	0	13
leaves/vegetation	0	17	10	4	0	0	0	0	13
pool	0	0	10	0	0	0	0	0	0
bare sand	0	0	10	4	4	0	0	0	13
sand/detritus	50	17	0	17	9	31	0	0	25
sand/coarse detritus	0	0	0	33	4	0	0	0	0
vegetation/mud	0	0	0	4	17	46	0	0	0
vegetation	0	0	0	0	4	0	14	50	13
leaves/iron deposit	0	0	0	0	0	0	71	50	25
spring source	50	42	10	46	52	85	57	50	63
spring stream	50	58	90	54	48	15	43	50	38

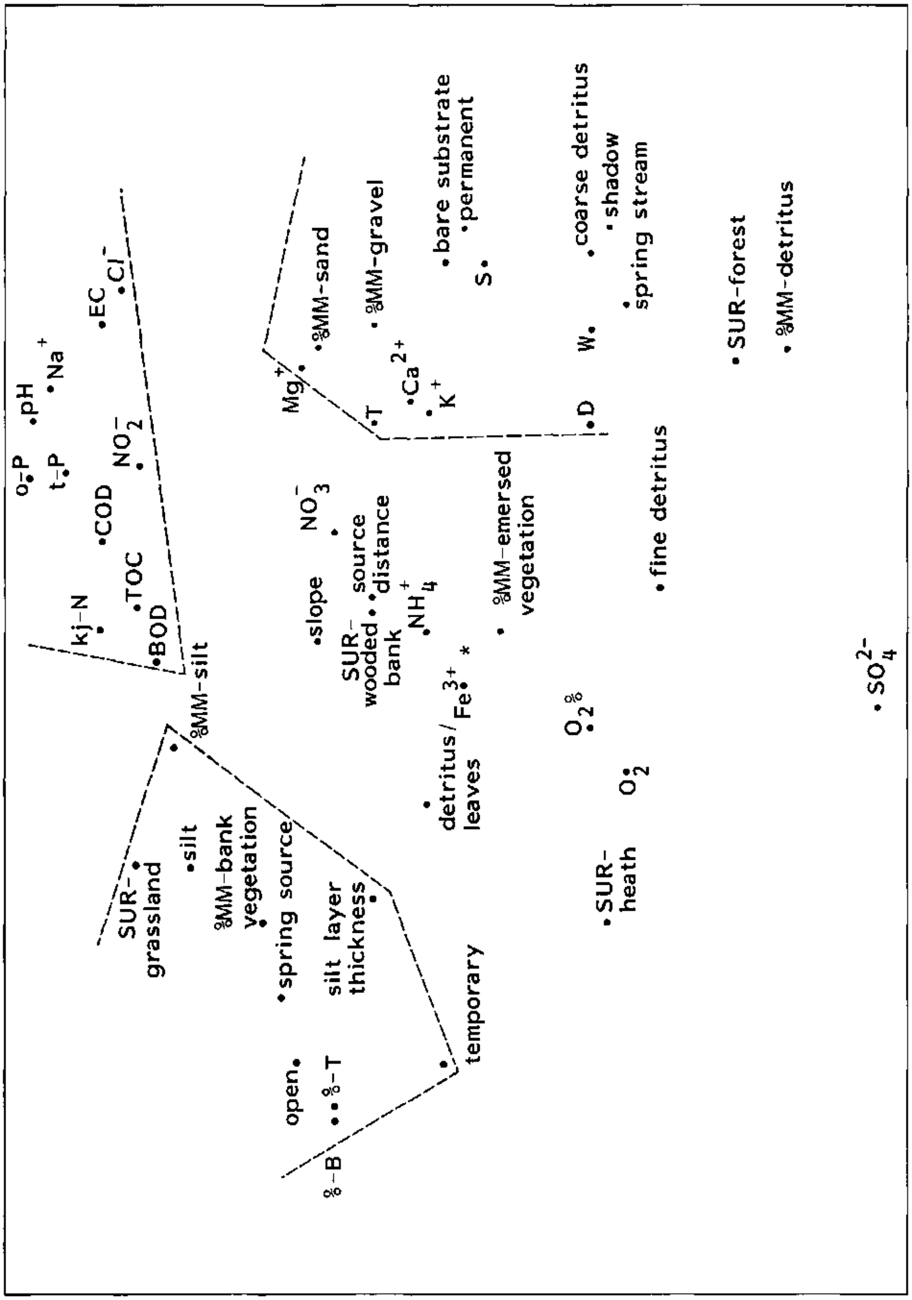

Figure 5.2 Helocrene springs; ordination (PCA) diagram for axes 1 (horizontally) and 2 (vertically) with only environmental variables indicated. Dotted lines indicate the environmental parameter complexes. For further explanation see Sections 3.4.2 and 5.2.3, and Figure 3.10. Abbreviations are explained in Table 10.5.

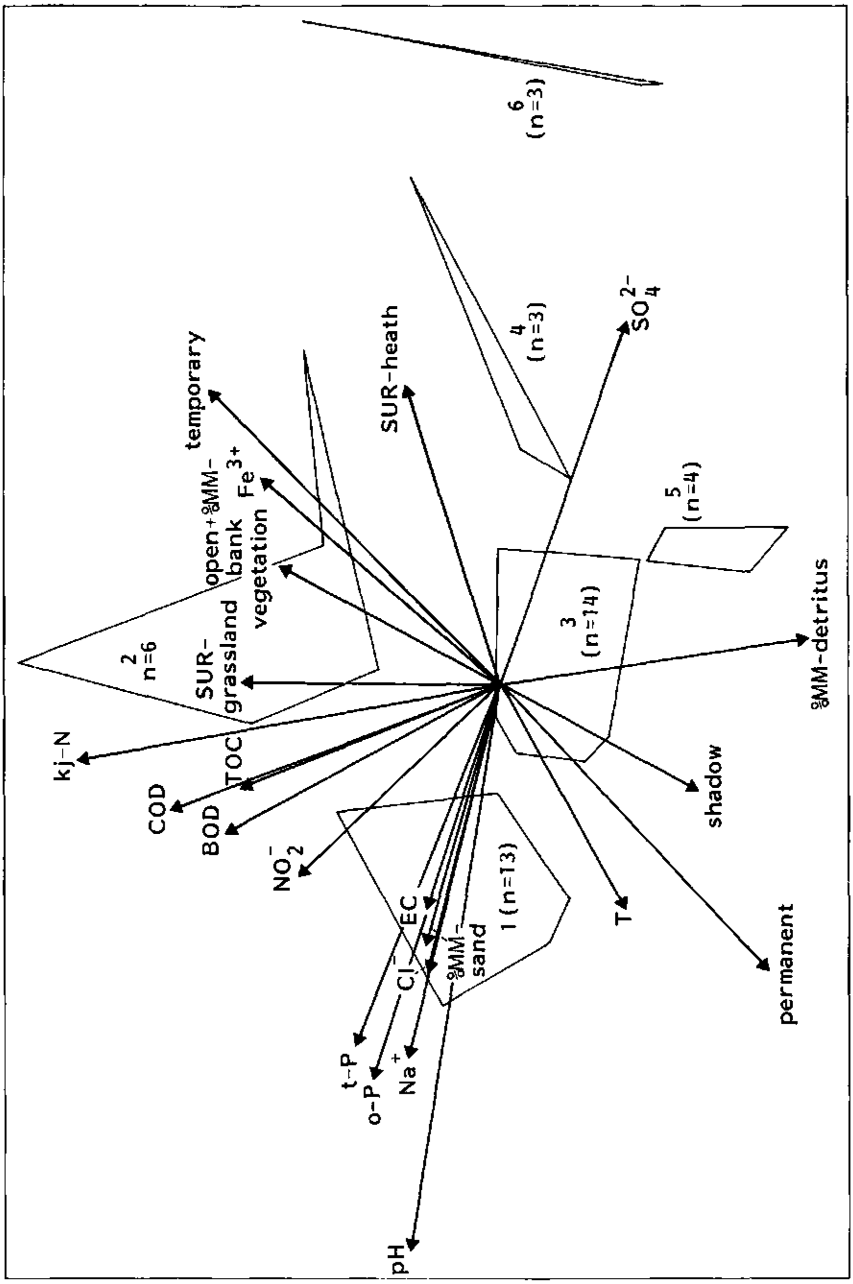

Figure 5.3 Helocrene springs; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically) with the habitat groups (contour lines) and the most important environmental variables (with an interset correlation greater than 0.3 (arrows)) indicated. For further explanation see Sections 3.4.2 and 5.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

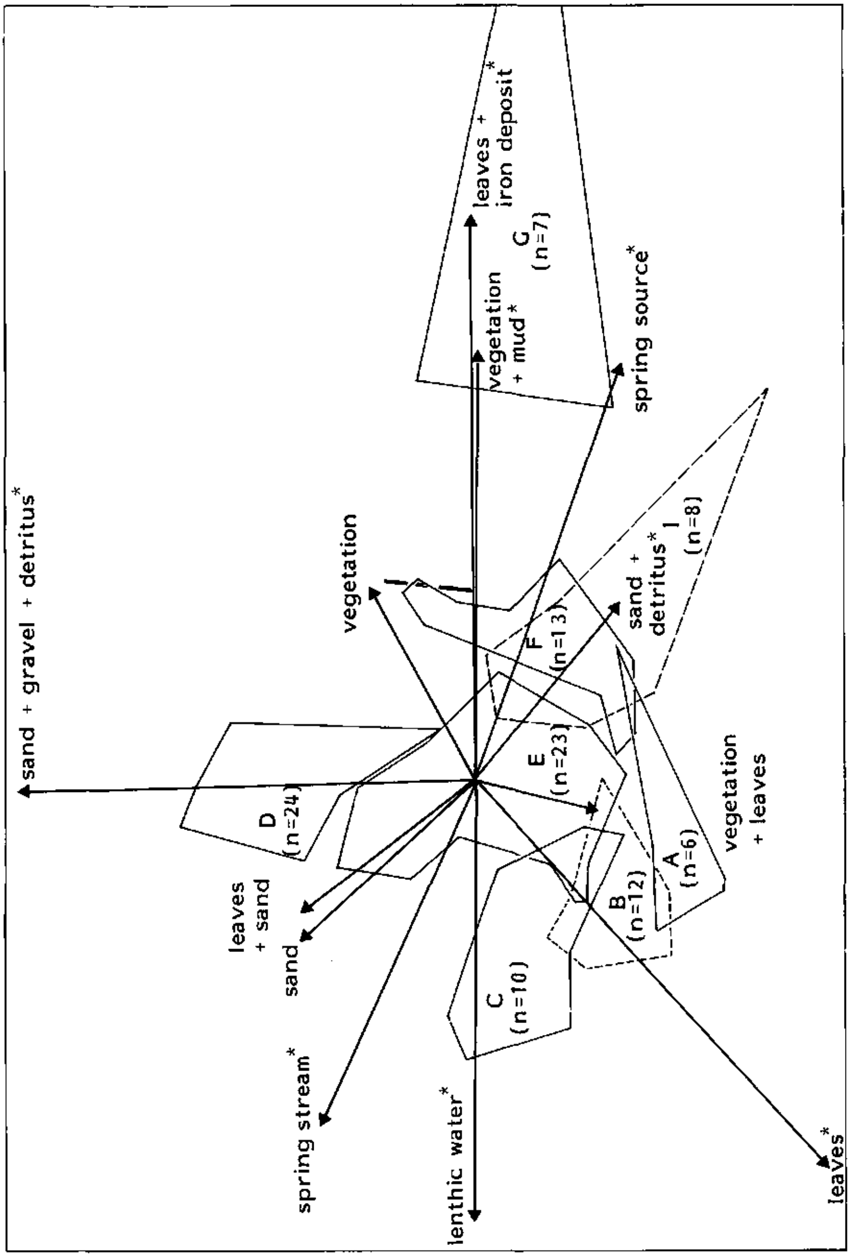

Figure 5.4 Helocrene springs; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically) with the microhabitat groups (contour lines) and the most important environmental variables (with an interset correlation greater than 0.3 (arrows)) indicated. For further explanation see Sections 3.4.2 and 5.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

indicated. For sixteen sites, the respective habitat sample from the spring source and the adjacent spring stream aggregate within one group. This indicates the dominance of common environmental factors in these seemingly different habitats, which is of course also reflected in the microhabitat groups. Therefore, the habitat groups are seen as site groups. Aberrant groups consisting of only one sample in both ordination diagrams will not be discussed.

Because of the dominance of common environmental factors on both site (habitat) and microhabitat groups, these groups are discussed together. On forehand, some similarities between the distribution of the site groups in Figure 5.3 and the distribution of microhabitat groups in Figure 5.4 can be seen. For example, the dominant variables related to site group 2 (Kj-N, temporary, Fe^{2+}, etc.) correspond with the variables related to microhabitat groups F, G and H (leaves, iron deposits, vegetation and mud). The relation between site and microhabitat will be dealt with further in the next section. Numbers between parentheses in the text indicate the relative frequency of occurrence of that environmental variable in the relevant group.

Site group 1

Within this data set group 1 is associated with a relatively high degree of eutrophication (high conductivity, high phosphate and ammonium concentrations, and high pH) (Figure 5.3). The sampled habitats consist mainly of coarse detritus and leaves on sand and gravel. They are predominantly (62%) situated in spring streams and vegetation cover is sparse. Most of the sites are situated on the northeastern hill-ridge. Typifying and indifferent species are mostly rheophilous (upper reaches and spring streams), and typical spring species are scarce. These rheophilous species also typify microhabitat group D, a group related to sand, gravel and detritus (Figure 5.4).

Site group 2

Sites within group 2 contain large amounts of organic material in solution and the iron concentration is high. Five of the six sites are temporary spring sources and four of them are vegetated. The main species are ubiquitous freshwater species, indifferent to habitat type, with a polysaprobic character, and most of them are drought resistant. Typifying species inhabiting silt appear in microhabitat group F, the polysaprobic and some semi-aquatic species appear in G and H. Microhabitat group F and parts of group H are associated with vegetation and mud in spring sources. Microhabitat groups H and especially G are associated with accumulations of leaves covered with iron deposits (71%).

Site group 3

Site group 3 consists of sites mostly (72%) situated on the southeastern hill-ridge. Potassium and magnesium concentrations are slightly elevated. This is the only group with a number of typifying and indifferent species from real springs, spring streams and hygropetric environments. The microhabitats are divided into two groups. Microhabitat group E contains the real spring species, and species of water films and spring streams. This group takes a central position in Figure 5.4, indicating the absence of any association with the extremes of any specific parameter, although the presence of leaves has some importance (48%). Microhabitat group C includes ubiquitous freshwater species and more common running water species. This group represents samples composed of leaves whether or not in combination with vegetation or sand (80%) and taken in spring streams (90%).

Site group 4

At sites within group 4 sulphate concentrations are high and ammonium and phosphate concentrations are low. Typifying and indifferent species are ubiquitous freshwater species. Some of the microhabitats belong to group C, the others to microhabitat group A, which is composed of indifferent lotic species resistent to drought. This group is associated with the variables sand and detritus.

Site group 5

All sites of group 5 are situated within one watershed on the northeastern hill-ridge (called Springendal). Although most of the samples were taken from detritus packages, concentrations of organic material in solution were low. The water is relatively poor in nutrients and weakly acid. There is only one typifying species, Nemurella picteti. The presence of many species from springs and spring streams is interesting, although all occur in low frequencies. Microhabitat group B, associated with leaves (81%), consists of the species combination of Nemurella picteti, Macropelopia sp. and Plectrocnemia conspersa. This microhabitat group together with microhabitat group I composes group 5. Microhabitat group I is typified by semi-aquatic species occurring in several substrates.

Site group 6

This group of temporary, acid and oligotrophic sites is situated entirely on the western hill-ridge. The chemical composition of the water at these sites indicates a direct input of rainwater. This group is typified by several Coleoptera and Diptera. No microhabitats were sampled at sites within this group.

5.3 Discussion of data

Illies (1952) reported that species living in the lower reaches of mountain streams also occurred in the upper reaches of streams of the western European plain. Within the region we studied, the ubiquitous freshwater species of mountain streams indeed have become typical spring species. According to Illies (1961) and Illies & Botosaneanu (1963), this transition depends on the latitude and altitude of the source and is due mainly to temperature and zoogeographical factors. This principle is generally accepted (Hawkes 1975), although there has been criticism of some aspects (Thorup 1966).

Compared with the faunistic composition of springs in a nearby region at a higher altitude and lower latitude, i.e. the region of Baumberge in Germany (Beyer 1932), the fauna in our region consists definitely of less typical spring inhabitants. However, the fauna of Baumberge consists in turn of less typical spring inhabitants compared to alpine and subalpine spring regions (Illies 1952). The results of this comparison are consistent with the above-mentioned principle. However, as Thorup (1966) argued pollution effects should not be disregarded. All of the springs under study are influenced by eutrophication to some degree.

Maas (1959) concluded that the southeastern hill-ridge in the study area was richer in nutrients (macro-ions) than the northeastern ridge. This difference, which was due to the nature of the local soil, seemed to have disappeared in 1982 (Table 5.3). Especially the

Table 5.3 Comparison of some average chemical parameters measured in helocrene springs on the southeastern hill-ridge and the northeastern hill-ridge in 1959 and in 1982. Aberrant number of sites are given between brackets.

		Southeastern hill-ridge		Northeastern hill-ridge	
		1959	1982	1959	1982
number of sites		4	9	3	11
pH		6.9	6.5	5.8	6.2
EC	µS	278	260	95	218
Ca	mg/l	22.7	47.2	9.5	42.8
Mg	mg/l	8.3	9.2	2.3	7.1
NO_3	mg/l	1.7	19.3	.8	10.7
SO_4	mg/l	39.6(2)	41.9(5)	17.1(3)	34.8(7)
NO_2	mg/l	0	0.04	0	0.02

calcium and nitrate concentrations in the springs of the southeastern hill-ridge have risen during the last twenty years. In the same period the values of all the measured variables on the northeastern ridge rose strongly, which abolished the local differences between them. Due to a strong increase in the intensity of the agricultural use of large parts of the ridge, the input of nutrients (especially nitrate) has apparently masked the natural differences of the soils.

Detailed knowledge on the autecology of typifying taxa supports the ecological validity of the groups. Many literature references gave only rough indications. Still differences between some groups of typifying taxa appeared, according to the literature and according to our observations, to be clearly associated with differences in the major environmental factors. In both site and microhabitat groups the master factors are the duration of drought and the pH. Within the occurring combinations of these factors the nutrient load has a diversifying function.

Figure 5.5 shows the typological relations within the springs under

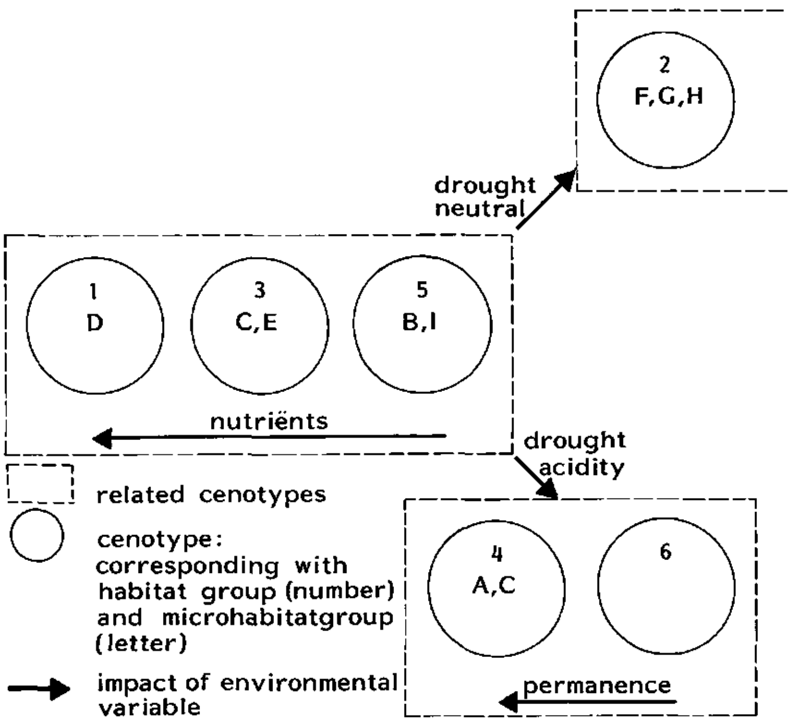

Figure 5.5 Helocrene springs; relations between site (figures) and microhabitat (characters) groups (circles) and cenotypological relations. The arrows indicate the direction of increase of the respective variables.

study. Since microhabitat groups mostly occur within one site group and since spring sources and spring streams (our original habitat samples) often group together, only the site groups, will be considered as cenotypes. A cenotype develops or becomes impoverished under the impact of environmental changes. Series of cenotypes, therefore, can occur in particular developmental stages (succession stages).

It is concluded that site groups 1, 3 and 5 are related cenotypes of helocrene springs. The group sequence (5, 3, 1) reflects an increase in eutrophication and/or (secondary) organic enrichment due to human activity as well as due to natural processes (e.g. input of leaves). But there are also differences in groundwater supply as can be seen from the lower pH in group H5. Site group 2 is described as the cenotype of temporary, neutral seepage marshes. Site groups 4 and 6 are related cenotypes of temporary, acid seepage marshes. The drought period is longer in 6 than in 4.

Most microhabitat groups occur within only one cenotype. For the helocrene springs studied, each cenotype is a specific combination of microhabitats. Furthermore, the microhabitat groups are related not only to 'substrate' (in a broad sense like leaves, mud, vegetation) differences but also to other dominant environmental variables (e.g. constancy in water flow, permanence, acidity). This can be explained by the fact that 'substrate' is determined on its turn by the dominant surrounding environmental variables, its character results from conditions pertaining to climatology, geology, history and hydrology. The last factor is the most strongly differentiated one within the region studied. Only microhabitat groups C and E can also be indicated as cenotypes of helocrene spring stream and helocrene spring source, respectively. Other microhabitat groups are more strongly associated with permanence, probably reflecting gradients within a marsh or spring from seepage source to dry bank. These groups can be seen as choriotypes (Section 2.3.2).

Illies & Botosaneanu (1963) divided a spring (crenon) into an eucrenon (spring source) and a hypocrenon (spring stream). This division was not supported by Thorup (1966). Our results show that such a division does not reflect a fundamental difference but depends strongly on local environmental master factors. Within the region studied hydrology is this local environmental master factor.

6. MACROFAUNAL COMMUNITY TYPES IN STREAMS

6.1 Introduction

Due to the gentle slope (fall averages between almost zero and five pro mille) of the terrain the streams in the study area are lowland streams like most running waters in The Netherlands (Tolkamp 1980, Higler & Mol 1985). Most streams are fed by rainwater, so they lack a well defined source. Their discharge shows a smoothed relation with the amount and frequency of precipitation in the various seasons. Current velocity varies from 5 to 30 cm/s in summer and early autumn, and from 30 to 60 cm/s in late autumn, winter and spring. Incidental, current velocities can reach up to 100 cm/s or more, for example after heavy rainfall or thunderstorms (Gardeniers & Tolkamp 1985). Especially, the rainwater fed upper reaches can dry up in summer. Some streams are fed by a helocrene spring and have a more constant discharge pattern. The studied lowland streams are up to 10 m wide and 1.5 m deep.

The natural lowland stream is situated mainly on a sandy soil; if the sand is mixed with gravel and/or clay, a mosaic pattern of substrate types occurs (Tolkamp 1980). The dynamic flow pattern further diversifies this mosaic (silt, detritus, leaves, dams, riffles, etc.). The natural lowland stream is often shaded by shrubs and trees, and its longitudinal profile meanders. Its transverse profile is irregular, differing from sandy shallows to strongly overhanging (hollow) banks. This complex of morphological and hydraulic characteristics will be called the 'stream-character' and it is best developed in natural streams.

Regulation of lowland streams implies:

- straightening of the bends,
- cutting of the trees/shrubs often followed by removal of the aquatic vegetation two to eight times per year,
- widening and deepening of the transverse profile to a standard 1:2/1:3 profile which results in a reduced current velocity (mostly lower than 5 cm/s) and a silty-muddy bottom,
- consolidation of the banks with concrete blocks, wooden frames or nylon mats,
- construction of movable weirs to adjust the water level.

The 'stream-character' in regulated streams is poorly developed.

6.2 Results

6.2.1 Data collection

Biotic and abiotic data were collected from 156 sites; 136 sites were visited only once and 22 sites were visited twice. The samples were collected from 1982 to 1984 inclusive, during spring, summer and autumn. A total of 56 abiotic variables was measured at each site.

6.2.2 Preprocessing of the data

Of the macrofaunal data (a total of 647 taxa) were, after careful individual weighing, 510 taxa included in the analysis. Further information on the preprocessing procedures is given in Section 3.4.1.

6.2.3 Multivariate analysis

The interpretation of the results of clustering (program FLEXCLUS) and ordination (program CANOCO) of the data leads to the description of 14 site groups (see below for further explanation). Numbers of sites, averages and standard deviations of the quantitative environmental variables, and relative frequency of the nominal variables per site group are given in Table 6.1. A list of all taxa present with their typifying weight per site group indicated (program NODES) is available from the author on request. The autecology of the most important typifying taxa will be discussed later.

The PCA-diagram (Figure 6.1) illustrates the relations between variables. Variables that are projected both close to each other and far from the center of the diagram follow similar patterns across sites. PCA also revealed site scores. Centroids of site groups, based on the site scores, are also indicated in Figure 6.1. The centroids of the site groups 1, 2, 3 and 4 relate to variables which characterize natural streams. Site groups 5 and 14 are related to variables which indicate the presence of organic pollutants. Site groups 7, 8 and 11 are related to variables which characterize regulated streams. Site groups 9 and 13 are related to variables characteristic of waters with a temporary character (often sampled in summer). Finally site groups 6 and 12 take an intermediate position between natural and regulated streams. The site groups enumerated so far are ordered along a gradient (indicated by the line AB which was fitted by eye) with an aberrant group of sites at the top of the figure. The position along the line AB is related to the transition from natural to regulated streams. The transition reflects the main pattern in this set.

The results of ordination of sites and environmental variables (DCCA; program CANOCO) are illustrated in Figures 6.2 and 6.3. The eigenvalues (respectively 0.41, 0.26, 0.18 and 0.17 for the first four DCCA ordination axes) indicate that there is a steep environmental gradient along the first axis and a less steep one along the second axis. The third and fourth axes are less important. The site groups will first be described with respect to the important related environmental variables (Table 6.1) and to the ordination results (Figures 6.2 and 6.3). Afterwards a validation of the groups will be based on knowledge present of the autecology of typifying taxa.

The first and most important environmental gradient in Figure 6.2 runs from site group 1 (right-hand lower corner) to site group 8 (left-hand lower corner). These site groups represent the extremes of the first axis shown in Figure 6.1. In site group 1, the fall is high, and the related variables, like irregular longitudinal and transverse profiles, occurrence of meanders and a substrate consisting of stones,

Table 6.1 Streams; number of sites, means, and standard deviations of the quantitative environmental variables and percentages of the nominal environmental variables per site group. Abbreviations are explained in Table 10.5.

Quantitative environmental variables

Site group		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Number of sites		19	5	5	21	12	16	21	16	9	15	4	3	11	1
T		7.	11.	7.	8.	9.	9.	9.	12.	16.	8.	7.	7.	19.	12.
	sd	3.	3.	3.	3.	2.	3.	3.	3.	4.	3.	2.	2.	1.	-
PH		7.1	7.7	7.4	7.5	7.4	7.1	7.3	7.3	7.5	7.0	7.3	6.0	7.0	-
	sd	0.4	0.4	0.5	0.4	0.3	0.4	0.3	0.6	0.5	0.3	0.6	0.6	0.4	-
EC		288	403	292	370	392	454	508	510	465	494	360	292	462	-
	sd	90	127	54	49	189	209	168	164	179	189	59	108	77	-
O2		11.	11.	9.	10.	8.	11.	10.	8.	6.	9.	11.	14.	4.	0.
	sd	1.	1.	2.	2.	1.	2.	2.	2.	5.	4.	3.	2.	1.	0.
O2%		87.	98.	73.	86.	69.	88.	84.	70.	60.	77.	89.	112	40.	0.
	sd	8.	15.	19.	18.	10.	18.	24.	19.	40.	27.	28.	13.	16.	0.
O-P		0.4	0.1	0.4	0.3	2.7	0.7	0.5	0.4	1.2	0.4	.02	.03	1.1	-
	sd	0.9	0.1	0.1	0.3	1.9	1.3	0.8	1.0	1.6	0.5	.01	.04	0.6	-
NH4		0.1	0.4	1.5	0.5	6.3	2.7	1.6	0.9	4.8	2.5	0.2	0.8	2.4	65.
	sd	0.1	0.2	1.6	0.4	5.1	4.5	1.8	0.7	9.0	2.1	0.1	0.3	2.3	-
NO3		12.	8.0	8.4	9.3	5.6	6.0	4.9	2.0	4.2	5.6	9.3	19.	8.8	-
	sd	7.2	1.7	3.6	5.6	2.4	3.5	2.7	1.4	3.8	3.6	7.6	16.	4.9	-
CL		33.	34.	36.	43.	124	42.	65.	44.	35.	39.	18.	18.	47.	82.
	sd	13.	12.	12.	13.	94.	15.	112	24.	10.	17.	4.	4.	4.	-
SO4		40.	60.	44.	49.	76.	63.	78.	62.	64.	76.	77.	81.	54.	-
	sd	15.	26.	13.	16.	27.	18.	20.	23.	26.	20.	15.	42.	16.	-
NA		18.	15.	22.	23.	76.	32.	38.	34.	23.	27.	12.	4.	17.	-
	sd	8.	9.	4.	8.	68.	31.	59.	34.	24.	21.	13.	4.	2.	-
K		10.	12.	12.	14.	14.	11.	11.	6.	21.	10.	5.	10.	42.	-
	sd	4.	2.	5.	5.	5.	3.	3.	2.	6.	3.	1.	2.	16.	-
MG		9.	8.	11.	9.	8.	8.	8.	6.	9.	9.	6.	7.	8.	-
	sd	4.	2.	3.	3.	2.	2.	2.	3.	4.	2.	1.	2.	1.	-
CA		27.	41.	25.	38.	50.	41.	64.	75.	38.	70.	60.	49.	27.	-
	sd	8.	18.	12.	9.	21.	13.	21.	19.	11.	34.	12.	19.	4.	-
HCO3		37.	47.	50.	79.	120.	61.	97.	125.	114.	90.	43.	7.	65.	-
	sd	18.	10.	42.	33.	54.	34.	54.	93.	57.	57.	20.	5.	14.	-
W		0.9	1.9	1.0	2.2	3.2	3.1	3.7	6.2	1.6	1.8	2.0	0.9	1.1	0.8
	sd	0.4	0.6	0.4	1.2	1.7	1.3	1.8	2.3	0.6	0.7	0.6	0.1	0.8	-
D		0.1	0.4	0.2	0.3	0.3	0.4	0.4	0.9	0.3	0.3	0.4	0.3	0.2	0.2
	sd	0.1	0.3	0.1	0.2	0.2	0.3	0.2	0.5	0.1	0.1	0.1	.05	0.1	-
S		25.	28.	17.	33.	27.	24.	18.	5.	4.	40.	2.	0.	0.	2
	sd	10.	14.	11.	18.	27.	14.	13.	3.	8.	130	2.	0.	0.	-
FALL		11.	3.0	4.4	2.8	1.9	1.2	0.8	0.1	2.1	1.4	0.9	1.6	3.1	.01
	sd	8.7	3.1	1.3	1.5	1.7	1.4	1.1	0.2	1.1	1.6	0.2	0.1	0.5	-
SOURDIST		1.0	4.3	0.9	3.8	4.0	6.4	6.9	7.9	2.9	1.5	2.4	0.3	3.8	.01
	sd	1.2	1.6	1.3	1.4	2.4	5.1	3.8	5.9	1.4	1.0	1.5	0.2	1.0	-
S-T		.00	.00	.00	.04	.10	.01	.14	.11	.07	.10	.01	.02	.00	.10

	sd	.00	.00	.01	.09	.16	.03	.21	.16	.17	.12	.00	.02	.00	-
%-A		0	0	0	0	4	6	8	16	0	9	60	23	0	20
	sd	0	0	0	1	14	22	18	26	0	24	39	33	0	0
%-F		0	0	0	0	1	4	3	14	0	6	1	2	0	0
	sd	0	0	0	0	3	10	6	18	0	20	1	2	0	0
%-S		0	0	18	3	14	11	14	34	0	7	32	20	0	0
	sd	1	0	31	9	20	23	27	29	0	17	40	28	0	0
%-E		4	1	2	2	1	1	3	7	1	2	5	0	0	10
	sd	10	0	4	5	2	1	8	7	3	5	9	0	0	0
%-B		15	3	2	2	2	2	4	2	0	0	0	0	0	0
	sd	27	4	2	2	2	3	9	2	0	1	0	0	0	0
%-T		20	3	22	7	17	16	21	49	1	23	95	33	0	10
	sd	29	4	31	12	22	26	32	30	4	38	5	47	0	0
%MM-B		5	6	6	6	17	7	26	22	7	18	15	13	0	0
	sd	6	8	5	9	16	10	20	18	13	13	17	19	0	0
%MM-E		7	11	4	8	0	5	5	11	0	12	18	33	0	0
	sd	14	16	8	13	0	8	12	11	0	22	18	9	0	0
%MM-F		0	0	0	0	0	0	1	6	0	2	8	0	0	0
	sd	0	0	0	0	0	0	4	11	0	9	13	0	0	0
%MM-S		3	4	8	6	5	6	9	24	0	21	45	7	0	0
	sd	11	8	16	10	12	15	13	18	0	18	15	9	0	0
%MMSILT		6	14	12	11	43	35	30	30	60	31	13	23	50	50
	sd	12	13	10	12	29	20	26	15	17	25	13	17	0	0
%MMSAND		30	18	24	30	19	31	18	5	33	8	0	0	50	0
	sd	15	18	13	15	22	19	19	11	24	11	0	0	0	0
%MMGRAVE		11	11	16	10	3	3	1	0	0	1	0	0	0	0
	sd	9	16	10	9	6	6	4	0	0	4	0	0	0	0
%MMSTONE		6	1	0	2	3	2	0	0	0	1	0	0	0	0
	sd	8	2	0	5	7	5	0	0	0	2	0	0	0	0
%MMDETR		33	36	29	29	12	12	10	2	0	5	3	23	0	50
	sd	21	15	11	13	16	11	14	8	0	11	4	17	0	0

Nominal environmental variables

Site group	1	2	3	4	5	6	7	8	9	10	11	12	13	14
SPRING	53	40	40	52	67	56	43	50	22	87	100	100	0	100
SUMMER	0	0	0	0	0	0	0	38	67	0	0	0	100	0
AUTUMN	47	60	60	48	33	44	57	13	11	13	0	0	0	0
SHAPLSRE	11	40	20	24	75	69	76	100	33	87	100	100	0	100
SHAPLSIR	89	60	80	81	25	31	24	0	0	13	0	0	0	0
SHAPIRR	0	0	0	0	0	0	0	0	67	0	0	0	100	0
TEMPOR	0	0	60	57	17	0	14	0	78	87	100	100	100	100
WATLF	0	40	0	05	25	38	48	56	11	27	0	0	0	100
SEE	11	0	0	05	25	31	29	06	0	40	50	33	0	0
COLORLES	47	0	0	10	08	19	05	13	11	20	25	0	0	0
YELLOW	42	100	60	81	25	56	62	81	0	73	75	100	0	0
GREEN	0	0	0	0	0	0	0	0	11	0	0	0	0	0
BROWN	11	0	40	10	25	13	24	06	0	0	0	0	0	0
GREYBLAC	0	0	0	0	42	13	10	0	11	07	0	0	0	100
SMELL	0	0	20	10	42	13	19	13	22	07	0	0	0	100
CLEAR	89	60	80	76	42	50	38	06	11	67	100	100	0	0
SLTURB	11	40	20	19	25	38	38	63	67	33	0	0	100	0
TURBID	0	0	0	05	33	13	24	31	22	0	0	0	0	100

BACTNONE	100	100	80	100	67	100	90	100	78	93	75	100	100	0
BACTSL	0	0	0	0	0	0	10	0	0	07	25	0	0	100
BACTABUN	0	0	20	0	33	0	0	0	22	0	0	0	0	0
POLLUT	05	20	20	19	75	13	24	31	22	07	0	0	0	100
CLEANIN	05	20	40	14	50	19	62	44	11	07	0	0	0	100
SAND	100	80	100	100	100	100	86	88	89	100	100	100	100	0
SILT	0	0	0	0	0	0	14	13	11	0	0	0	0	100
CLAY	0	0	20	0	08	0	05	0	0	07	0	0	0	0
STSAND	95	40	100	95	50	81	38	25	67	20	25	0	100	0
STSILT	0	0	0	0	0	0	10	0	0	0	0	0	0	0
STCM	74	40	80	43	17	31	05	06	0	07	0	0	0	0
STCDLE	42	80	100	62	17	06	19	0	0	0	0	0	0	100
STCMCDLE	26	0	0	10	08	19	05	0	0	07	0	0	0	0
STFDPE	42	40	20	29	0	0	0	06	0	07	0	0	0	0
STCMDELE	26	0	0	10	0	0	0	0	0	0	0	0	0	0
STSILT	11	60	60	52	75	69	76	88	100	87	50	33	100	100
STCMI	0	0	0	05	17	0	0	0	0	0	0	0	0	0
STFDPESI	05	20	0	0	0	06	05	0	0	0	0	0	0	0
STCDLESI	16	40	20	19	25	38	24	0	0	0	25	67	0	0
MEANDNT	0	40	20	14	75	44	67	100	100	60	100	100	100	100
MEANDSL	26	0	20	38	17	31	29	0	0	33	0	0	0	0
MEAND	74	60	60	48	08	25	05	0	0	07	0	0	0	0
REGULNT	89	60	80	71	17	31	24	0	67	07	0	0	100	0
REGULSL	05	0	0	05	08	19	0	0	0	13	0	0	0	0
REGUL	05	40	20	24	75	50	76	100	33	80	100	100	0	100
PSIRR	95	60	80	81	25	50	19	0	0	13	0	0	0	0
PS30	0	0	0	0	0	0	10	0	67	0	0	0	100	0
PS45	0	0	20	05	25	13	29	50	0	47	100	67	0	0
PS75	05	40	0	14	42	31	38	50	33	27	0	33	0	0
PS90	0	0	0	0	08	06	05	0	0	13	0	0	0	100
PROCON	05	40	20	10	67	44	48	19	11	13	0	0	0	0
SHADOW	79	60	100	76	67	81	43	13	89	27	0	33	64	100
SURURB	05	20	0	14	17	19	0	06	11	20	0	0	0	0
SURFOR	47	40	100	52	17	38	29	0	67	0	0	0	18	0
SURWOB	47	0	0	38	42	31	38	13	78	20	0	0	64	0
SURFIE	05	0	0	0	17	06	24	06	22	40	25	0	0	0
SURGRA	42	60	20	43	58	56	57	100	56	67	75	100	55	100
ISOL	0	0	0	0	0	0	0	0	67	0	0	0	100	0

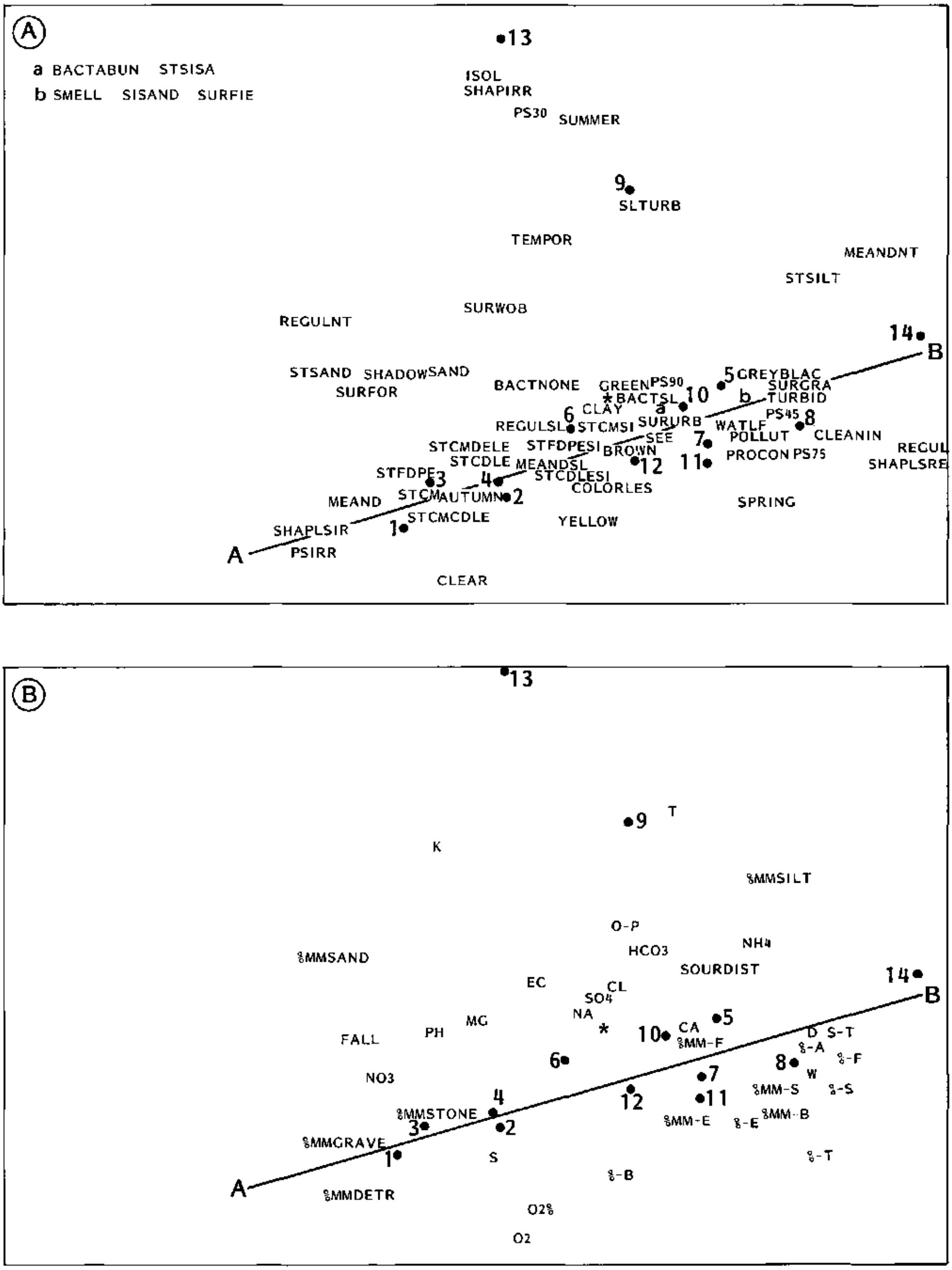

Figure 6.1 Streams; ordination (PCA) diagram for axes 1 (horizontally) and 2 (vertically) for nominal (A) and quantitative (B) environmental variables. For further explanation see Sections 3.4.2 and 6.2.3, and Figure 3.10. Abbreviations are explained in Table 10.5.

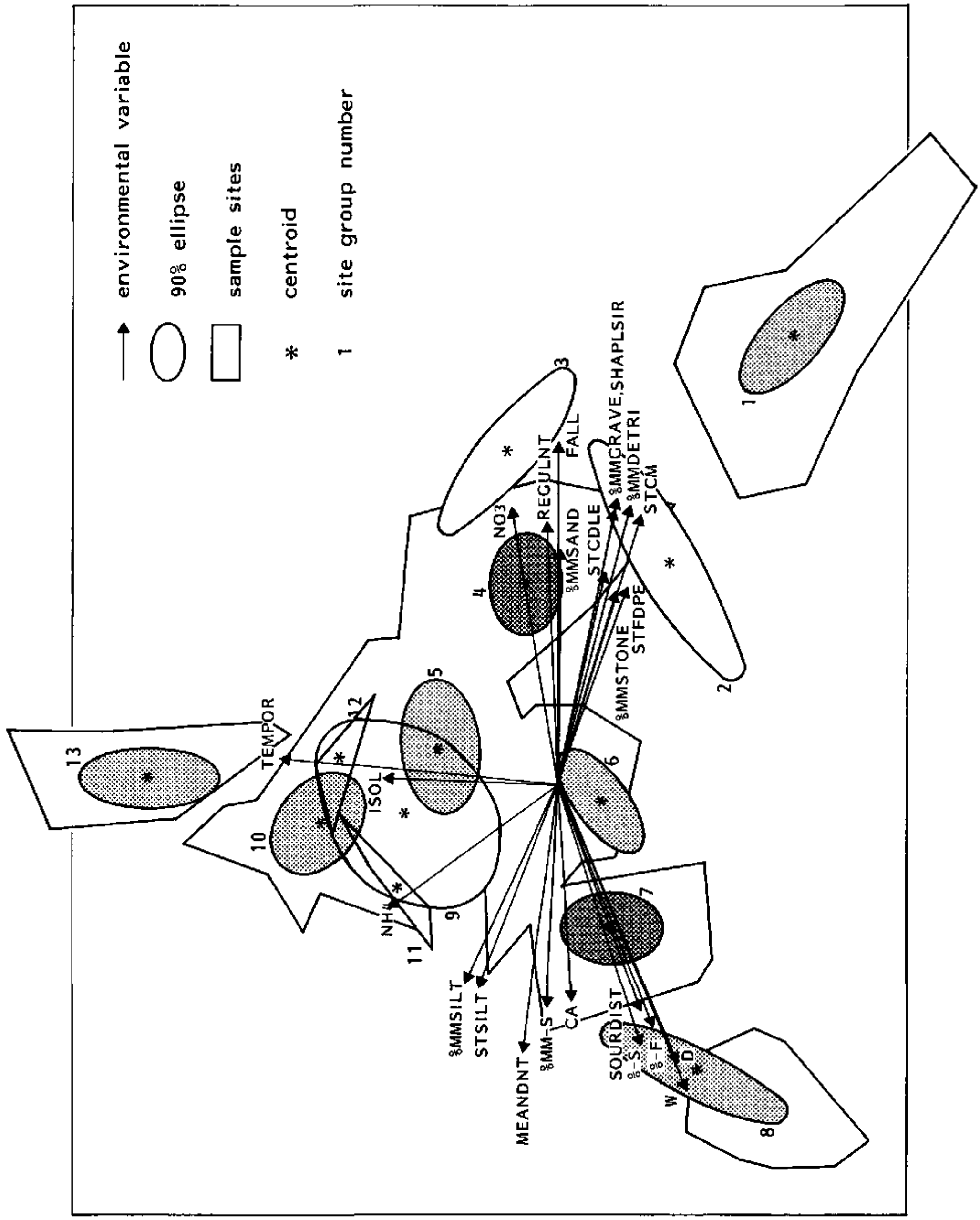

Figure 6.2 Streams; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically). The contour line describes the total variation of site scores. Only environmental variables with an interset correlation greater than 0.4 are shown (arrows). For further explanation see Sections 3.4.2 and 6.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

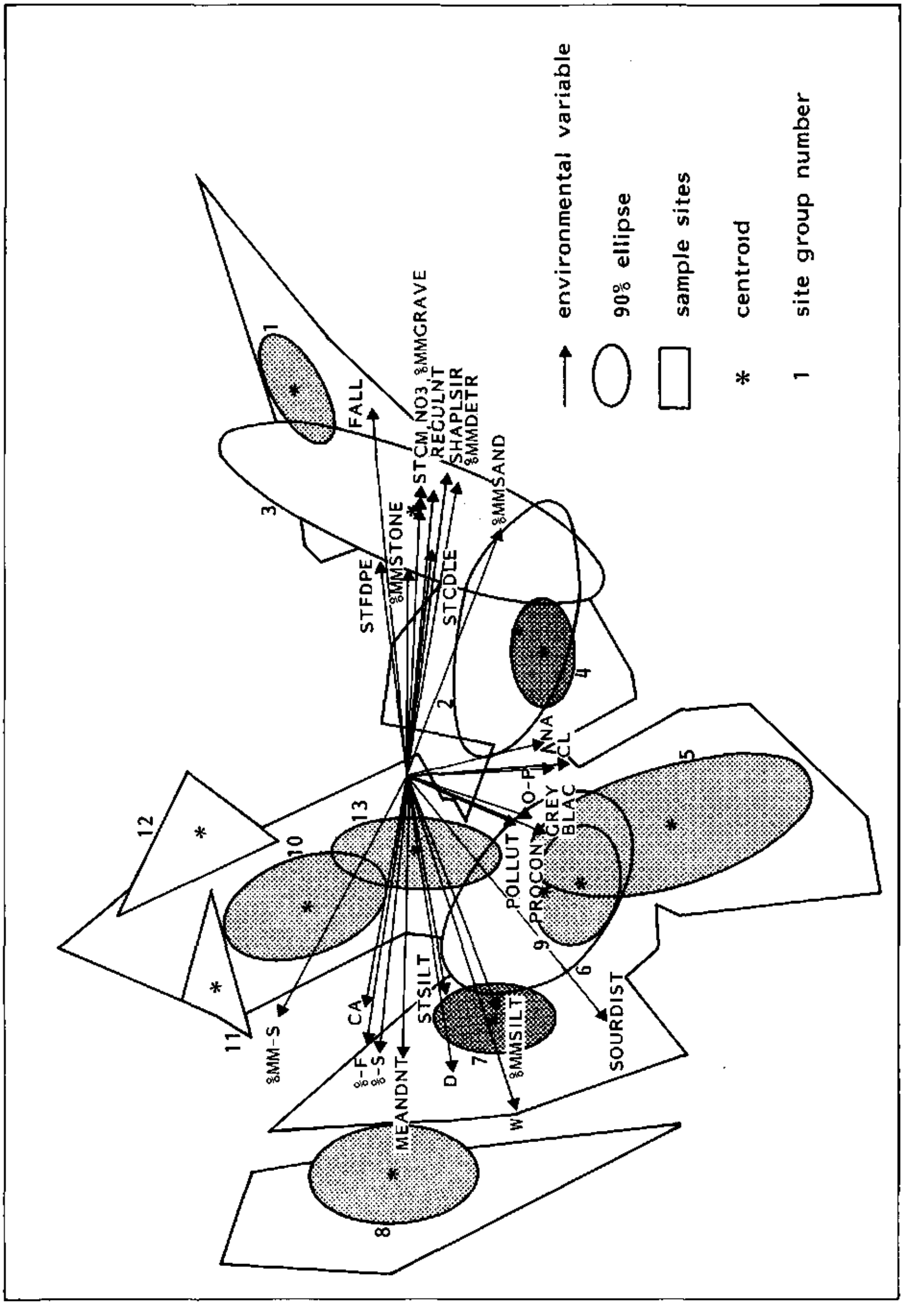

Figure 6.3 Streams; ordination (DCCA) diagram for axes 1 (horizontally) and 3 (vertically). The contour line describes the total variation of site scores. For further explanation see Sections 3.4.2 and 6.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

gravel and sand are pronounced. The sites are also shaded. Nitrate concentration is high, and ammonium and sulphate concentrations are low (Table 6.1). At the other side of the figure (site group 8) the waters are deep, wide and regulated. This corresponds with a silty bottom, a dense vegetation, an average conductivity, and high calcium and bicarbonate concentrations. Site groups 2, 3 and 4 resemble group 1. In these site groups, however, the fall is much lower, there is more silt, and most chemical variables indicate more anthropogenic influence. Sites in group 2 are slightly wider and much deeper compared with those in group 1. Physically site group 2 tends towards groups 6, 7 and 8. Site groups 3 and 4 may dry up in summer, and ammonium concentrations are higher in site group 3. Sites in group 3 are all situated in woods and have more submerged vegetation (especially mosses) than group 4. Physically site group 3 is similar to group 1. Sites in group 4 represent wider streams than those in group 3. Site groups 6 and 7 are like group 8. In this group order average concentrations of ammonium, nitrate and phosphate decrease whereas calcium and bicarbonate concentrations increase as does the total vegetation cover. The dimensions of sites in groups 6 and 7 are smaller than those in group 8. In the group order 8, 7 and 6, sites become more irregularly shaped, are more often shaded, and the fall and current velocity increase, but are still low compared to the first five groups.

The second important gradient runs from site group 9 (above the centre of Figure 6.2) to site group 13 (at the top). All these site groups represent temporary waters. Site group 13 represents pools that remain after the natural stream has dried up. Even these pools may disappear. The pools data revealed high potassium and low oxygen and calcium concentrations. All were sampled in summer. Site group 9 is comparable to group 13 although the sites have higher ammonium and phosphate concentrations and less vegetation. These organically enriched pools and some enriched, temporary, regulated streams are shaded. The organic enrichment is illustrated in Figure 6.3 where site group 9 is situated close to site group 5. Sites of groups 10, 11 and 12 are temporary, regulated streams. Site group 12 is small and the water is slightly acid with low concentrations of chloride, sodium, bicarbonate and phosphate. Although the neutral sites in group 11 are also poor in nutrients, their dimensions are larger. Site group 10 resembles group 11 but is more organically enriched.

The third gradient is illustrated in Figure 6.3. The third ordination axis shows that site group 5 consists of organically polluted sites which are situated in natural and regulated streams (Table 6.1). Average ammonium, phosphate, chloride and sodium concentrations are high. The stream bottom consists of a thick silt layer. The water smells and it is grey/black and polluted. Site group 14 is not shown in Figures 6.2 and 6.3, being one aberrant site which is heavily polluted.

The data set is described by three important gradients. The first gradient is related to the physical and hydraulic conditions of the streams. Site groups are not arranged in a straight line but on an arc along this gradient. This is due to the more temporary character of site groups 3 and 4, which both also fit into the second gradient related to drought, and the pollution status of site groups 6 and 7 which corresponds to the third gradient related to organic pollution.

For a biological verification of the above gradients, the typifying taxa (resulting from NODES) of each site group will be discussed with respect to published data.

Site group 1 is inhabited by a number of rheophilic species living on or in stony substratum (e.g. Amphinemura standfussi/sulcicollis, Hynes 1977), leaf packs (e.g. Brillia modesta, Cranston et al. 1983; Chaetopteryx villosa, Tolkamp 1980; Pedicia sp., Pomeisl 1953), detritus (e.g. Polypedilum laetum, Tolkamp 1980) or sand (Sericostoma personatum, Higler 1975). Part of the typical taxa immigrate from spring areas and are cold stenothermic (e.g. Sperchon spp., Viets 1974; Dixa maculata, Illies 1952; Parametriocnemus stylatus, Lehmann 1971). Most other taxa are common and/or abundant in unpolluted small streams.

Site group 8 is inhabited by a large number of taxa common in slowly flowing or stagnant waters, with a rich vegetation (e.g. Anisus vortex, Macan 1977; Mystacides longicornis, Hickin 1967; Ophidonais serpentina, Verdonschot 1984) and well oxygenated (e.g. Limnesia undulata, Kreuzer 1940; Anabolia nervosa, Lepneva 1971). There are several interesting taxa which are often found in slowly flowing waters and/or the littoral zone of lakes (wave action) (e.g. Mideopsis orbiculare, Berg 1948; Glossiphonia heteroclita, Elliott & Mann 1979; Triaenodes bicolor, Lepneva 1971). Most other taxa are common but especially their population numbers indicate a well developed, eutrophic, unpolluted environment (e.g. Plea minutissima, Nieser 1982; Piona alpicola/coccinea, Viets 1936; Corixa punctata, Macan 1976; Cyrnus flavidus, Edington & Hildrew 1981).

Site group 2 has much in common with group 1, including some corresponding typifying taxa (Brillia modesta, Chaetopteryx villosa, Gammarus pulex and Polypedilum laetum). Baetis vernus, Hygrobatus nigromaculatus, Lebertia inaequalis/insignis and Paratrichocladius rufiventris are found in large, slowly flowing streams (see Macan 1970, Smissaert 1959 and Hirvenoja 1973, respectively). Only one taxon (Beraeodes minuta) is typical of small streams (Lepneva 1971). Some other taxa indicate more saprobic conditions (e.g. Limnodrilus hoffmeisteri, Kennedy 1965).

All the typifying taxa of site group 3 mostly inhabit semi-aquatic environments (e.g. Ephydridae, Scatophagidae, Merrit & Cummins 1984; Eiseniella tetraedra, Brinkhurst & Jamieson 1971).

Site group 4 is also characterized by taxa which are resistant to desiccation (e.g. Nais elinguis, Rhantus sp., Klausnitzer 1984; Chaetocladius piger agg., Cranston et al. 1983). Several taxa are clearly bound to water flow (Diplocladius cultriger, Cranston et al. 1983; Rhyacodrilus coccineus, Chekanovskaya 1962; Micropsectra fusca, Klink 1982).

Site group 5 is typified by oligochaetes and chironomids. Their representatives are all resistant to organic pollution and/or become abundant in organically enriched sediments. Examples are Chironomus sp., Tubifex tubifex (Hynes 1960), Limnodrilus spp. (Chekanovskaya

1962), Cricotopus gr. sylvestris (Saether 1979) and Prodiamesa olivacea. Under circumstances of organic pollution the last one is especially common in flowing waters (Tolkamp 1980).

The taxa typical of site group 6 all have a wide distribution with respect to water flow. They inhabit mostly lentic as well as lotic waters (e.g. Mideopsis crassipes, Berg 1948; Paracladopelma camptolabis agg., Lehmann 1971; Cryptochironomus sp., Pinder & Reiss 1983). Some taxa can be found in organically enriched conditions, e.g. Limnodrilus claparedianus (Pfannkuche 1977), Paratendipes gr. albimanus and Procladius sp. (Fittkau & Roback 1983).

Many more typifying taxa can be found in site group 7. Site group 8 is even richer. Site group 7 is inhabited by more or less ubiquitous taxa (e.g. Cloeon dipterum, Macan 1979; Potamothrix hammoniensis, Brinkhurst 1964; Bathyomphalus contortus, Macan 1977), some of which are bound to a dense vegetation (Physa fontinalis, Macan 1977; Graptodytes pictus, Freude et al. 1971), others to a silty substratum (e.g. Sphaerium sp., Ellis 1978; Sialis lutaria, Elliott 1977; Caenis horaria, Macan 1970), to water flow (e.g. Hygrobates longipalpus, Viets 1936) or to the littoral zone (e.g. Limnephilus decipiens, Lepneva 1971). Glossiphonia complanata occurs in all types of water, including fast flowing streams, but is most abundant in waters with a large population of snails (Elliott & Mann 1979).

Site group 13, an extreme in Figure 6.2, is typified by a number of common coleopterans (Agabus spp., Helophorus spp., Hydrobius fuscipes). Cold stenothermic taxa are Hydroporus discretus (occurring in springs and small streams), Hydroporus memnonius and Agabus didymus (Freude et al. 1971).

Site group 9 has few typifying taxa. Psectrotanypus varius favours the sediments of small, nutrient-rich, standing or slowly flowing waters, and also those streams which dry up in summer (Fittkau & Roback 1983, Schleuter 1986). Limnophora sp. occurs at the banks of streams (Johannsen 1969).

Site group 12 is inhabited by several taxa which prefer swamps and temporary pools (Limnephilus centralis and L. auricula, Hiley 1976; Paralimnophyes hydrophilus and Limnophyes sp., Cranston et al. 1983; Hydroporus planus and H. nigrita, Freude et al. 1971). Lumbriculus variegatus (Verdonschot 1987) and Paralimnophyes hydrophilus are more abundant in slightly acid waters.

Site group 11 has several taxa in common with groups 10 and 12. Most taxa in this group prefer small, running or standing waters (e.g. Ochtebius minutus, Freude et al. 1971; Haliplus lineatocollis, Cooling 1981) some may often be intermittent (Hydroporus discretus, Freude et al. 1971; Limnephilus affinis, Lepneva 1971). Some are characteristic of small acid pools (e.g. Hydroporus erythrocephalus, Freude et al. 1971; Lumbriculus variegatus, Macropelopia spp. and Callicorixa praeusta, Bernhardt 1985) or vegetated pools (e.g. Planorbarius planorbis, Macan 1977; Polycelis tenuis, Reynoldson 1978).

Site group 10 is also inhabited by taxa typical of temporary waters (e.g. Aplexa hypnorum, den Hartog & de Wolf 1962; Anisus leucostoma/spirorbis, Garms 1961; Pilaria sp., Brindle 1967; Trissocladius sp., Cranston et al. 1983; Hydryphantes dispar/ruber, Wiggins et al. 1980). Some taxa inhabit detritus-rich or muddy sediments (e.g. Zavrelimyia sp., Fittkau & Roback 1983; Dina lineata, Elliott & Mann 1979). Stylodrilus heringianus is indicative of unproductive habitats (Brinkhurst & Jamiesson 1971); Dugesia lugubris of productive ones (Reynoldson 1978).

Finally, site group 14 consists of one site that contains only three taxa. Most significant is Eristalis sp. which can survive anaerobic conditions by means of air-breathing.

6.3 Discussion of data

A typological description is based on a recurring combination of taxa under comparable environmental circumstances. Major environmental variables are the results of climatological, geological and topographical processess. The presented site groups are clearly a result of some of these major factors. The major environmental variables within the streams studied are dimensions, duration of drought and 'stream-character'. Within the occurring combinations of these factors the load of organic material or nutrients diversifies. The three major variables mentioned, however, do not occur in every independent combination. Regulation not only affects the 'stream-character' but also implies increase of size, and an increased drainage capacity can result in intermittant stream flow. So, when size increases, 'stream-character' will decrease and discharge patterns can become even more irregular. The allochthonous energy source of the natural stream (Cummins 1973) becomes an autochthonous one, especially when the wooded banks are cleared. But there is more than a local interaction. As a stream follows its course it becomes larger and regulation of an upper reach will affect the middle and lower reaches. The energy input (nutrient spiralling; Wallace et al. 1977) is changed and the flow pattern is disrupted. Taxa depositing their eggs in the upper reach may disappear despite the possibility that a suitable habitat for the larvae exists in the middle reach. Regulation as well as drought greatly diminish the natural stream community and often result in a more or less ubiquitous fauna, also present in stagnant waters and which is capable of resisting periods of drought.

Does this general pattern fit the site groups described? Site group 1 has an optimal 'stream-character'; all sites are fed by helocrene springs throughout the year. These small-sized streams are inhabited by a rheophilic and a spring-inhabiting fauna. The fauna is comparable to the community of helocrene springs described by Verdonschot & Schot (1987). As dimensions increase the spring fauna gradually disappears. A few representatives remain in site group 2 where not only width but especially depth is much larger.

For a long time, streams have been influenced by man mainly through agricultural activity in the catchment area. Agricultural activity is especially developed in the naturally level areas. Hill-ridges are less appropriate except for the more level tops. Sites in site group 1 are all situated on the steep slopes of the ridges (fall is high) and therefore their natural character is preserved. Because springs in this province arise from a perched groundwater table (Verdonschot & Schot 1987), discharge is fairly constant throughout the year. But as these spring streams flow down hill, the slope decreases and man's influence strongly increases. This process is already present in site group 2 (e.g. regulation is traceable). Since the earlier investigations were carried out most of the characteristic inhabitants of the upper and middle reaches have disappeared (Mol 1986b).

Agricultural activity and drinking water extraction drain the land and lower the groundwater table. Streams which are not fed by an apparent groundwater aquifer can become intermittent. These sites are found in site group 3. True rheophilic taxa are absent. These truly rainwater-fed streams show a very fluctuating discharge pattern in which even larger, downstream parts may dry up (site group 4). Sometimes small isolated pools remain in these intermittent streams in summer. These isolated pools are inhabited by a poor aquatic fauna of mainly coleopterans, not restricted to a running water environment. Site groups 13 and 9 represent the summer aspects of site groups 3 and 4, respectively. However, the difference between 9 and 13 is also due to organic load. The macrofauna in highly organically-enriched pools in 9 looks like that in some small, intermittent, organically-enriched regulated streams.

Further downstream, as dimensions increase, there are no undisturbed catchment areas or streams in the province of Overijssel. Those larger streams with a high 'stream-character' are always influenced by nutrient/organic input and/or are regulated in (parts of) the upper reaches. Site group 6 consists of sites that have kept the physical part of their natural 'stream-character' together with sites that are regulated but which have retained their current velocity. Most sites are shaded contrary to the sites of group 7. Site group 7 represents regulated, slowly flowing streams with vegetation. The difference between site groups 6 and 7 is also seen in taxon composition. Site group 7 is inhabited by a number of vegetation-related taxa, while group 6 represents a combination of common, sub-rheophilic taxa and indicators of saprobity due to the presence of a wooded bank.

Sites in group 8 are wide and contain a zone with well aerated open water which, together with a large littoral zone and a low organic enrichment, explains the high taxon diversity.

Organic enrichment causes a decrease in diversity and a change in taxon composition. As organic enrichment increases, it increasingly dominates all the other, even the major, environmental variables and thus sites from site groups 4, 6 and 7 begin to look more like site group 5. Only saprobic taxa are to be found.

Finally, site group 14 represents a state of almost completely 'dead' water (Verdonschot 1983).

Regulated, temporary small streams fed by rainwater, become slightly more acid in the absence of other anthropogenic disturbance (site group 12). Sites in site groups 10 and 11 are neutral and the sites in group 10 are even slightly organically enriched. The taxa collected are typical of temporary waters but their distribution pattern sometimes looks more stochastically determined within the extreme conditions of drought and acidity.

The relations found between the site groups are a complex web resulting from interactions between some major environmental variables and fit the general patterns indicated earlier in this section. Within this web cenotypes, as defined in chapter 2, can be described. Since cenotypes should be described independent of season, some site groups were combined in one cenotype. Further, some cenotypes are related, often reflecting an increase in amount of organic material. The following scheme of cenotypes is proposed (Figure 6.4):

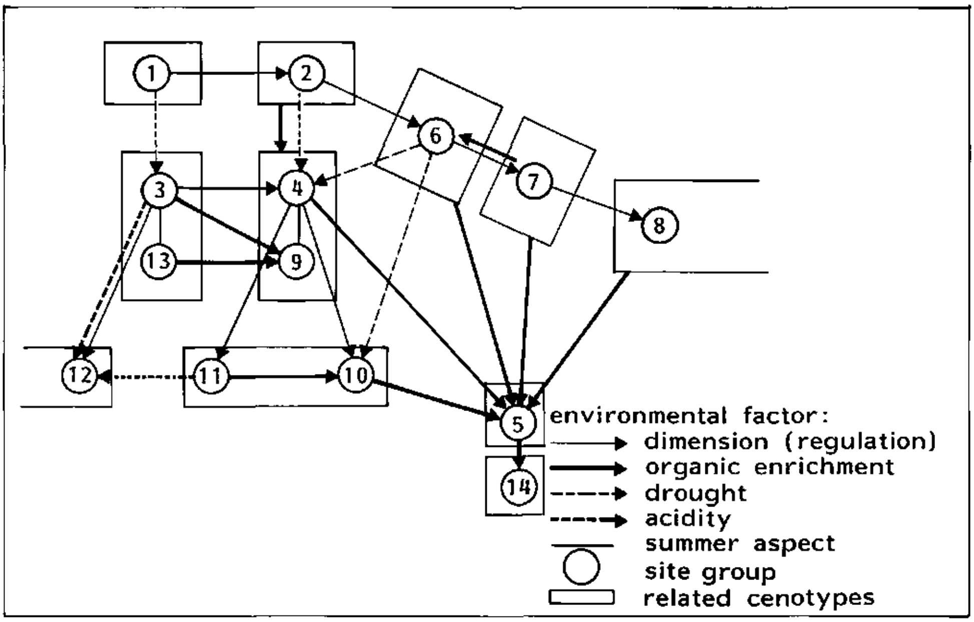

Figure 6.4 Streams; cenotypological relations. The arrows indicate the direction of increase of the respective variables.

- permanent spring streams (site group 1),
- permanent, rainwater-fed upper reaches of natural streams (site group 2),
- temporary, small upper reaches of natural streams (site group 3 its summer aspect, site group 13),
- temporary, upper reaches of natural streams (site group 4 and its summer aspect, site group 9),
- temporary, small upper reaches of regulated streams (site group 12),
- temporary, upper reaches of regulated streams (site group 10 and 11),
- permanent, middle reaches of semi-natural streams (site group 6),
- permanent, middle reaches of regulated streams (site group 7),

-permanent, lower reaches of regulated streams (site group 8),
-organically-enriched streams (site group 5),
-heavily organically-enriched streams (site group 14).

The middle reaches (site group 6) together with the described upper reaches of natural streams (site groups 1, 2, 3, 13, 4 and 9) can be generally indicated as natural streams. The middle (site group 7) and lower (site group 8) reaches together with the upper reaches (site groups 12, 10 and 11) of regulated streams can be generally indicated as regulated streams. When upper and middle reaches become organically enriched, they move into both related cenotypes of organically-enriched streams (site group 5 or even into site group 14).

All streams studied are more (e.g. site group 5) or less (e.g. site group 1) influenced by human activities. Regulation, especially, has caused a dramatic change in community composition and from a social-political point of view is almost irreversible. In planning the aims and methods of management of natural and regulated streams, one should keep in mind the natural origin of regulated streams. Even in regulated streams it is possible to improve 'stream-character' without losing their agricultural function. It is unrealistic to strive for an original pristine state at all sites for both natural and regulated streams but the web of cenotypes (Figure 6.4) indicates directions in which the stream ecosystem can be made more natural. A simplification of the previously given scheme is illustrated in Figure 6.5, where transverse and longitudinal profiles of a natural and a

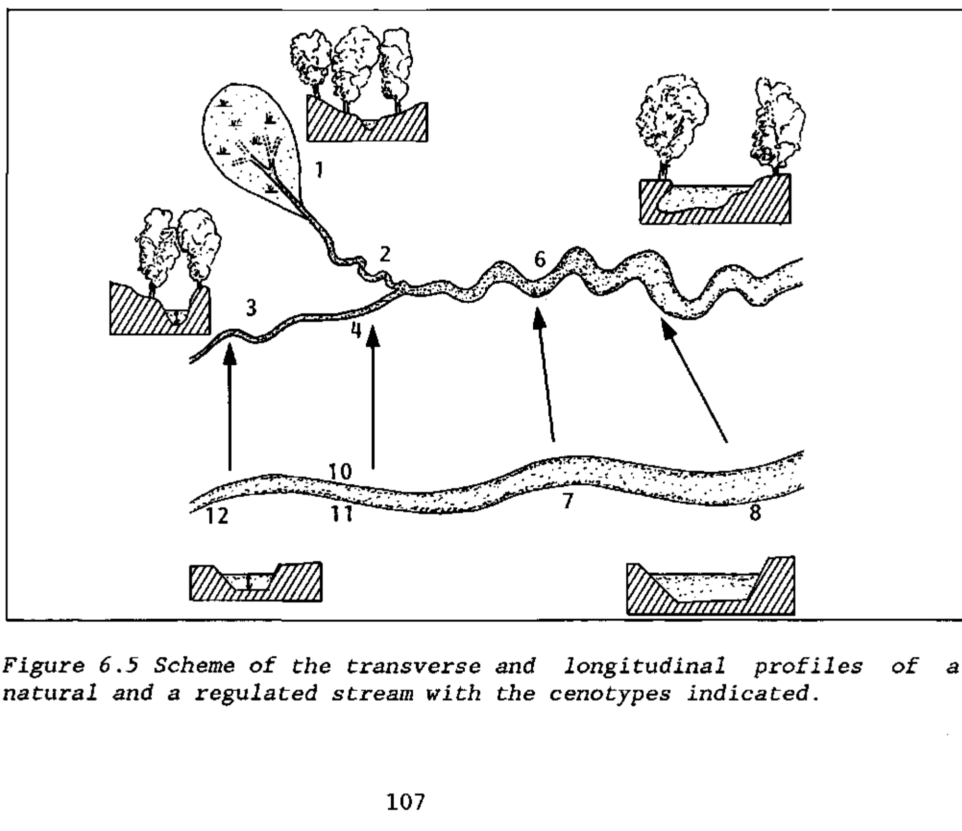

Figure 6.5 Scheme of the transverse and longitudinal profiles of a natural and a regulated stream with the cenotypes indicated.

regulated stream are given on which the cenotypes are projected. Planning and management may be directed towards improvement especially because only about 2% of the total length of streams in the province of Overijssel has a more or less natural 'stream-character' and corresponding community. These 2% are only preserved because of their geographical positions on the steepest parts of the slopes. In general, an attempt at improvement of 'stream-character' should be directed towards the physical and hydraulic conditions. This direction is indicated in Figure 6.5 by arrows.

As already mentioned, the presented cenotypes are provisional; in Chapter 10 they will be elaborated with all the other data collected.

It is difficult to compare the results of our study with other classifications of small streams because of the different approach. Yet, the major environmental factors responsible for the cenotypes have already been mentioned individually as master factors, e.g. duration of drought (Pennak 1971, Williams & Hynes 1977), water source (Illies 1955), dimensions (Strahler 1957) and regulation (Gardeniers & Tolkamp 1985).

7. MACROFAUNAL COMMUNITY TYPES IN DITCHES

7.1 Introduction

Despite the 350,000 km of ditches to be found in The Netherlands, knowledge is limited about the distribution of macrofauna in these small, shallow, linear waters which are made and intensively influenced by man (Higler 1976a; Beltman 1976; Beltman 1984; Scheffer et al. 1984; Verdonschot 1987). There exists no integrated, systematic approach for studying the considerable variability between and within ditches (Higler, Torenbeek & Verdonschot 1986).

Ditches are the most abundant physico-geographical water type present in the province. Some general physico-geomorphological characteristics of the ditches studied are:

- -a regular, linear shape,
- -regulated or dug,
- -a stream direction in none or two ways (velocity 0-0.05 m/s),
- -a width up to 10 m and depth up to 1 m.

Bottom composition is regarded as one of the most important environmental variables affecting the macrofauna composition in ditches. The 126 sampling sites were a priori spread over the bottom types; sand, clay, ombrotrophic and minerotrophic (fenland) peat. Within each occurring bottom type, the sampling sites were situated in ditches of different water quality, profile and other important variables.

7.2 Results

7.2.1 Data collection

Macrofauna and environmental data were collected from 126 sites, sampled in 1981 and 1983. Most sites were visited once, only 5 sites were visited twice, and sampling dates were spread over the four seasons. Forty sites were sampled in spring, 59 in summer, 22 in autumn and 5 in winter. A total of 71 environmental variables were used in this analysis.

7.2.2 Preprocessing of the data

This study revealed 666 taxa which is a high number compared with other studies in ditches (Garms 1961, Beltman 1984, Caspers & Heckman 1981, 1982). After careful individual weighing 606 taxa were finally included in the analysis. Further information on the preprocessing procedures is given in Section 3.4.1.

7.2.3 Multivariate analysis

The interpretation of the results of clustering (program FLEXCLUS) and ordination (program CANOCO) of the data led to the description of 11 site groups. Numbers of sites, arithmetical means and standard deviations of the quantitative environmental variables, and relative frequency of the nominal variables per site group are given in Table 7.1. The resulting list of all taxa with their typifying weight per site group (program NODES) is available from the author on request. The important typifying taxa are discussed below.

The PCA-diagram (Figure 7.1) is an illustration of the correlation matrix and shows the most obvious relations between variables, e.g. the development of different vegetation layers in summer (higher temperatures), the relation between conductivity, calcium and chloride, the relation between width and depth, and so on. Site groups are not projected because almost all of them are scattered over the whole diagram and are therefore not related to certain complexes of environmental variables, except for site groups 1 and 2b. Those groups have high values of the variables in the lower left corner, such as reedland, fenland and irregular profile.

The ordination results (DCCA) are given in Figures 7.2 and 7.3. The low eigenvalues (0.21, 0.14, 0.12 and 0.09, respectively, for the first four axes) mean that the extracted environmental gradients are short. The lengths of gradient of the axes lie in the range of 2-3 SD suggesting a 75-80% turnover of taxa along the environmental gradients represented by the axes. The scores (optima) of most taxa therefore lie outside the region of the site scores and the probability of occurrence of such taxa increases or decreases uniformly along the sampled gradients instead of being unimodal (ter Braak 1986). Comparison of DCA and DCCA shows only a slight decrease in eigenvalues which means that the environmental variables describe the species variability well. The species-environment correlations of the axes are all high (about 0.95). The measured environmental variables are sufficient to explain the major variations within the data set. The first 4 axes together account for approximately 25% of the known variation in species distributions along the measured variables. The first axis accounts for approximately 9% which indicates that there is no important primary environmental gradient.

Although sites can be classified into groups due to differences in frequency and abundance of the taxa present, the distribution pattern of these taxa is not discontinuous. This is shown in Figures 7.2 and 7.3 where the dotted lines indicate the total variation within a site group. The ellipses represent the 95%-confidence regions of the means of site scores per group.

The relations presented by the site groups will be described with respect to the important environmental variables (Table 7.1) and the ordination results (Figures 7.2 and 7.3). A validation of the site groups will be based on knowledge present of the autecology of typifying taxa.

Site group 1

From Figures 7.2 and 7.3 and Table 7.1 it can be concluded that site group 1 is related to ditches with a large cross-section (width and depth), often situated on peat (65%) and within reedland. The bank profile was often vertical (65%). Samples were mostly taken in summer (88%) which explains the high average temperature. Conductivity was

Table 7.1 Ditches; number of sites, means, and standard deviations of the quantitative environmental variables and percentages of the nominal environmental variables per site group. Abbreviations are explained in Table 10.5.

Quantitative environmental variables

Site group	1	2a	2b	3	4	5	6	7	8	9	10	11
Number of sites	17	14	16	41	3	4	4	6	8	2	2	1
PH	7.7	7.6	7.1	7.5	6.9	5.9	5.8	7.7	7.0	5.9	5.6	7.6
sd	0.4	0.7	0.9	0.7	0.4	1.8	1.2	0.9	1.1	0.3	0.1	-
NH4	0.4	0.7	1.0	1.5	0.7	1.4	5.4	1.3	1.8	2.0	2.9	28.
sd	0.1	1.0	0.7	2.5	0.2	0.9	2.7	0.9	1.9	0.1	0.4	-
NO3	0.2	0.1	0.7	0.6	6.2	0.3	3.0	2.0	2.2	9.8	5.7	0.0
sd	0.3	0.9	0.1	1.3	4.3	0.2	2.0	1.8	3.3	0.3	6.1	-
O-P	.03	.12	.03	.18	.08	.13	.27	.07	.02	.04	1.4	2.5
sd	.02	.04	.12	.42	.03	.08	.47	.08	.01	.03	1.9	-
T-P	.23	.35	.18	.37	.33	.16	.52	.32	.08	.18	1.5	11.
sd	.16	.17	.18	.47	.15	.11	.57	.32	.05	.11	1.7	-
O2	8.6	8.7	12.	7.2	9.5	4.8	11.	11.	7.1	12.	8.0	4.0
sd	3.7	5.6	4.8	3.6	0.9	2.9	1.7	5.5	2.4	0.1	0.8	-
O2%	94	93	94	68	74	57	87	94	80	92	65	32
sd	45	47	59	35	7	37	17	41	35	1	11	-
EC	556	369	344	460	348	176	199	469	548	240	283	650
sd	147	132	155	164	150	119	38	156	223	28	152	-
CL	73	61	51	75	31	29	53	133	44	43	47	51
sd	43	32	44	50	19	22	46	186	11	1	33	-
CA	77	60	50	57	62	15	64	63	58	30	30	75
sd	33	20	21	18	39	12	78	20	30	4	13	-
FE	.30	.34	.36	.30	.17	.38	1.5	.62	.14	.10	.90	.60
sd	.36	.33	.54	.38	.21	.33	1.1	.84	.29	.00	.57	-
T	20	18	8	14	5	24	7	9	20	5	6	6
sd	3	4	7	8	0	4	2	6	6	0	2	-
W	6.0	5.2	3.6	2.7	3.8	3.7	3.6	2.7	1.1	1.8	2.4	1.9
sd	2.9	3.1	1.2	1.3	5.3	1.3	3.5	1.3	0.5	0.2	0.2	-
D	.59	.50	.42	.35	.37	.28	.36	.33	.13	.45	.48	.35
sd	.24	.20	.17	.22	.06	.17	.43	.17	.11	.21	.11	-
S	.5	.0	.0	2.9	.0	.0	.0	.5	.5	2.5	1.5	.0
sd	1.4	.0	.7	16.	.0	.0	.0	.8	.8	.7	2.1	-
S-T	.11	.10	.18	.12	.35	.25	.03	.05	.08	.02	.01	1.0
sd	.25	.26	.30	.22	.22	.50	.05	.09	.17	.02	.00	-
%-A	6	5	2	10	0	5	30	16	1	11	31	0
sd	15	14	3	25	0	10	41	24	4	13	42	-
%-S	22	45	23	32	0	20	0	11	7	8	1	0
sd	22	30	33	39	0	40	0	12	14	11	0	-
%-F	20	68	6	12	0	25	13	26	0	3	1	0
sd	17	31	9	22	0	50	25	38	1	4	1	-
%-E	5	20	3	13	63	26	7	9	14	0	0	0
sd	7	23	5	22	25	34	15	16	14	0	0	-
%-B	2	3	2	3	5	3	3	1	1	1	1	0

sd	1	3	3	4	5	5	5	2	2	0	0	-
%-T	49	94	32	54	68	55	40	51	22	18	31	0
sd	25	11	38	41	27	42	43	29	27	18	41	-
%MM-B	19	13	33	18	13	15	30	13	21	20	40	0
sd	13	13	20	18	11	30	35	16	17	0	0	-
%MM-E	12	16	16	18	67	25	18	30	25	0	20	0
sd	16	16	22	20	12	30	21	28	26	0	0	-
%MM-F	27	24	5	11	0	10	15	10	8	55	0	0
sd	19	11	10	13	0	20	30	17	10	7	0	-
%MM-S	20	25	20	29	0	25	23	17	15	0	10	0
sd	17	11	22	22	0	19	29	20	18	0	14	-
%MMSILT	14	10	18	19	20	10	5	25	21	15	20	100
sd	12	10	14	15	0	12	10	12	14	21	28	-
%MMSAND	2	0	1	2	0	0	5	5	9	10	10	0
sd	7	0	5	6	0	0	10	10	15	14	14	-
%MMPEAT	6	10	4	1	15	5	0	0	0	0	0	0
sd	9	10	11	4	19	10	0	0	0	0	0	-

Nominal environmental variables

Site group	1	2a	2b	3	4	5	6	7	8	9	10	11
SPRING	0	7	44	37	0	0	100	67	13	100	100	100
SUMMER	88	71	6	42	0	100	0	17	88	0	0	0
AUTUMN	12	21	44	20	0	0	0	0	0	0	0	0
WINTER	0	0	6	2	100	0	0	17	0	0	0	0
SHAPREG	94	64	94	98	100	100	100	100	100	100	100	100
SHAPIRR	6	6	6	2	0	0	0	0	0	0	0	0
TEMPOR	0	7	0	0	0	50	25	33	63	0	100	0
WATLF	0	0	19	12	33	25	0	17	25	100	50	0
SAND	24	7	44	42	0	25	50	83	100	100	50	100
CLAY	18	21	13	34	0	0	26	17	0	0	0	0
PEAT	65	71	38	24	100	0	0	0	0	0	0	0
FENLAND	0	0	6	0	0	75	25	0	0	0	50	0
SEE	0	7	19	17	0	0	25	17	63	0	0	0
COLORLES	18	7	44	27	0	0	0	33	38	0	0	0
YELLOW	77	86	56	63	100	50	75	33	63	100	0	0
BROWN	0	7	0	7	0	50	25	17	0	0	100	0
GREEN	6	0	0	2	0	0	0	17	0	0	0	0
SMELL	0	0	0	2	0	25	0	0	0	0	0	100
CLEAR	71	64	75	73	67	50	50	83	88	100	50	0
SLTURB	18	36	19	17	33	50	50	0	13	0	50	0
TURBID	12	0	6	10	0	0	0	17	0	0	0	100
POLLUT	18	0	6	5	0	0	25	17	0	0	0	100
CLEANIN	47	7	31	37	0	0	75	50	50	100	100	0
STNONE	18	7	19	17	0	25	25	17	25	0	0	0
STDEPE	18	64	13	2	0	0	25	0	13	50	0	0
STSILT	29	7	44	68	67	25	50	83	63	50	50	100
STDEPES	35	14	25	12	33	50	0	0	0	0	0	0
PSIRR	6	50	25	12	33	25	25	0	0	0	0	0
PS45	0	14	6	0	0	0	0	0	0	0	0	0
PS75	35	7	38	59	67	25	50	83	88	100	100	100
PS90	65	29	38	29	0	50	25	0	13	0	0	0
SHADOW	24	21	19	15	67	25	25	0	38	50	0	100

SURURB	0	0	0	5	0	0	0	0	0	0	0	100
SURFOR	6	0	6	5	0	0	0	0	0	0	0	0
SURWOB	6	0	6	0	0	25	25	0	0	0	0	0
SURFIE	0	0	0	7	0	0	50	0	38	50	50	0
SURGRA	71	79	94	93	100	50	50	100	75	50	50	0
SURREE	35	21	13	2	0	0	0	0	0	0	0	0
PROCON	0	0	13	2	0	0	0	0	0	0	50	0

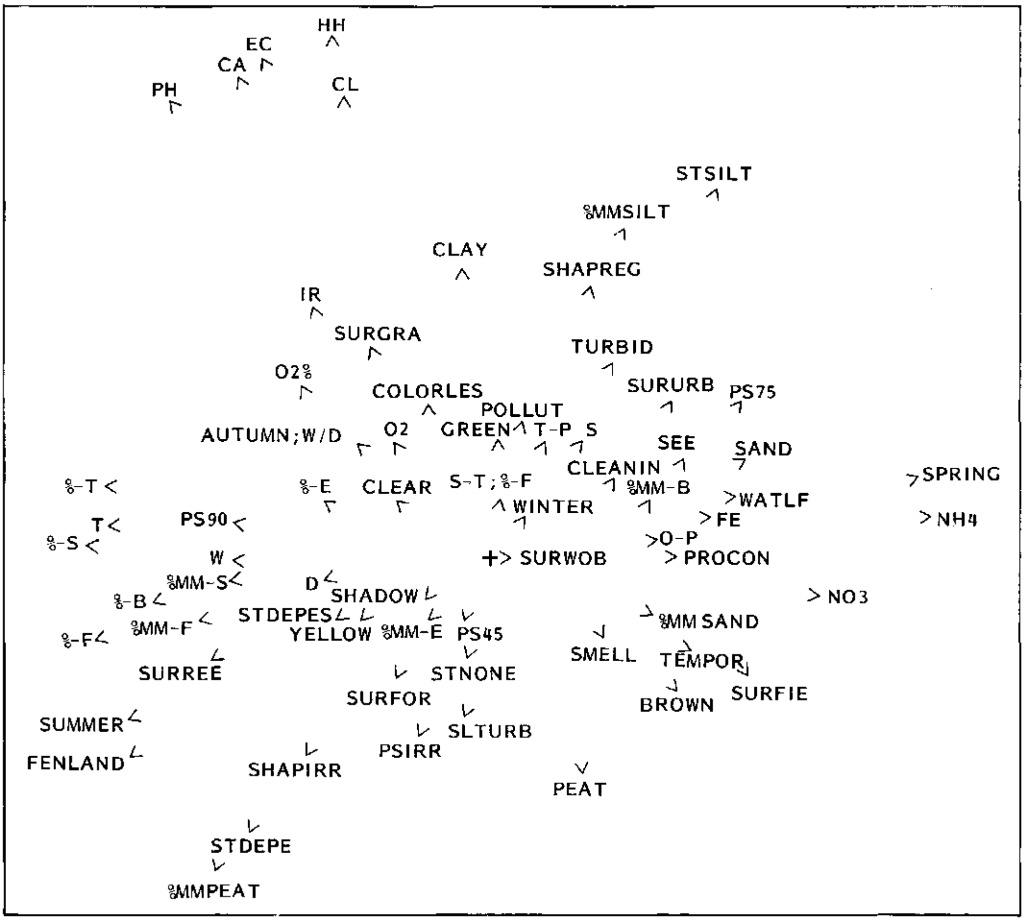

Figure 7.1 Ditches; ordination (PCA) diagram for axes 1 (horizontally) and 2 (vertically) with only environmental variables indicated. For further explanation see Sections 3.4.2 and 7.2.3, and Figure 3.10. Abbreviations are explained in Table 10.5.

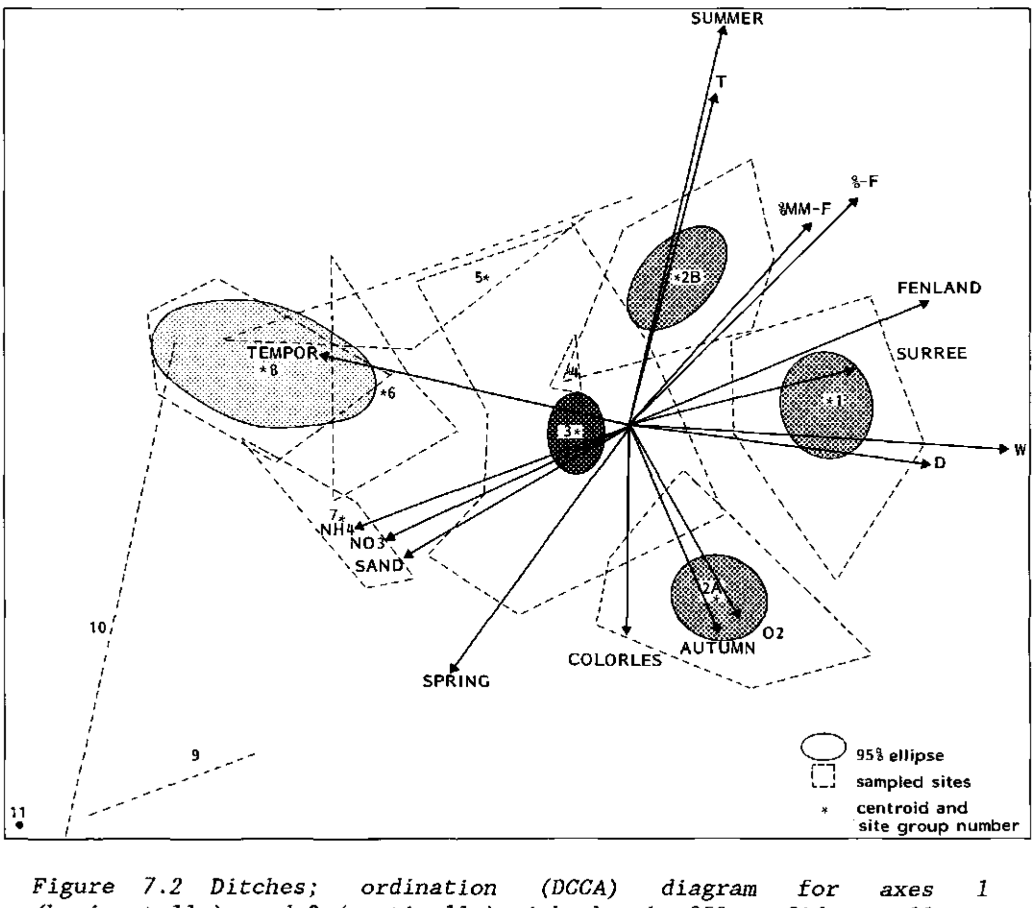

Figure 7.2 Ditches; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically) with the the 95% confidence ellipse of the mean of site scores per site group. Only environmental variables with an interset correlation greater than 0.35 are shown (arrows). For further explanation see Sections 3.4.2 and 7.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

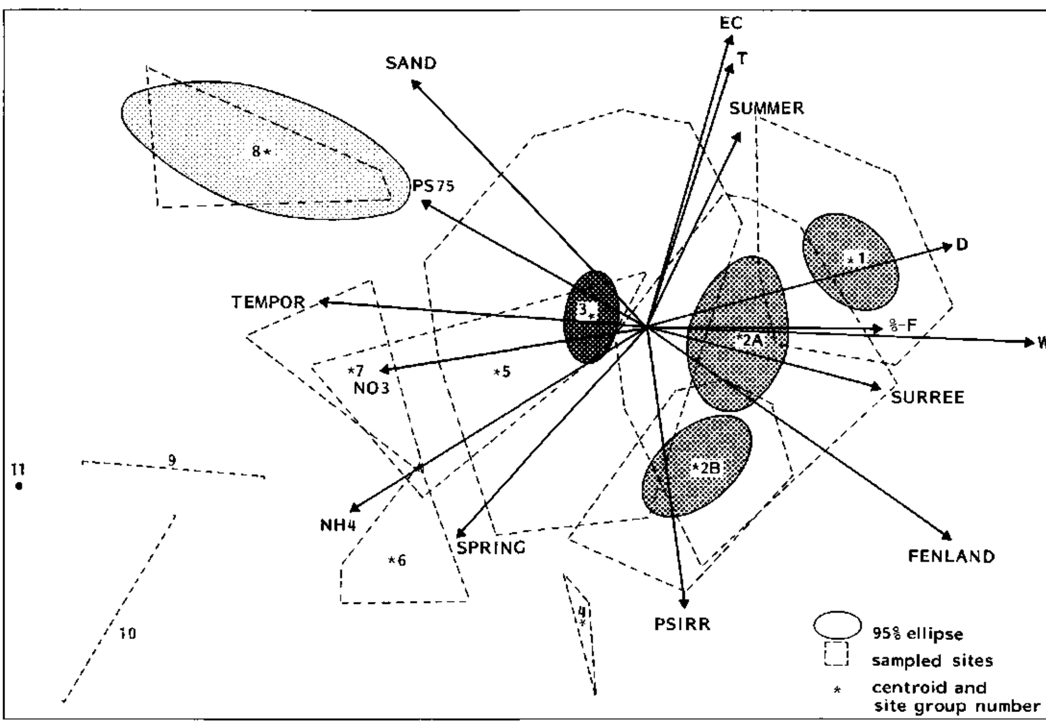

Figure 7.3 Ditches; ordination (DCCA) diagram for axes 1 (horizontally) and 3 (vertically) with the 95% confidence ellipse of the mean of site scores per site group. For further explanation see Sections 3.4.2 and 7.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

relatively high and ammonium, nitrate and total phosphate concentrations were relatively low within this data set.

Filter feeders like Endochironomus albipennis, Glyptotendipes sp., Parachironomus gr. arcuatus and Polypedilum gr. sordens often inhabit plant stems and build nets at the end of their tubes to feed on algae and detritus particles (Walshe 1948; Shilova 1968). Unionicola crassipes needs Spongae to complete its life cycle (Böttger 1972). Spongae, in general, need clear water to develop (Harrison 1974). Cymatia coleoptrata was only found in lakes and large permanent ponds by Brown (1951) and in mesotrophic waters by Bernhardt (1985). Spercheus emarginatus lives in vegetation-rich, stagnant waters (Klausnitzer 1984). Ophidonais serpentina is abundant in waters with a dense, submerged vegetation and a high transparancy (Verdonschot 1984). Species like Limnesia undulata and Piona alpicola/coccinea avoid small waters due to high fluctuations in the environmental conditions (Viets 1936; Kreuzer 1940). Marstoniopsis scholtzi is limited to canals (Macan 1977) and lakes (Higler 1976b). Gyraulus albus is regularly to be found in clear ditches (Garms 1961). Several other typifying taxa, especially the Hydrachnellae and Trichoptera, are found in clear, stagnant, eutrophic waters often rich in macrophytes. Piscicola geometra prefers clean, larger, less weedy waters due to its association with fish (Garms 1961).

Based upon the abiotic and the biotic description, site group 1 consists of larger, clear, permanent, eutrophic ditches with different well-developed vegetation layers and a recognizable open water column. Higler (1977) described a similar macrofauna-cenosis on Stratiotes plants in a broad-lake.

Site group 2a

Sites within group 2a were mostly sampled in summer (71%) and therefore had an average total vegetation cover of 94% and a high average temperature. Often the profile was irregular (36%). In comparison with site group 2b, these sites had a higher average total phosphate concentration and a lower average oxygen, ammonium and nitrate concentration. This is probably a seasonal effect. Most ditches of this group are situated upon peat (71%) and surrounded by grassland (79%) and/or reedland (21%).

Hygrotus decoratus prefers marshes (Freude et al. 1971). Segmentina nitida flourishes chiefly in marsh-draining ditches. It is uncommon in rivers, streams and canals (Boycott 1936). Holocentropus picicornis is common in stagnant waters with a rich vegetation (Tobias & Tobias 1981); this is also true of Limnesia connata (Besseling 1964). Arrenurus cuspidator is a typical summer species (Stechmann 1977). Nais variabilis and Stylaria lacustris feed on algae (Moore 1979) and occur in waters with a fairly well developed vegetation or an algal bloom (Verdonschot 1984). Both are common in summer (Bülow 1955). Cataclysta lemnata lives in a tube of Lemna particles or parts of reed stems and feeds on Lemna (Hasenfuss 1960). Valvata cristata is common in eutrophic pools (Benthem Jutting 1959) and requires mud (Boycott 1936). Endochironomus gr. dispar is common in meso- and eutrophic ditches and ponds (Moller Pillot 1984). Guttipelopia guttipennis lives primarily in shallow standing waters (Fittkau & Roback 1983).

Site group 2b

Sites in group 2b were mostly sampled in spring (44%) and autumn (44%). Oxygen concentration was relatively high. Width and depth were slightly larger than in site groups 2a and 3. There was little vegetation development and the water was clear. Most sites are situated on a peat (38%) or sand (44%) bottom and surrounded by grasslands (94%).

Microtendipes gr. chloris, Polypedilum gr. bicrenatum and Clinotanypus nervosus are common inhabitants of bottom sediments (Reiss 1968). The latter species often occurs in fenlands (Moller Pillot 1984). The genus Cladotanytarsus occurs abundantly in the littoral zone of the Bodensee (Reiss 1968). Caenis horaria is common in stagnant waters (Macan 1970; Mol 1986a). Cloeon dipterum is also common in small pools with a dense vegetation or in littoral zone (Garms 1961, Macan 1979). Adults emerge in late spring (Caspers & Heckman 1981). Paraponyx stratiotata is a ubiquitous lepidopteran living in macrophytes like Elodea, Ceratophyllum and Callitriche (Hasenfuss 1960). Gammarus pulex is intolerant of low oxygen concentrations (Liepolt 1953) but is able to resist some organic enrichment (Liebmann 1951). Sigara falleni is a common inhabitant of stagnant waters. Savage & Pratt (1976) indicated a preference for slightly larger waters with a vegetation-rich littoral zone. They can be collected en masse during autumn and spring (Caspers & Heckman 1981). Both Athripsodes aterrimus and Mystacides sp. prefer vegetation-rich, stagnant waters (Hickin 1967). This is also true for Erythromma najas (Gardner 1954) which is not found in summer (Garms 1961).

Site groups 2a and 2b both consist of small, shallow, clear, eutrophic permanent ditches with a densely developed vegetation. Seasonal differences between 2a and 2b are recognizable.

Site group 3

Site group 3 represents the most centrally situated group within both the diagrams. Its centroid is situated (Figures 7.2 and 7.3) to the right of the centre of the diagrams. This indicates a smaller profile compared with site groups 1 and 2. Oxygen concentration was relatively lower and ammonium and total phosphate concentrations were slightly higher. Samples were spread over spring (37%), summer (42%), and autumn (20%). Note that sites sampled in summer are mainly situated above the centroid and autumn and spring sites below. Samples were taken on all bottom types :sand (42%), clay (34%), and peat (24%). The substrate often contains silt (68%). Most other variables take an intermediate position.

Site group 3 is best characterized by the absence of any significant typifying taxa with respect to all the other site groups described. There is an interesting abundance of species with an overall frequency larger than 50% and with a frequency between 30% and 50%. Both groups of taxa are frequently and abundantly encountered at sites within this site group. Most gastropods and leeches within these taxa groups are resistant to oxygen depletion and organic enrichment (Hart & Fuller 1974; Berg 1961; Learner et al. 1983; and others). This is also known of Asellus aquaticus (Birstein 1951), Limnodrilus hoffmeisteri (Kennedy 1965), Haliplus ruficollis (Seeger 1971), Arrenurus globator (Besseling 1964) and Procladius sp. (Moller Pillot & Krebs 1981).

Site group 3 consists of small, shallow, eutrophicated, permanent ditches with a weedy, fairly homogeneous vegetation in summer.

Site group 4

The three sites for site group 4 were all sampled in winter. Many variables are like those in site group 2b except for the presence of much, mostly dead, emergent vegetation.

Larvae of Dixella amphibia were recorded in December and January in swamps, pools and ditches (Disney 1975). Aeshna cyanea has a two-year cycle, so full-grown larvae can be found in winter (Schiemenz 1953). Trissocladius sp. lives in temporary and permanent puddles, it builds loose tunnels of mud and plant remains (Saether 1983). This chironomid emerges in early spring (Cranston 1982). Several typifying taxa are common in pools, lakes, ditches and slowly flowing streams, e.g. Acroloxus lacustris and Hippeutis complanata (Boycott 1936), Paramerina cingulata (Moller Pillot 1984) and Limnodrilus profundicola (Brinkhurst 1964). The latter two species are often common but of low abundance. Agabus sturmi is typical for the early spring (Galewski 1971). Microvelia umbricola is common in weedy waters (Macan 1976).

Site group 4 probably represents the winter situation of site group 3.

Site group 5

Site group 5 consists of four sites which are spread in two pairs over the diagrams. The bottom was peaty (75%) or sandy (25%). At two of the sites the water colour was brown. The sites were sampled in summer and two were temporary waters. Calcium, chloride and oxygen concentrations were very low. For this site group calcium is important on axis 4, which is not shown in the diagrams. Conductivity and pH were also low, indicating an acid environment.

Hesperocorixa linnei and H. sahlbergi occur in weedy waters with a thick organic layer (Macan 1976; Bernhardt 1985). Sigara semistriata can be found in all water types but especially in peaty places (Macan 1976). Callicorixa praeusta lives in temporary pools, often acid, and with a sparse vegetation (Bernhardt 1985). This species is also common in eutrophic or even polluted, vegetation-rich waters, which is also true for Microvelia reticulata and Ilyocoris cimicoides (Macan 1976). Gerris odontogaster occurs in permanent and temporary pools and swamps (Bernhardt 1985). Chaoborus obscuripes is restricted to shallow and small waters (Parma 1969). Eristalis sp. and Culex sp. are air-breathing and often occur in still waters with much decaying organic material (Johannsen 1969). Chironomus gr. plumosus also indicates high organic enrichment (Liebmann 1951; Hynes 1960). Erpobdella testacea is found in dystrophic localities which seem to exclude E. octoculata (Mann 1955). Cyphon sp. occurs in swamps (Klausnitzer 1984). Guignotus pusillus prefers oligo- and mesotrophic ponds. Hydroporus tristis occurs in shaded ponds (Larson 1985) or peaty areas (Freude et al. 1971). Enochrus coarctus, E. affinis and Hydroporus erythrocephalus are acidophilic species (Freude et al. 1971; Galewski 1971). Hyphydrus ovatus can be found in larger ponds and lakes (Galewski 1971). Oligotricha striata lives in stagnant waters, usually swampy, with brown peaty (acid) water (Lepneva 1971). Tricholeiochiton fagesii occurs in stagnant weedy waters (Tobias and Tobias 1981). Sympetrum flaveolum, Lestes sponsa and Aeshna mixta are common in meso- to eutrophic ponds, peat pits, canals and weedy ditches (Gardner 1954).

Site group 5 consists of acid, soft, oligo-ionic, vegetated ditches with a substrate rich in organic material.

Site group 6

Site group 6 is also composed of four sites, all sampled in spring. Conductivity and pH were relatively low. Ammonium, nitrate, total phosphate and iron concentrations were high. Despite the low pH, calcium concentrations were not low. Only one site is temporary. The bottoms consist of sand, peat or clay and the sites are surrounded by grassland or fields.

Chaoborus crystallinus inhabits small and shallow ponds (Parma 1969). Ptychoptera sp. can be found in pools and swamps which are often shaded (Stubbs 1972). Paralimnophyes hydrophilus occurs in eutrophic lowland pools and ditches (Cranston et al. 1983), especially in temporary ones (Moller Pillot & Krebs 1981). Xenopelopia sp. occurs in small waters and the littoral zone of lakes (Fittkau & Roback 1983). Culiseta sp. and Aedes sp. are air-breathing, pollution-tolerant taxa often occurring in temporary waters (Johannsen 1969). Hydroporus umbrosus and Acilius canaliculatus inhabit swamps and small, shaded, often acid pools (Freude et al. 1971). Proasellus meridianus is a common species but less tolerant of organic enrichment than Asellus aquaticus (Higler 1977). Lumbriculus variegatus is also widespread (Brinkhurst and Jamieson 1971) but is often abundant in temporary (Wiggins et al. 1980), even acid pools (Garms 1961; Verdonschot 1987).

Site group 6 consists of acid, eutrophic, vegetated ditches.

Site group 7

Sites in group 7 were mainly sampled in spring (67%), situated on a sandy bottom (83%) with a substrate rich in organic material (83%) and surrounded by grassland (100%). Average ammonium, nitrate and total phosphate concentrations were high.

Most typifying species of this group are tolerant to extreme organic pollution. This holds for Tubifex tubifex (Brinkhurst & Jamieson 1971), Limnodrilus claparedianus (Verdonschot 1981), Haemopsis sanguisuga (Mann 1955) and Psectrotanypus varius (Kreuzer 1940). H. sanguisuga is characteristic for littoral zones or temporary waters; it tends to be a more semi-aquatic species (Elliott & Mann 1979). Haliplus heydeni prefers small hypertrophic ponds (Seeger 1971).

Site group 7 consists of highly eutrophic, organically enriched, more or less vegetated ditches with a substrate rich in organic material.

Site group 8

Most sites of this group are temporary (63%), the ditches are situated on a sandy bottom (100%) with a silt layer (63%) and surrounded both by grasslands (75%) and fields (38%). Seepage occurs at most sites (63%). Samples were mainly taken in summer (88%). Vegetation was mainly restricted to emergent macrophytes. The profile was steep and regular, width and depth were relatively small. Total phosphate concentration was low, ammonium concentration and electrical conductivity were high.

This site group is best typified by the presence of many coleopterans. Common species, also occurring in weedy, small and shallow waters elsewhere, are Anacaena globulus (Jackson 1952), Rhantus suturalis, Laccobius bipustulatus, Helophorus flavipes/obscurus, H. aquaticus/grandis, H. brevipalpis, Hydrobius fuscipes, and Colymbetus fuscus (Freude et al. 1971). Hydroporus nigrita, Anacaena limbata and Agabus bipustulatus also occur in temporary waters (Jackson 1973; Galewski 1971; Williams & Hynes 1976). Hydroporus planus prefers ditches and pools with a sandy or clay bottom (Galewski 1971). Hydroporus striola prefers shaded pools with a silty bottom (Freude et al. 1971). Acricotopus lucens is common in small waters (Moller Pillot 1984). Macropelopia sp. often prefers acid, temporary waters and the upper reaches of lowland streams (Moller Pillot & Krebs 1981). Chaetocladius piger agg. is restricted to springs and streams with a sandy bottom (Moller Pillot 1984). This is also true for Micropsectra sp. (Klink 1982) and Conchapelopia sp. Anisus spirorbis/leucostoma inhabits still waters, temporary ponds and ditches (Boycott 1936; Garms 1961). Gerris lacustris can be found in all types of waters (Bernhardt 1985).

Site group 8 consists of very small, shallow, eutrophic and/or organically-enriched, temporary, slightly flowing ditches on a sandy bottom with an organically rich substrate and only emergent vegetation.

Site group 9

Both sites were situated on a sandy bottom in an agricultural landscape. Samples were taken in spring. Water was slightly flowing. Calcium and total phosphate concentration, conductivity and pH were low. The nitrate concentration was extremely high.

Enchytraeidae are mainly terrestrial or semi-terrestrial (Brinkhurst & Jamieson 1971) and often occur in temporary waters. Limnophila sp. and Geosargus sp. are mainly found in wet earth and sandy soils near the water edge (Johannsen 1969; Rozskosny 1973). Limnephilus flavicornis lives in ponds and puddles, L. lunatus in clear ponds near the shore or slow, clear brooks and L. centralis in temporary pools, especially in acid areas but it is also found elsewhere (Lepneva 1971; Hiley 1976). Nemoura cinerea is often found in temporary and permanent, especially flowing waters (Kreuzer 1940; Beyer 1980). Hydroporus pubescens is found in temporary Sphagnum pools and ditches (Jackson 1973). Limnophyes sp. is eurytopic and is found in aquatic, semi-terrestrial and terrestrial habitats (Cranston et al. 1983).

Site group 9 consists of acid, soft, temporary, slightly flowing ditches on sandy bottoms.

Site group 10

Both sites were temporary and acid. Ammonium, nitrate, phosphate and iron concentrations were high but oxygen and calcium concentrations were relatively low within the data set. Samples were taken in spring. The water colour was brown. The bottoms consisted of sand or sandy peat, both organically enriched.

The typifying taxa resemble those in site group 9. Sigara distincta is common but prefers slightly oligotrophic or clear, slowly running waters (Bernhardt 1985). Scatophagidae mostly live in decaying vegetation or dung (Johannsen 1969). Stylodrilus heringianus is common in stagnant and running waters with sandy, low-productive habitats and is intolerant to pollution (Brinkhurst & Jamieson 1971).

Site group 10 consists of acid, eutrophicated, temporary, slightly flowing ditches.

Site group 11

This site had a low oxygen concentration, but the ammonium and phosphate concentrations were extremely high. Conductivity was high as well. There was a thick mud layer and the water colour was grey/black. Vegetation was absent. The site was sampled in spring.

This site group consists of only one site. This site is taken into consideration because of its intense pollution, which is reflected by the absence of almost all taxa. In this respect the presence of Tubifex tubifex is interesting; it is widespread but expands in more or less extreme environments (Verdonschot 1987). Also, some Ceratopogonidae occur in waters where life becomes unbearable for most other species at certain times (Johannsen 1969).

Site group 11 consists of an extremely eutrophicated ditch with a thick, black mud layer and without vegetation.

7.3 Discussion of data

It can be assumed that the habitat of organisms, which are found nowadays in stagnant waters, was one of marshes, bogs, lakes and stranges before man settled and modified the West European plain. Those stagnant waters normally slowly filled with sediments to become terrestrial (Welch 1952; Hutchinson 1957). Ditches are artificial water bodies which prove to be ideal habitats for many taxa that were formerly confined to shallow lentic zones surrounding lakes and stranges (Caspers & Heckman 1982) or confined to marshes. Ditches need to be periodically dredged to keep them open (Beltman 1984). Otherwise these small and shallow waters will be filled and become terrestrial within 7 to 10 years (Garms 1961). Garms (1961) described five successive stages in ditches near Hamburg. First stage ditches contain either clean water with various organisms that drift in from adjacent ditches or they consist of an anaerobic habitat beneath a solid layer of lemnids. The second and third stages are characterized by a large number of organisms belonging to a wide variety of taxa. The fourth and fifth stages show a sharp decline of aquatic biota and frequently occurring anaerobic and H_2S-rich water. A process of eutrophication and accumulation of organic material runs parallel to this succession.

Welch (1952) described a succession in ponds, which followed some general stages from:

(1) young, exposed, permanent, bare bottom ponds.
(2) adolescent, permanent ponds with increasingly muddy bottoms and invading aquatic vegetation.
(3) mature muck-bottom, permanent ponds with abundant aquatic vegetation in clear layers.
(4) senescent ponds, becoming temporary, completely vegetated.
(5) marsh ponds, becoming increasingly dry.
(6) dry.

The successions described by Welch (1952) and Garms (1961) are closely alike. Caspers & Heckman (1981, 1982) further developed this idea of succession in ditches. They not only described such a succession in time but also in space. Within a ditch they recognized a gradient from the "deep" centre of the ditch to the supralittoral zone. This gradient consists of a complex system of distinct small habitats in close interaction with each other and in an almost constant state of change. This great diversity in habitats accounts for the presence of such large numbers of taxa in ditches (Caspers & Heckman 1982). Such successions in space and time also hold true for the ditches studied.

A typological description is not based upon individual taxa but upon combinations of taxa. These combinations or typifying groups of taxa can be related to differences in important environmental variables. Within the ditches studied the important environmental variables are dimensions, duration of drought, acidity and current. The nutrient load (eutrophication, organic enrichment) diversifies within the occurring combinations of these variables. Although the structure of community-types is mainly determined by the abiotic environment, it is greatly influenced by biotic processes; for example in ditches by a quick succession. This constant interaction is responsible for a number of different ecological niches to be encountered throughout the ditch system. Even under stable conditions of the known major environmental variables, taxa separation occurs due to spatial and temporal segregation (structural niche) and food resource and food utilization (functional niche) (Ramacharan & Paterson 1978; Pianka 1978). Within the scope of this thesis, the functional relations will not be dealt with further. The structural relation between macrofauna and, for example, macrophytes has been stressed by Korinkova (1971), Scheffer et al. (1984), Higler et al. (1986) and Engel (1986).

The ecological validity of the resulting site groups could be strongly supported by detailed knowledge of the autecology of the typifying taxa. Unfortunately, there is insufficient information available to determine this with any great certainty. Many literature references are restricted to global indications like "eutrophic pond", "weedy water" and "littoral zone". A great number of the collected taxa, especially those of site groups 1, 2 and 3, are to be found in most site groups and thus show some overlap in ecological tolerance. This is emphasized by the low eigenvalues. Despite this overlap, taxa are divided into different typifying groups due to differences in the frequency of occurrence and abundance. These differences are, as discussed, the result of the dominance of major environmental variables and/or the presence or absence of certain habitats. By extracting the major habitats from the different site groups, the following gradient results. Site group 1 contains a zone with a well aerated, open water column due to its larger cross-section. This open water column is much less developed in site groups 2 and 3. The open water column is inhabited by taxa which can withstand fish predators, or are related to fish (Piscicola geometra), or migrate through the water column, or are themselves predators (e.g. Cymatia coleoptrata and Plea minutissima). The open water column is followed by a zone of floating and submerged vegetation, which is inhabited by many herbivores. Due to eutrophication, this vegetation is more weedy and less diverse in site group 3 than in site groups 1 and 2. In the more weedy habitats fluctuations in environmental parameters will be greater and only the more tolerant herbivores will be present. The littoral zone is inhabited by emergent macrophytes. In site group 1 this zone is only weakly developed due to the vertical bank profile prevalent in the fenlands. But in site group 2, ditches with a mainly irregular profile, this zone is well developed. The littoral zone is inhabited by taxa which are aquatic or semi-aquatic detritivores. Between the macrophytes, dead plant remains will accumulate. In this littoral zone, large fluctuations in environmental parameters like temperature and oxygen concentration will occur, resulting in temporary anaerobic conditions (Kreuzer 1940). The inhabitants prefer organically-enriched waters (the organic material is their food supply) and can tolerate anaerobic or toxic (H_2S) conditions. In this habitat, taxa characteristic of site groups 7 and 11 can occur, such as Tubifex tubifex and Psectrotanypus varius. The supralittoral zone is a transition between aquatic environment and moist soil. Many of the occurring taxa are semi-aquatic or prefer marshes and they also appear in site group 8. A comparable gradient is present in the acid site groups. This acid environment (site group 5) can be more vegetated in the littoral zone (site group 6) and organically-enriched (site group 10) or mineral (site group 9) in the supralittoral zone.

It should be noted that the bottom, a priori considered as an important variable, is related to many other variables. The fenland consists for the greater part of nature reserves, so the input of nutrients will be low. Further, it has a stable water level and most of the ditches are larger than in other areas and they have vertical banks. The sandy region has a gentle slope, rain water easily infiltrates the bottom, and the bottom itself is poor in nutrients. This results in ditches with small dimensions, the presence of some water movement, and acid conditions at places where rain water meets a soil which is poor in minerals and where agricultural influences are less dominant. The clay region is rich in nutrients and therefore generally intensively cultivated, which implies that these sites do not have their own characteristic fauna.

The gradient based on major habitats combined with the above major environmental variables and diversified by eutrophication and/or organic enrichment accounts for differences between cenotypes.

Site group 1 represents the cenotype of large, permanent, stagnant, neutral, eutrophic ditches. In this chapter these waters are called ditches; it should be noted that this term does not reflect the physico-geomorphological water type ditch but represents the general biotic and abiotic condition belonging to the cenotypes described further. This cenotype probably reflects a mature stage in the sense of Welch (1952).

Site groups 2, 3, 7 and 11 are related cenotypes of small, shallow, permanent, stagnant, neutral ditches. The sequence in cenotypes reflects an increase in eutrophication and/or organic enrichment due to antropogenic activity. It can also be seen as representing the adolescent/mature, senescent and marshy stages (Welch 1952) in succession.

Site group 4 cannot be described accurately enough to be included in the cenotypological scheme.

Site groups 5 and 6 are related cenotypes of small, shallow, permanent, stagnant, acid ditches. The latter is more eutrophicated and/or organically enriched.

Site group 8 represents the cenotype of (very) small, shallow, temporary, slowly running, neutral ditches.

Site groups 9 and 10 are related cenotypes of small, shallow, temporary, acid ditches. The latter is more eutrophicated and/or organically enriched.

These cenotypes are not only interrelated, they even form a continuum. Figure 7.4 reflects the typological relations within the

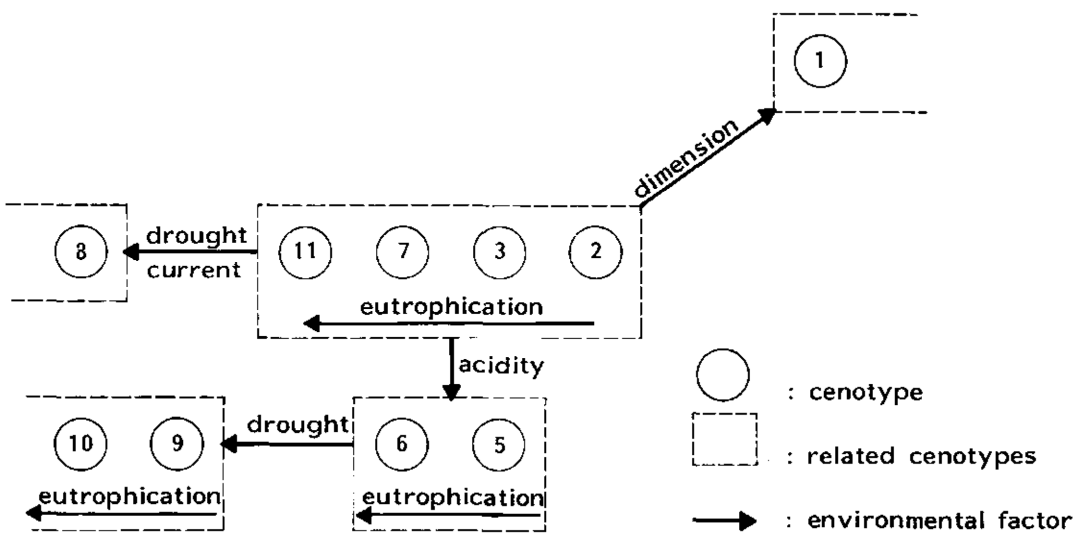

Figure 7.4 Ditches; cenotypological relations. The arrows indicate the direction of increase of the respective variables.

ditches studied. Both central groups of related cenotypes (the closed dotted blocks) are centroids of true ditches. The cenotypes are described in more detail in Chapter 10.

8. MACROFAUNAL COMMUNITY TYPES IN RIVERS, CANALS AND LARGE LAKES

8.1 Introduction

The province of Overijssel is crossed by a system of canals, dug for shipping purposes. Only a few canals have retained their function as a waterway; most of them are now used in water quantity management for the benefit of agricultural activities. Water movement in canals can be two-way: in winter the water is directed towards the rivers and in summer it is pumped from the rivers into the canals. The bottoms consist of peat, clay or sand.

Most catchment areas are fed by rainwater and the medium-sized rivers show corresponding hydrological patterns of low discharges in summer and high ones in winter. Most medium-sized rivers are regulated, canalized and/or more or less polluted. The bottoms consist mainly of sand. The catchment areas vary from 150 to 5120 km^2 and average annual discharges range from 1.2 to 35 m^3/s. The falls average between almost zero and 0.25 m/km.

The river IJssel, a distributary of the river Rhine, is also included. The main characteristics of this river were described by Urk (1981).

Finally, the lakes situated between the main land mass of the province and the polders in Lake IJssel (IJsselmeer), as well as the littoral zone of Lake IJssel itself (Figure 1.10) were included in this chapter. These lakes have a large surface area and are shallow, except for deep navigation channels.

8.2 Results

8.2.1 Data collection

Biotic and abiotic data were collected from 178 sites, sampled between 1981 and 1984; 156 sites were visited only once, 22 sites were visited twice and sampling dates were spread over spring, summer and autumn. A total of 74 variables were measured at all sites.

8.2.2 Preprocessing of the data

After careful individual weighing, 594 taxa were finally included in the analysis. Further information on the preprocessing procedures is given in Section 3.4.1.

8.2.3 Multivariate analysis

The interpretation of the results of clustering (program FLEXCLUS) and ordination (program CANOCO) of the data led to the description of 11 site groups (see below). Numbers of sites, arithmetical means and standard deviations of the quantitative environmental variables, and relative frequency of the nominal variables per site group are given in Table 8.1. The resulting list of all taxa with their typifying weight per site group (program NODES) is available from the author on request. The important typifying taxa are discussed later.

The PCA-diagram (Figure 8.1) illustrates the interrelated variables. Variables that are projected both close to each other and far from the center of the diagram follow similar patterns across sites. The centroids of site scores per site group are projected in this diagram. Some obvious relations between environmental variables and site groups can be seen. Site group 2 is related to macrophytes, peat, oxygen, temperature and a vertical slope profile. Site group 8 is related to width, depth, irregular shape and a weak slope profile. Site group 11 has a high electrical conductivity, the profile is consolidated and there is a sand/silt substrate. Site group 9 was sampled in autumn and shows a high nitrogen and phosphate concentration as well as current, meandering and a fluctuating water level. This is, to a lesser degree, also true for site group 3. Site group 5 includes silty substrates and the sites are often situated in urban areas. Sites of groups 1 and 4 are scattered over the diagram and do not differ in environmental conditions. The other site groups have too few sites to permit conclusions.

The results of ordination of sites and environmental variables (DCCA; program CANOCO) is illustrated in Figures 8.2 and 8.3. The eigenvalues (respectively 0.18, 0.11, 0.11 and 0.07 for the first four DCCA ordination axes) indicate that the environmental gradient is weak along the first axis and even weaker along the second and third axes. The eigenvalue of the fourth axis is very low and therefore this axis is not discussed. This means that the whole data set is reasonably homogeneous. Differences in macrofauna composition of the sites are small. Sites were classified into groups although the distribution patterns of the individual taxa are not discontinuous. Therefore, in the ordination diagram each site group is represented by a centroid which is surrounded by a 90% confidence region (hatched) of the mean of site scores. The contour lines indicate the total variation of all site scores within the data set. The ordination diagrams represent the main structure of the data set.

The relations presented by the site groups are described below with respect to the important environmental variables (Table 8.1) and the ordination results (Figures 8.2 and 8.3). A validation of the site groups is based on knowledge present of the autecology of typifying taxa.

Site group 2

The sites in group 2 are inhabited by a number of typifying species which are common in stagnant waters (e.g. Scirtes sp., Klausnitzer 1984; Noterus crassicornis, Spercheus emarginatus, Hyphydrus ovatus (especially in larger water bodies), Freude et al. 1971; Tanypus kraatzi, Bathyomphalus contortus, Beedham 1972; and several other

Table 8.1 Rivers, canals and large lakes; number of sites, means, and standard deviations of the quantitative environmental variables and percentages of the nominal environmental variables per site group. Abbreviations are explained in Table 10.5.

Quantitative environmental variables

Site group	2	4	1	7	3	11	8	9	5	6	10
Number of sites	35	46	26	4	12	10	9	28	6	1	1
T	20	15	15	18	12	12	12	10	15	16	21
sd	2.8	4.0	3.9	0.9	3.2	4.0	1.1	3.2	5.4	0	0
PH	7.6	7.8	7.5	8.7	7.9	7.8	8.4	7.7	7.7	7.2	7.9
sd	0.4	0.6	0.3	0.3	0.5	0.3	0.2	0.5	0.6	0	0
EC	427	483	437	418	493	695	569	588	466	1300	480
sd	115	133	205	93	72	255	181	293	102	0	0
O2	12.	10.	14.	11.	12.	11.	9.8	9.6	6.7	6.5	6.5
sd	4.5	3.2	4.4	4.7	2.3	3.1	1.9	2.3	3.5	0	0
O2%	129	102	96	116	102	86	91	83	71	65	72
sd	55	33	39	49	13	16	18	24	38	0	0
NH4	0.9	0.5	0.8	0.1	1.7	0.7	0.2	1.8	1.9	1.6	0.1
sd	1.1	0.4	0.5	.03	1.4	0.6	0.1	1.9	1.4	0	0
NO3	.19	1.8	1.8	3.3	3.8	2.9	2.5	14.	2.8	.12	2.3
sd	.13	1.7	1.6	1.8	1.5	1.6	1.8	28.	1.9	0	0
O-P	.17	.04	.14	.01	.20	.16	.04	.63	.10	0	.01
sd	.48	.05	.23	0	.12	.12	.06	.83	.12	0	0
T-P	.27	.32	.30	.17	.53	.39	.34	1.2	.59	.18	.15
sd	.55	.48	.27	.03	.39	.17	.14	1.3	.31	0	0
CL	50	50	74	54	29	94	99	64	76	325	59
sd	16	28	59	14	8	69	46	92	20	0	0
W	12	23	28	38	29	96	1550	14	68	8	20
sd	7	22	18	10	13	52	1447	7	17	0	0
D	.73	1.5	2.4	3.4	2.5	4.1	4.9	1.5	4.7	0.5	3.0
sd	.31	.83	1.1	.41	1.1	0.8	4.0	.73	0.5	0	0
TRANSPAR	.38	.58	.70	.38	.41	.50	.44	.74	.54	.30	.80
sd	.19	.33	.31	.13	.18	.17	.14	.41	.20	0	0
S-T	.10	.02	.08	.13	0	.05	.40	.11	.15	.03	0
sd	.20	.04	.24	.22	0	.15	0	.19	.21	0	0
%-A	1	2	2	1	0	1	0	3	1	1	0
sd	1	7	6	1	0	1	0	15	1	0	0
%-F	30	10	10	1	4	1	0	3	0	1	5
sd	24	13	19	1	8	1	0	10	0	0	0
%-S	5	4	5	1	1	3	0	5	0	1	5
sd	11	9	12	1	1	9	0	13	0	0	0
%-E	9	3	19	1	1	3	3	3	2	1	1
sd	13	4	22	1	1	6	3	10	4	0	0
%-B	12	1	1	0	2	1	0	1	1	0	1
sd	12	3	3	0	2	1	0	4	1	0	0
%-T	47	17	33	1	5	7	3	10	2	1	10
sd	26	18	31	1	8	15	3	22	3	0	0
%MM-B	36	30	40	40	38	0	6	24	17	20	16

sd	35	27	30	40	35	0	12	28	37	0	0
%MM-E	5	18	23	3	16	40	23	10	33	0	16
sd	13	23	25	4	24	29	13	19	47	0	0
%MM-F	43	21	13	5	3	8	0	7	0	40	0
sd	36	23	14	9	7	17	0	17	0	0	0
%MM-S	2	7	7	21	7	8	0	23	13	20	32
sd	9	18	13	25	22	24	0	31	30	0	0
%MMSILT	3	10	8	13	5	6	37	17	28	20	0
sd	7	12	12	8	8	9	10	13	37	0	0
%MMSAND	2	8	4	19	22	20	27	12	8	0	36
sd	7	11	8	27	25	27	15	14	19	0	0
%MMPEAT	5	1	2	0	0	0	0	0	0	0	0
sd	7	3	5	0	0	0	0	0	0	0	0
%MMCLAY	1	1	1	0	0	7	0	1	0	0	0
sd	2	3	4	0	0	13	0	5	0	0	0
%MMDETR	5	3	2	0	6	4	7	1	0	0	0
sd	6	6	9	0	12	6	8	4	0	0	0
%MMGRAVE	0	0	1	0	0	0	0	1	0	0	0
sd	0	0	3	0	0	0	0	2	0	0	0
%MMSTONE	0	1	0	0	3	8	1	2	0	0	0
sd	0	4	0	0	4	10	2	6	0	0	0
FALL	.0	.11	.7	.0	.25	.14	.0	.41	.1	.0	.0
sd	.0	.30	.18	.0	.12	.29	.0	.39	.0	.0	.0
SOURDIST	0	11	22	0	97	212	0	37	20	0	0
sd	0	19	20	0	51	366	0	21	14	0	0
S	0	.01	.01	0	.20	.30	.01	.17	0	0	0
sd	0	.03	.02	0	.30	.46	.02	.19	0	0	0

Nominal environmental variables

Site group	2	4	1	7	3	11	8	9	5	6	10
SPRING	97	72	46	25	83	70	100	25	50	100	100
SUMMER	3	26	42	75	17	20	0	4	33	0	0
AUTUMN	0	2	12	0	0	10	0	71	17	0	0
SHAPLSRE	91	87	100	100	92	90	0	82	100	100	100
SHAPLSIR	9	4	0	0	8	0	0	18	0	0	0
SHAPIRR	0	7	0	0	0	10	100	0	0	0	0
SHAPREG	0	2	0	0	0	0	0	0	0	0	0
SEE	14	9	0	0	0	0	0	4	0	0	0
COLORLESS	3	0	0	0	0	10	0	0	0	0	0
YELLOW	60	87	73	50	100	70	33	82	33	0	100
BROWN	11	13	23	25	0	0	22	14	17	100	0
GREEN	23	0	4	25	0	10	44	0	17	0	0
GREYBLAC	3	0	0	0	0	10	0	7	33	0	0
SMELL	3	7	0	0	33	30	0	14	33	0	0
CLEAR	20	46	0	0	33	20	22	18	0	0	100
SLTURB	49	43	73	50	42	80	67	46	50	0	0
TURBID	31	9	27	50	25	0	11	36	50	100	100
BACTNONE	94	91	100	100	100	100	100	100	100	100	100
BACTSL	0	7	0	0	0	0	0	0	0	0	0
BACTABUN	3	2	0	0	0	0	0	0	0	0	0
POLLUT	11	13	19	100	0	30	0	29	67	0	0
CLEANIN	74	41	69	0	25	20	100	21	67	0	0

SAND	20	67	69	75	100	70	100	96	100	0	0
SASILT	6	4	8	0	0	20	0	4	0	100	0
CLAY	29	24	27	0	0	40	0	11	0	0	0
FENLAND	57	13	15	25	0	0	0	4	0	0	100
PEAT	3	2	0	0	0	0	0	0	0	0	0
STSAND	6	35	0	0	83	40	89	21	0	0	100
STSASI	3	0	0	0	0	10	0	0	0	0	0
STPEAT	20	2	0	0	0	0	0	0	0	0	100
STCLAY	6	7	0	0	0	30	0	0	0	0	0
STSILT	46	70	65	50	33	40	89	71	100	0	0
STFDPESI	6	9	8	50	0	0	11	0	0	0	0
STFDEPE	0	0	12	0	0	0	0	0	0	0	0
STCM	0	9	12	0	8	10	11	4	0	0	0
STCMDLPE	6	2	0	0	0	0	0	4	0	100	0
STCMDELE	0	0	0	0	0	10	0	0	0	0	0
STCMSI	0	0	0	0	0	0	44	0	0	0	0
STCDLE	0	0	0	0	0	0	11	0	0	0	0
STCDLESI	0	2	0	0	0	0	11	0	0	0	0
STCOMB	11	2	0	0	0	0	0	0	0	0	0
MEANDNT	100	93	81	100	33	90	0	75	100	100	100
MEANDSL	0	4	19	0	33	0	0	7	0	0	0
MEAND	0	2	0	0	33	0	0	18	0	0	0
REGULNT	0	2	12	0	25	0	0	18	0	0	0
REGULSL	0	0	12	0	25	0	0	4	0	0	0
REGUL	100	98	77	100	50	90	0	79	100	100	100
WATLF	03	22	15	75	42	30	0	64	0	0	100
PS30	0	7	19	0	17	20	89	7	17	0	0
PS45	0	15	15	0	17	20	11	14	0	0	0
PS75	3	43	27	0	50	20	0	61	0	0	0
PS90	89	24	23	100	8	30	0	0	67	100	100
PSCON	9	2	0	0	0	0	0	0	0	0	0
PSIRR	0	2	15	0	8	10	0	18	17	0	0
PROCON	3	26	42	100	33	100	11	25	100	100	100
SHADOW	14	35	4	50	33	10	0	21	0	100	0
SURURB	6	13	19	50	8	20	11	18	50	0	100
SURFOR	11	4	0	0	33	10	0	11	0	0	0
SURWOB	3	11	0	25	0	0	0	11	0	0	0
SURFIE	3	9	8	0	8	10	0	25	17	100	0
SURGRA	46	80	92	50	83	80	44	64	33	0	100
SURREE	60	2	4	0	0	0	89	0	0	0	0
ISOL	0	9	0	0	0	0	0	0	0	0	0

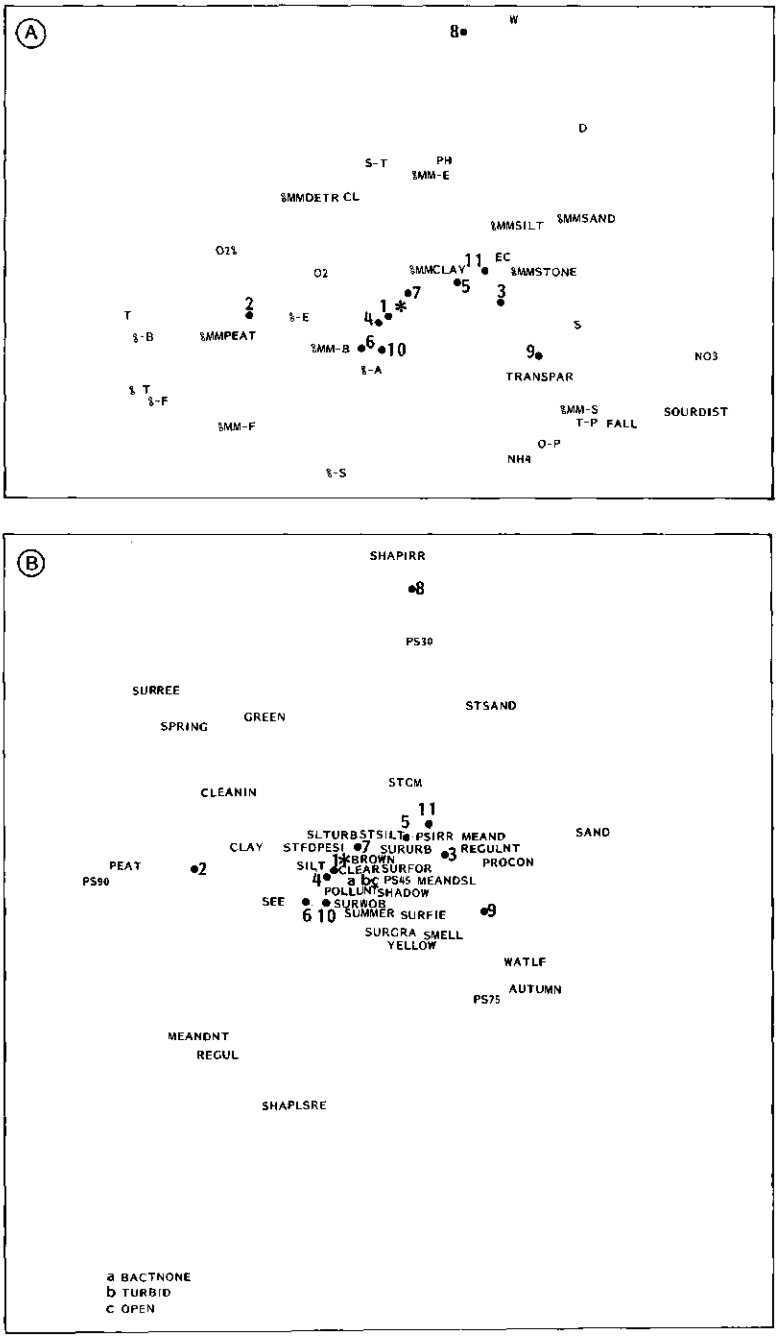

Figure 8.1 Rivers, canals and large lakes; ordination (PCA) diagram for axes 1 (horizontally) and 2 (vertically) for nominal (A) and quantitative (B) environmental variables. For further explanation see Sections 3.4.2 and 8.2.3, and Figure 3.10. Abbreviations are explained in Table 10.5.

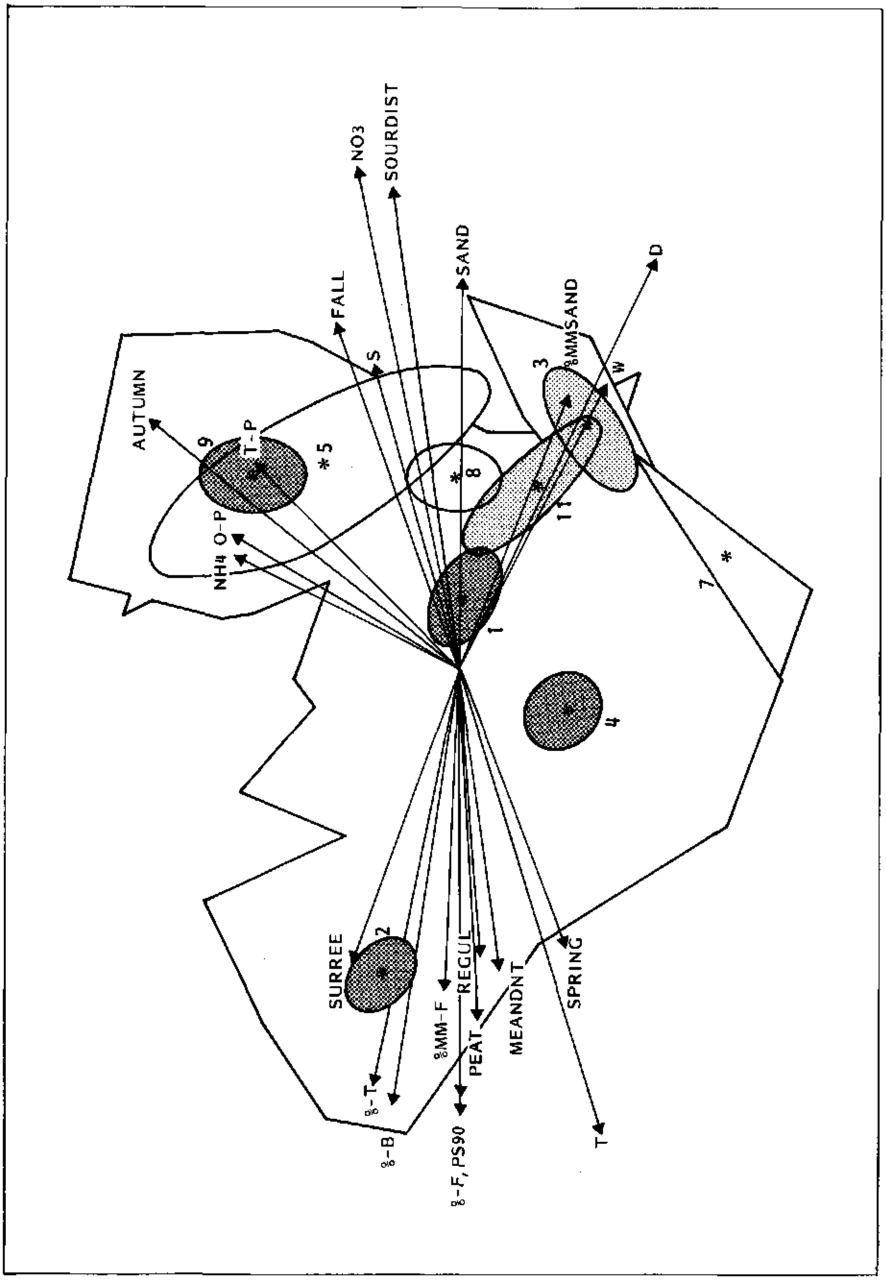

Figure 8.2 Rivers, canals and large lakes; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically). The contour line describes the total variation of all site scores. Only environmental variables with an interset correlation greater than 0.4 are shown (arrows). For further explanation see Sections 3.4.2 and 8.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

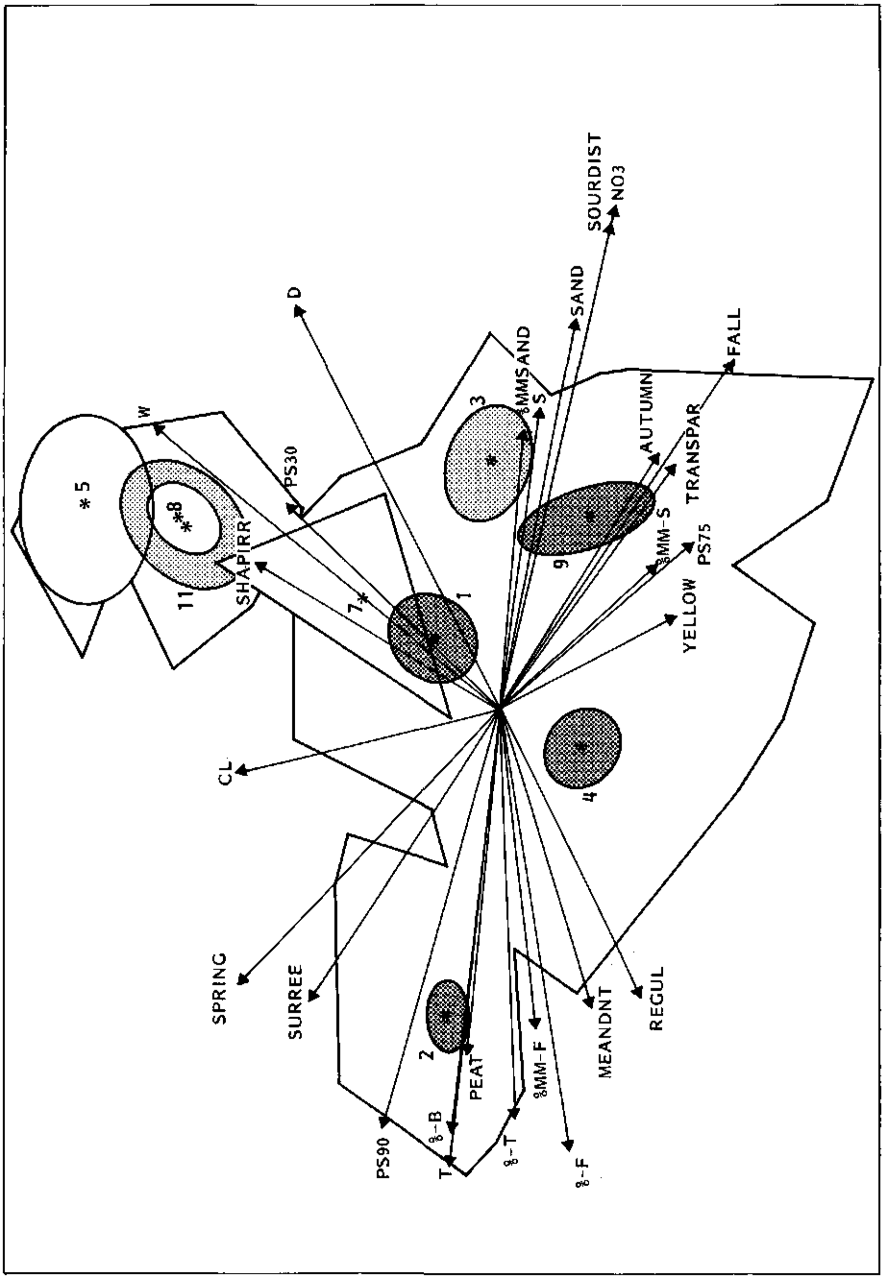

Figure 8.3 Rivers, canals and large lakes; ordination (DCCA) diagram for axes 1 (horizontally) and 3 (vertically). The contour line describes the total variation of all site scores. Only environmental variables with an interset correlation greater than 0.4 are shown (arrows). For further explanation see Sections 3.4.2 and 8.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

eurytopic gastropods, here abundantly present). More specific for the vegetation at these sites are Anatopynia plumipes (Fittkau 1962), Hippeutis complanata, Segmentina nitida (Macan 1977), Planorbis planorbis (Beedham 1972) and Eylais extendens/tantilla (Besseling 1964). Anatopynia plumipes and Caenis robusta are more abundant in waters with a minerotrophic peaty substrate (Fittkau 1962, Mol 1985). Proasellus meridianus and Asellus aquaticus (Hynes 1960) are more abundant in organic detritus.

Most sites in group 2 are vegetated, well oxygenated, surrounded by reedlands (60%), and situated on a peaty substrate (57%). The waters have a vertical profile (89%) without consolidation, and the high temperatures (although most samples were taken in spring) were probably related to the small dimensions. The nitrate concentrations were low.

Site group 2 consists of small, linear, stagnant waters on a peaty substrate. Biotic and abiotic characteristics indicate a less diverse fauna, a more dense vegetation and some eutrophication compared to the large, permanent, stagnant, neutral ditches (Chapter 6) and peat lakes (Higler 1977). The less diverse fauna is most probably due to eutrophication (a larger algal biomass reduces light penetration and therefore growth of macrophytes) and to a lesser extent to recreational navigation (due to the physical destruction of macrophytes). A reduction of macrophytes implies a reduction of physical structure and thus a reduction in macrofauna diversity.

Site group 4

The sites in group 4 are inhabited by only a few typifying taxa, although the total number of taxa per site is relatively high within the total data set. Most species are widespread and ubiquitous. There are some typifying mites (Piona pusilla, Limnesia undulata, Eylais hamata) which often occur in the littoral zones of larger, hard water bodies (Kreuzer 1940). Triaenodes bicolor, Arrenurus globator, and Ilyocoris cimicoides are common inhabitants of weedy, stagnant waters (Hickin 1967, Besseling 1964, Macan 1965). Other very widespread taxa but typifying site group 4 are Pionopsis lutescens, Haliplus ruficollis, and Graptodytes pictus (also in slowly flowing waters)(Freude et al. 1971). Their typifying character is less significant.

The sites in this group have average concentrations of most variables measured within this study. The sites are widely scattered over the diagram (Figures 8.2 and 8.3) indicating the intermediate position of this site group. Most sites were sampled in spring (72%), have a silty substrate (70%), are surrounded by grassland (80%), and are slightly turbid to transparant.

Site group 4 consists of small to medium-sized, linear, stagnant waters. The presence of only widespread taxa indicates, to a certain extent, a chronic environmental stress due to navigation, eutrophication, and/or organic wastes.

Site group 1

Most typifying taxa occur in stagnant and/or slowly flowing waters like Cyrnus flavidus and Cyrnus insolutus (Lepneva 1970, Eddington &

Hildrew 1981). Within the vegetation there are taxa like Hemiclepsis marginata (Dresscher & Higler 1982) and Phryganea bipunctata (with detritus substrate)(Tobias & Tobias 1981). Haliplus fluviatilis lives in running waters (Freude et al. 1971). On the other hand, stagnant inhabitants are Ecnomus tenellus (ponds and canals) (Hickin 1967) and Gammarus tigrinus. The latter species occurs in large, especially ion-rich, water bodies in the Netherlands since 1965 (Nijssen & Stock 1966).

The sites of group 1 are well oxygenated and transparancy is intermediate (73%). The sites are reasonably vegetated in the littoral zone and the substrate often consists of silt (65%). The sites are surrounded by grassland (92%).

Site group 1 consists of medium-sized, linear, stagnant or very slightly flowing waters and the differences with site group 4 are small.

Site group 7

Site group 7 consists of four sites. A number of typifying taxa occur in stagnant and slowly flowing waters (e.g. Nais pardalis, N. barbata, N. variabilis, Ripistis parasita (all more abundant in the middle and lower reaches of rivers), Learner et al. 1978; Tinodes waeneri, Eddington & Hildrew 1981, Hickin 1967; Limnesia maculata (especially in vegetation), Böttger 1972; Mideopsis orbicularis, Berg 1948; Unionicola aculeata, Hevers 1978). Some others are eurytopic (e.g. Limnophyes sp., Cranston et al. 1983; Hygrobates nigromaculatus, Berg 1948), or are common in large stagnant water bodies like Glyptotendipes gr. signatus (in Ectoprocta colonies)(Shilova 1968), Potamothrix bedoti (in silty muck substrates)(Stimpson et al. 1982) and Branchiura sowerbyi (especially in canals where the temperature does not drop very low in winter)(Brinkhurst 1964). Stictotarsus duodecimpustulatus lives in pools of streams on sand and gravel substrates (Freude et al. 1971). Piscicola geometra prefers clean, larger, less weedy waters due to its association with fish (Garms 1961).

The sites (all in canals) mostly had slightly turbid to turbid water with a high pH and a fluctuating water level. The ammonium and orthophosphate concentrations were low and the iron and nitrate concentrations were high. The sites are relatively wide, deep and have very little vegetation. They are sometimes shaded (50%), always polluted, and the substrate often consists of silt. There is always a vertical profile consolidation. The sites are situated in urban (50%) or agricultural areas (50%) and were sampled in summer (75%).

Site group 7 consists of medium to reasonably large, stagnant waters with a regular linear shape.

Site group 11

The sites of group 11 are also inhabited by typifying taxa which are common in lakes and slowly flowing waters (e.g. Psammoryctides barbatus (needs a reasonable oxygen concentration), Brinkhurst 1964; Dicrotendipes gr. nervosus, Lehman 1971; Chaetocladius sp., Cranston et al. 1983; Uncinais uncinata, Learner et al. 1978; Dreissena polymorpha and Unio pictorum, Ellis 1978) but are most abundant in larger water bodies. Hydropsyche contubernalis is a typical inhabitant of the lower reaches of rivers (Eddington & Hildrew 1981), as is Parachironomus Kampen which is associated with Ectoprocta (Pinder & Reiss 1983). The genus Cricotopus, also typifying, is very eurytopic.

All sites have a high electrical conductivity and chloride concentration. They are wide, deep, and the bottoms consist of sand or clay. There is always a profile consolidation, some fall and a high current. Most samples were taken in spring (70%). Most sites are surrounded by grassland (80%). This site group includes the only sample taken in the exposed littoral zone of the very large Lake IJssel.

Site group 11 consists of large, linear, slightly flowing or stagnant waters.

Site group 8

The taxa typifying site group 8 are again common in lakes and rivers (e.g. Cryptochironomus sp., Pinder & Reiss 1983; Psammoryctides albicola (in mud and gravel), Chekanovskaja 1962; Limnodrilus claparedianus (in mud and muddy sand, saprobic), Dzwillo 1966; Noterus clavicornis, Freude et al. 1971; Limnodrilus profundicola (in mud and sand), Kennedy 1965; Lipiniella arenicola (in sand), Pinder & Reiss 1983; Lithoglyphus naticoides (on solid substrate and sand)). Some taxa are inhabitants of lakes and reservoirs (e.g. Einfeldia gr. insolita (in mud), Lenz 1962; Gyraulis laevis, Macan 1977; Fleuria lacustris (in soft sediments), Pinder & Reiss 1983), are eurytopic (e.g. Peloscolex ferox, Stimpson et al. 1982; Cladotanytarsus sp., Pinder & Reiss 1983; Limnophyes sp., Cranston et al. 1983) or inhabit the lower reaches of rivers (e.g. Potamothrix moldaviensis (in mud and muddy sand), Timm 1970, Moroz 1977; Potamopyrgus jenkinsi, Macan 1977; Valvata macrostoma and Microchironomus tener).

Site group 8 is related to very large dimensions, a very weak slope profile (89%), a high chloride and a low ammonium concentration, a wide littoral zone with reed vegetation and a round or irregular shape. All samples were taken in spring on partly silt or sand substrates. The water colour was sometimes green (44%) and the pH was high.

Site group 8 consists of very large, round or irregular shaped, stagnant waters.

Site group 5

Site group 5 has no typifying taxa. The only two indifferent taxa are Limnodrilus claparedianus and Potamothrix moldaviensis (see site group 8). All sites were characterized by the presence of only a few taxa and low abundance.

Site group 5 had low oxygen and high ammonium concentrations. The sites are wide, deep, linear, have little vegetation and a vertical profile consolidation (67%). The water is often turbid (50%), polluted (67%), sometimes grey/black (33%) and the substrate is silty. The sites are situated in urban or agricultural areas.

Site group 5 consists of polluted, rather large, linear, stagnant or slightly flowing waters.

Site group 3

Most typifying taxa of site group 3 are more or less subrheophilic (e.g. Laccophilus hyalinus, Galewski 1971; Nanocladius sp., Cranston et al. 1983; Cyrnus trimaculatus, Eddington & Hildrew 1981; Polypedilum breviantennatum, Lindegaard-Petersen 1972; Zavrelimiyia sp. (in sand and detritus), Fittkau & Roback 1983; Uncinais uncinatum, Learner et al. 1978; Haliplus fluviatilis, Freude et al. 1971; Cricotopus bicinctus, Mackay 1976; Rheotanytarsus sp., Pinder & Reiss 1983), though some also occur, often less abundantly, in stagnant waters (e.g. Phaenopsectra (in sand and mud), Pinder & Reiss 1983; Nemoura cinerea, Illies 1955; Nais elinguis, Learner et al. 1978; Conchapelopia, Fittkau & Roback 1983).

Several sites in group 3 are situated in rivers which are not or slightly regulated (50%), more or less meander (66%) and are surrounded by grassland (83%). The profile is often reasonably steep and fall and current are fairly high. The chloride concentration is low and the nutrient concentrations are relatively high compared to the other groups. Little silt is deposited. The samples were taken in spring (83%).

Site group 3 consists of medium-sized, meandering, linear, flowing waters.

Site group 9

Sites of group 9 are inhabited by taxa of ponds and small rivers like Micropsectra sp. (especially in muddy deposits of streams) (Pinder & Reiss 1983), Limnephilus rhombicus (in weedy, oxygen-rich water) (Hickin 1967), Procladius sp. (in mud, and abundant in autumn)(Fittkau & Roback 1983), Polypedilum gr. nubeculosum (Lehmann 1971), Aulodrilus pluriseta (in sand, mud and peat) (Brinkhurst 1964, Pfannkuche 1977), Limnodrilus udekemianus (in organic mud) (Chekanovskaja 1962). Baetis vernus occurs in slowly flowing, weedy rivers (Macan 1970), together with Potthasia longimanus (on sand) (Lehmann 1971) and Centroptilum luteolum (on sand) (Macan 1979). Neumania deltoides, Cloeon dipterum (in dense vegetation) (Garms 1961, Macan 1979), and Potamothrix hammoniensis (in mud) (Brinkhurst 1964) are common in stagnant, productive waters. Finally, Tubifex tubifex often occurs under extreme conditions, e.g. organic pollution or drought.

Site group 9 consists of samples mostly taken in autumn (71%; low temperature), in small, relatively shallow, nutrient-rich waters (especially high nitrate concentrations) with a fairly strong current due to a steep fall. The water is slightly turbid (46%), the water level fluctuates (64%), the substrate is silty (71%), and the profile is not steep.

Site group 9 consists of small to medium-sized, linear, flowing waters.

Site group 6

Site group 6 consists of only one site dominated by tubificids, some gastropods and Chironomus sp.

This site is small, shallow and poorly oxygenated. The water was turbid and had a high chloride (oligohaline) concentration (correlated with a high conductivity) and a low nitrate concentration. The site is shaded, has a vertical profile consolidation, and was sampled in spring.

Site group 6 consists of a small, linear, stagnant, oligohaline water.

Site group 10

Site group 10 consists also of only one site, a canal, which is rich in species partly like site group 1 and partly like site group 7.

The nutrient concentrations were relatively low, the profile was consolidated and the water was transparant. The site was sampled in spring. Water inlet takes place from an adjacent regulated river. This explains the unusual aberrant species combination.

Site group 10 consists of a medium-sized, linear, stagnant water.

8.3 Discussion of data

The site groups show a great overlap in collected taxa and thus of conditions. This is stressed by the extremely low eigenvalues. The fauna concerns mostly opportunistic taxa. In running and linear, (temporarily) stagnant waters increasing size implies an increasing drainage area. The larger bodies which transport water therefore function as collectors of nutrients, organic materials, and toxicants. This cumulative process causes chronic stess and the disappearance of most of the original taxa. Despite the strong overlap between the site groups, different groups of typifying taxa could be distinguished due to differences in their frequency of occurrence and abundance (Figure 8.4).

Site group 4 probably best represents the cenotype with the greatest number of opportunistic taxa. It consists of sites with a broad range of major environmental conditions (e.g. profile shape, dimensions, isolation) present in linear waters. Chronic stress in such an environment overrules the natural master factors (current, dimensions). This is also illustrated by the extremely small number of typifying taxa despite the large variety of taxa present. This cenotype represents chronically stressed, small to medium-sized, stagnant canals.

If environmental conditions in small stagnant canals on a peaty substrate improve, the typifying taxa of site group 2 should reappear. These inhabitants of stagnant water with a dense vegetation are all relatively tolerant of fluctuations in environmental variables. This site group represents the cenotype of less chronically stressed, small, stagnant canals on a peaty substrate.

If the dimensions of these stagnant waters increase, the taxa assemblage of site group 4 will gradually grade into that encountered in site group 7. Sites of this site group are situated on a sandy substrate and are less polluted. The type of substrate does play a role in the development of a taxa assemblage but this factor is difficult to eliminate in this study because of the level of pollution present at all sites. Site group 7 represents the cenotype of less

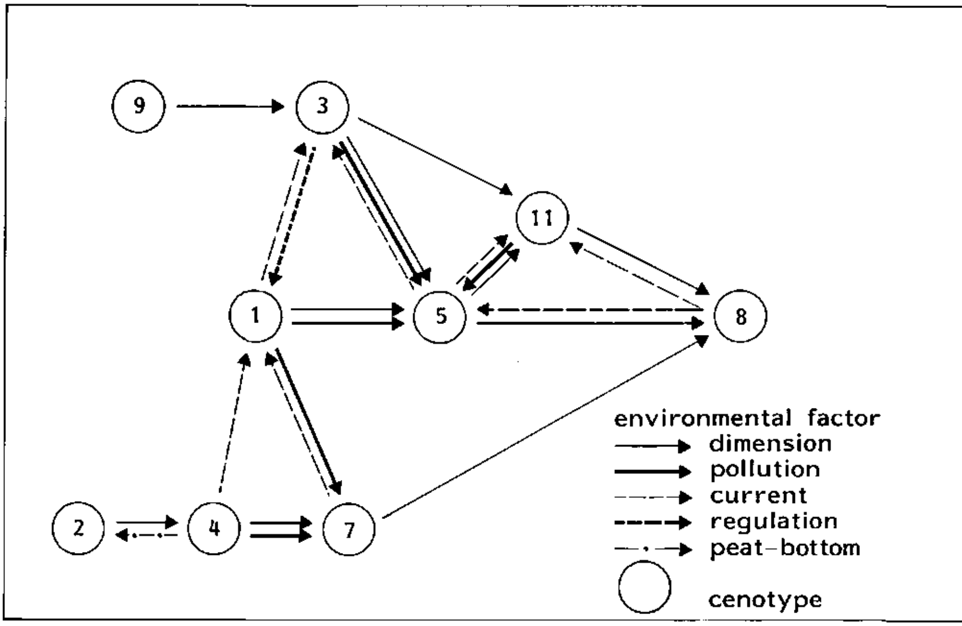

Figure 8.4 Rivers and canals; cenotypological relations. The arrows indicate the direction of increase of the respective variables.

stressed, medium to fairly large, stagnant canals.

The importance of dimensions in the gradient of small to large, linear, stagnant waters can be seen in Figure 8.2, where site groups 2, 4 and 7 are situated along a diagonal line (from upper left to lower right corner) in the diagram. Another important discriminating variable is current, which separates these three site groups (mainly canals and a few very slightly flowing, regulated rivers) from all the others (natural and regulated rivers), in the upper right area.

Site group 1 is slightly different from site group 4. The average dimensions and current are slightly higher and most sites are more vegetated, especially in the littoral zone. This agrees with the different predatory trichopterans and the occurrence of typifying taxa characteristic of larger water bodies. Chronic stress is responsible for the poorly specified taxa assemblage. Site group 1 represents the cenotype of chronically stressed, medium-sized, very slowly flowing, regulated rivers or stagnant canals.

The sites of site group 5 are severely and chronically stressed and larger in dimensions. Only the oligochaete P. moldaviensis typically inhabits such large water bodies. Site group 5 represents the cenotype of severely and chronically stressed, fairly large, slightly flowing, regulated rivers or stagnant canals.

Site group 9, despite the higher nutrient concentrations (a seasonal effect), is chronically less stressed. This is reflected in the presence of inhabitants from medium-sized rivers. Only some oligochaetes indicate (organic) pollution. This site group represents the cenotype of chronically less stressed, small to medium-sized, flowing rivers.

As the size of these rivers increases, the taxa assemblage gradually changes towards the subrheophilic taxa assemblage encountered in site group 3. Pollution levels and/or disturbances may be smaller. Site group 3 represents the cenotype of chronically less stressed, medium-sized, meandering, flowing rivers.

Dimensions increase as the river follows its course. A large river will always be more or less chronically stressed because it will reflect the summation of all human activities in a large catchment area. Only a few original inhabitants of large rivers were found in site group 11. Site groups 3 and 11 do not overlap because rivers with intermediate dimensions are lacking in the studied region. Some large canals and the exposed littoral zone of a large lake are also represented in site group 11. The level of pollution makes it impossible to discriminate between large lakes and some large canals. So site group 11 can also be projected in the sequence of site groups 1 and 5. Site group 11 represents the cenotype of chronically fairly stressed, large, slightly flowing rivers or stagnant canals.

Most waters of the province of Overijssel finally discharge into Lake IJssel via smaller lakes in open connection with each other. Sites sampled in these smaller lakes all belong to group 8. Several taxa indicate the influence of river discharge into these lakes. Pollutants present in the rivers are deposited in the lakes. Site group 8 represents the cenotype of chronically stressed lakes.

The nine cenotypes described are schematically illustrated in Figure 8.5. The physical state (longitudinal and transverse profile) of the waters is more or less fixed and the cenotypes are projected upon these physical structures. Originally, especially the natural river at the top of this figure and the stagnant canal (comparable to a oxbow lake) at the bottom must have had their characteristic taxa assemblages. It is still possible to extract some information from the cenotypes. They represent more or less stressed stages of assemblages which could have developed there. The cenotypes 9, 3 and 11 follow the original course of a river. The cenotypes 2, 4 and 7 represent a gradient in size of dug canals, and the cenotypes 1 and 5 represent a gradient in size of strongly regulated rivers or canals. Pollution has often caused the disappearance of all original taxa. The presented cenotypes are provisional. They should be compared to the cenotypes for other water bodies described in the other chapters.

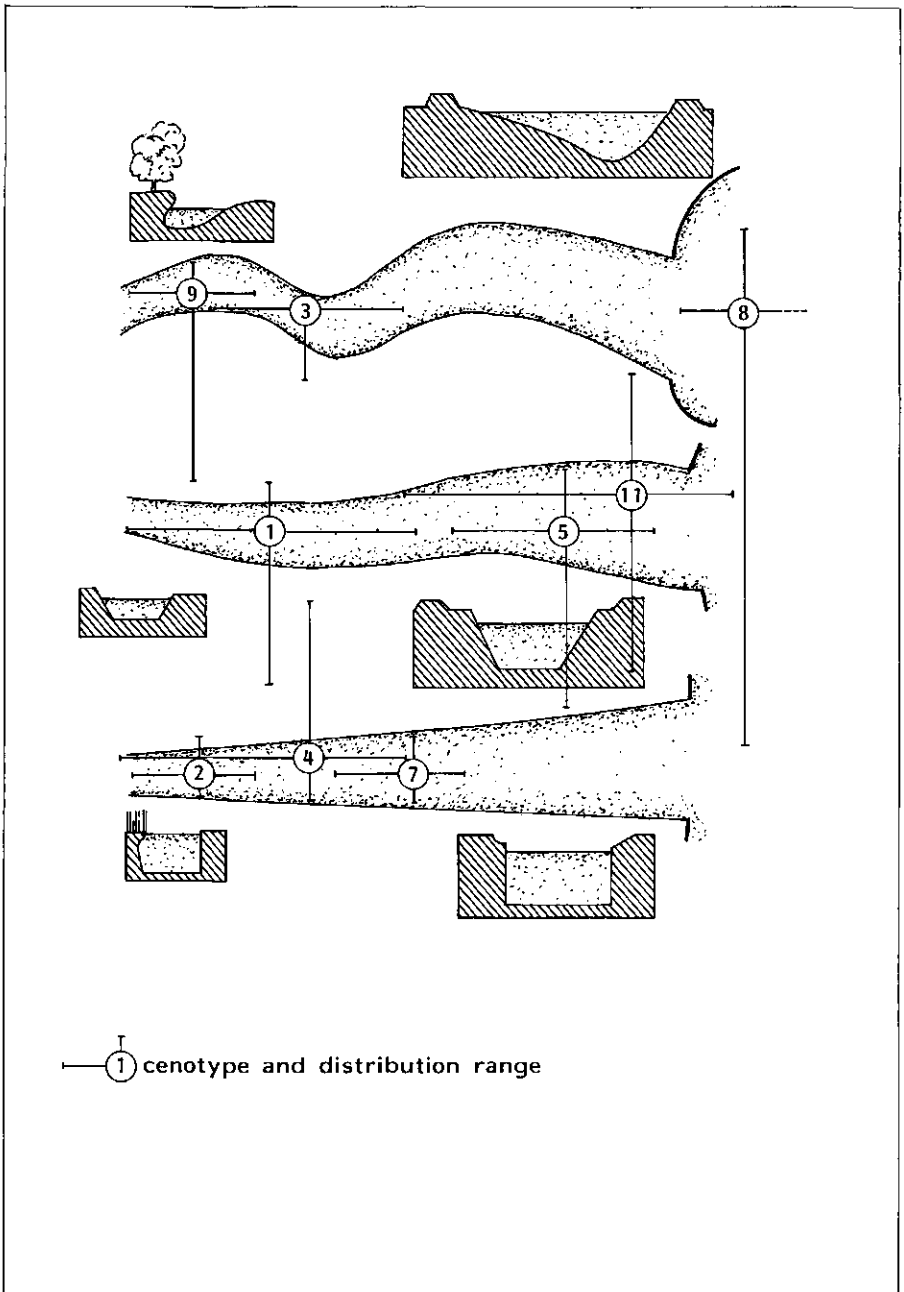

Figure 8.5. Scheme of the transverse and longitudinal profiles of a natural river, a regulated river and a canal with cenotypes and their respective distribution ranges, with respect to longitudinal and transverse profile shapes, width, depth, and 'stream character'.

9. MACROFAUNAL COMMUNITY TYPES IN PONDS AND SMALL LAKES

9.1 Introduction

Ponds and small lakes may be formed by natural processes or by anthropogenic ones. The natural ponds are a result of aeolian or fluvial processes. In the Pleistocene part of the province the wind eroded depressions on the cover-sands and percolating water deposited an impermeable iron-pan layer, above which moorland pools were formed. Meandering streams form large shallow ponds in an 'oxbow' when the meander is cut off. The man-made ponds and small lakes result from former rural (e.g. drinking pools for cattle, water holes) and industrial (e.g. sand-, clay- and peat-extraction) activities. Deeper ponds were formed along the dikes of the rivers IJssel and Vecht and the former inlet of the North Sea (the 'Zuiderzee') where dikes had burst during storms and floods.

The ponds and small lakes have an average depth of 1.8 m and an average surface area of 42,000 m^2. Some important differentiating physical and chemical parameters are permanence, morphometry, acidity, vegetation cover, and human influence. The bottom consists of clay, sand or peat. Some of the ponds are fed by rainwater and correspondingly show water level fluctuations - low in summer and high in winter. The mineral content of the bottom together with human activity determine whether these ponds contain chemically rainwater or not. Some other ponds are connected to ditches or canals and are, therefore, less dependent on rainwater input; they have a more constant water volume. A third part, also with a constant water volume, is isolated and fed by groundwater flow; they contain therefore chemically groundwater.

Human activities in the province of Overijssel are mainly concerned with agriculture and since 75 % of the total area of the province is cultivated, this strongly affects the nutrient load of many ponds.

9.2 Results

9.2.1 Data collection

The data were collected from 157 sites, sampled between 1982 and 1985. Most sites were visited once, only 6 sites were visited twice, and sampling dates were spread over spring, summer and autumn. A total of 61 abiotic variables was measured at all sites.

9.2.2 Preprocessing of the data

After careful individual weighing of the macrofaunal data, a total of 774 taxa, 608 taxa were finally included in the analysis. Further information on the preprocessing procedures is given in Section 3.4.1.

9.2.3 Multivariate analysis

The interpretation of the results of clustering (program FLEXCLUS) and ordination (program CANOCO) of the data lead to the description of 9 site groups (see below). Numbers of sites, averages and standard deviations of the quantitative environmental variables, and relative frequency of the nominal variables per site group are given in Table 9.1. A list of all taxa present with their typifying weight per site group (program NODES) is available from the author on request. The autecology of the most important typifying taxa will be discussed below.

The ordination (PCA) diagram for the axes 1 and 2 illustrates the relation between site groups and environmental variables (Figure 9.1). Variables that are projected both close to each other and far from the center of the diagram follow similar patterns across sites. Only centroids of site groups, based on the site scores, are indicated. In general, the diagram shows two main patterns. The first pattern follows the first axis and divides the diagram into a group of acid, oligo-ionic, mesotrophic sites (left half of the diagram) versus a group of neutral, ionrich, eutrophic to hypertrophic sites (right half of the diagram). The second pattern is spread along the second axis and is a complex combination of morphometry (depth and surface area) and bottom (minerotrophic peat (fenland), clay and sand) factors.

The centroids of site groups 1, 2 and 3 are related to variables which describe moorland pools. The bottom consists of peat, there is a rich vegetation (often Sphagnum spp.) and sites are surrounded by heath or woods. Electrical conductivity, concentrations of associated ions and pH are low. Ammonium concentration is high. Sites were mainly sampled in spring. Site groups 4 and 7 are irregularly shaped, isolated ponds situated on a sandy bottom and surrounded by grassland. Especially sites of group 7 are shaded, deep ponds with a silty substrate. Site group 5 takes an intermediate position in the diagram which indicates its aberrant character. Site group 6 consists of sites situated in the fenlands (a minerotrophic peaty bottom, a steep profile, surrounded by reedland and in open connection with other waters). Site groups 8 and 9 take intermediate positions between groups 7 and 6, respectively. Site group 9 partly consists of sites with a clay, sand or peat bottom and a large surface area, while the sites of group 8 are slightly smaller.

The ordination of sites, based on taxon composition, and environmental variables (DCCA; program CANOCO) is presented in Figure 9.2. The eigenvalues (0.42, 0.23, 0.14 and 0.12 for the first four DCCA ordination axes respectively) indicate that there is a strong environmental gradient along the first and a weaker one along the second axis. The ordination diagram (Figure 9.2) represents the main structure of the data set. Due to the heterogeneity of the site groups 1, 2, 3, 4 and 5 with respect to the groups 6, 7, 8 and 9, the last four groups are projected within one contour line. The variation in the third and fourth axes is also surpressed in the diagrams (not included) due to the presence of some more heterogeneous sites within the first five groups. Therefore, the groups 6, 7, 8 and 9 were ordinated separately (Figure 9.3). The eigenvalues (respectively

Table 9.1 Ponds and small lakes; number of sites, means, and standard deviations of the quantitative environmental variables and percentages of the nominal environmental variables per site group. Abbreviations are explained in Table 10.5.

Quantitative environmental variables

Site group		1	2	3	4	5	6	7	8	9
Number of sites		9	13	14	21	3	26	21	24	26
T		14.	13.	12.	14.	26.	18.	19.	18.	19.
	sd	5.	7.	3.	2.	3.	3.	2.	3.	3.
PH		4.2	4.2	5.1	6.7	6.0	7.4	7.9	7.4	7.8
	sd	0.3	0.2	0.8	0.6	0.0	0.5	0.6	0.8	0.6
EC		121	84	77	241	200	378	405	553	492
	sd	50	30	28	97	99	118	140	225	179
O2		-	-	9.	6.	15.	15.	10.	8.	13.
	sd	-	-	1.	3.	5.	3.	1.	4.	5.
O2%		-	-	86.	56.	183.	161.	108.	86.	140.
	sd	-	-	12.	31.	66.	35.	15.	56.	56.
NH4		5.9	4.3	1.9	1.8	0.6	0.4	0.2	0.7	1.2
	sd	6.2	3.1	2.0	2.7	0.0	0.2	0.1	0.7	1.8
O-P		.01	.03	.03	0.4	.06	.03	.03	.18	.05
	sd	.01	.02	.03	.84	0.0	.04	.02	.29	.04
T-P		.06	.13	.21	.58	.06	.10	.08	.37	.24
	sd	.03	.11	.40	.92	-	.07	.05	.53	.27
CL		9.	8.	10.	21.	65.	56.	43.	70.	70.
	sd	4.	3.	4.	17.	33.	21.	25.	39.	33.
SO4		17.	12.	12.	6.	15.	16.	33.	29.	35.
	sd	8.	5.	6.	8.	0.	27.	20.	24.	17.
FE		0.4	0.5	0.2	0.4	0.5	0.6	0.5	0.9	0.8
	sd	0.1	0.3	0.2	0.5	0.0	1.1	0.3	1.0	1.1
NA		4.	5.	6.	12.	10.	22.	24.	32.	33.
	sd	2.	2.	2.	9.	7.	15.	13.	27.	19.
K		1.7	1.6	3.0	15.7	2.7	4.3	5.3	7.1	6.4
	sd	0.7	0.6	2.0	11.5	0.6	1.9	3.2	7.6	5.6
MG		0.9	1.0	2.8	8.4	7.2	7.4	7.4	9.1	7.7
	sd	0.5	0.6	2.1	2.3	1.7	2.2	2.7	4.6	2.3
CA		1.	2.	5.	23.	70.	52.	49.	61.	54.
	sd	1.	1.	4.	12.	0.	24.	20.	25.	18.
NO3		.05	.09	.18	.12	.70	1.6	.36	.62	1.2
	sd	.01	.07	.15	.09	.00	3.3	.71	.88	2.5
IR		24	28	44	68	68	60	67	61	58
	sd	13	8	22	15	10	13	13	12	13
HN		4	5	14	52	115	89	86	106	92
	sd	2	2	9	19	4	36	31	42	28
SA		0.1	0.5	0.8	.01	-	2.4	3.8	1.3	18.
	sd	0.1	0.6	1.1	.01	-	4.5	4.9	2.7	43.
W		22.	45.	57.	13.	1.7	58.	140.	50.	227.
	sd	9.	47.	50.	12.	0.5	82.	106.	69.	421.
D		0.6	0.7	1.5	1.2	0.1	1.0	5.6	0.9	2.0

sd	0.1	0.1	0.7	0.7	0.0	0.7	3.2	0.5	2.2
L	43.	103.	85.	17.	3.7	370.	215.	276.	746.
sd	29.	52.	83.	14.	1.9	246.	113.	420.	1058.
S-T	0.1	0.0	0.2	0.1	-	0.3	0.1	0.4	0.2
sd	0.1	0.1	0.3	0.1	-	0.3	0.2	0.3	0.3
%-A	0	0	8	4	-	1	2	0	0
sd	0	0	19	17	-	4	6	1	1
%-F	-	-	2	34	-	42	3	32	12
sd	0	0	6	40	-	28	3	34	18
%-S	40	23	26	9	97	4	10	13	1
sd	39	24	37	23	5	8	28	24	2
%-E	23	15	11	16	-	4	2	11	6
sd	19	13	15	19	-	6	2	11	17
%-B	33	32	23	2	-	8	0	6	3
sd	30	21	25	11	-	5	0	11	5
%-T	97	65	62	59	30	55	14	61	17
sd	5	25	25	37	42	27	29	33	21
%MM-B	2	7	3	-	-	21	17	15	18
sd	6	13	8	-	-	20	19	19	21
%MM-E	34	46	37	42	11	14	32	23	15
sd	20	24	25	25	16	16	25	23	17
%MM-F	-	-	9	24	-	41	17	22	32
sd	-	-	12	20	-	19	17	17	21
%MM-S	36	21	29	8	11	7	8	16	8
sd	22	16	26	14	16	11	15	22	16
%MMSILT	-	-	6	17	-	4	12	15	12
sd	-	-	10	20	-	8	10	12	12
%MMSAND	1	5	4	2	-	-	7	2	4
sd	4	10	8	4	-	-	10	6	9
%MMPEAT	9	20	6	2	11	7	1	2	1
sd	13	10	11	5	16	10	4	6	3
%MMCLAY	-	-	-	1	-	-	1	-	1
sd	-	-	-	4	-	-	6	-	5
%MMSTONE	-	-	-	-	-	-	-	-	1
sd	-	-	-	-	-	-	-	-	2
%MMDETRI	18	1	7	5	-	6	4	5	5
sd	13	3	9	8	-	6	7	10	8

Nominal environmental variables

Site group	1	2	3	4	5	6	7	8	9
SPRING	89	85	43	5	0	0	0	0	0
SUMMER	11	15	14	10	100	81	100	100	100
AUTUMN	0	0	43	86	0	19	0	0	0
SHAPVIR	0	0	14	0	0	0	0	4	0
SHAPIRR	78	23	36	33	0	31	14	50	69
SHAPREG	22	77	50	67	0	69	86	33	31
SHAPLSRE	0	0	0	0	0	0	0	13	0
TEMPOR	33	0	0	0	0	0	0	0	0
WATLF	67	23	50	14	0	15	5	8	27
SEE	0	0	0	10	0	0	5	8	0
COLORLES	44	15	43	14	33	15	10	4	0
YELLOW	44	62	7	43	67	50	86	63	42

BROWN	11	23	43	29	0	8	0	13	15
GREEN	0	0	7	10	0	27	5	13	42
BLACK	0	0	0	5	0	4	0	4	0
SMELL	22	31	7	0	0	0	0	8	8
CLEAR	89	92	79	57	0	81	90	50	42
SLTURB	11	0	21	33	0	8	10	38	38
TURBID	0	8	0	10	100	12	0	13	19
BACTNONE	78	100	100	100	67	100	100	100	100
BACTSL	11	0	0	0	0	0	0	0	0
BACTABUN	11	0	0	0	0	0	0	0	0
POLLUT	0	0	7	14	0	0	5	8	12
CLEANIN	0	0	0	5	0	62	0	8	31
SAND	56	62	79	71	0	0	62	42	46
SASILT	33	0	7	0	0	0	10	8	0
CLAY	33	15	7	33	33	35	19	21	38
FENLAND	0	0	0	0	67	96	10	25	35
PEAT	33	62	36	0	0	0	0	0	0
STCDLE	0	0	0	0	0	0	10	0	0
STSILT	0	0	14	57	0	12	52	79	46
STCMSI	0	0	0	0	0	23	5	0	12
STSAND	33	15	21	10	0	0	19	0	15
STPEAT	0	46	14	0	100	8	0	0	0
STFDPESI	0	0	21	19	0	38	0	17	8
STCOMB	0	0	0	0	0	23	0	4	19
STCLAY	0	0	0	5	0	0	0	0	8
STFDPE	67	38	29	14	0	0	14	0	0
STCDLESI	0	0	7	10	0	0	0	0	0
PSIRR	100	100	57	19	67	0	100	63	54
PS90	0	0	0	0	0	100	0	33	50
PS75	0	0	7	24	0	0	0	4	0
PS45	0	0	21	33	0	0	0	0	0
PS30	0	0	14	24	0	0	0	0	0
SHADOW	33	31	79	29	33	27	81	54	31
SURFOR	89	69	79	5	0	19	19	29	15
SURWOB	0	0	0	0	0	4	48	8	12
SURGRA	0	0	14	86	0	4	67	63	54
SURREE	0	0	0	0	33	81	0	17	42
SURHEA	67	69	36	0	0	0	0	0	0
SURFIE	11	0	7	10	0	0	10	0	0
SURURB	0	0	0	10	0	0	0	8	0
ISOL	100	100	100	95	100	35	100	67	38

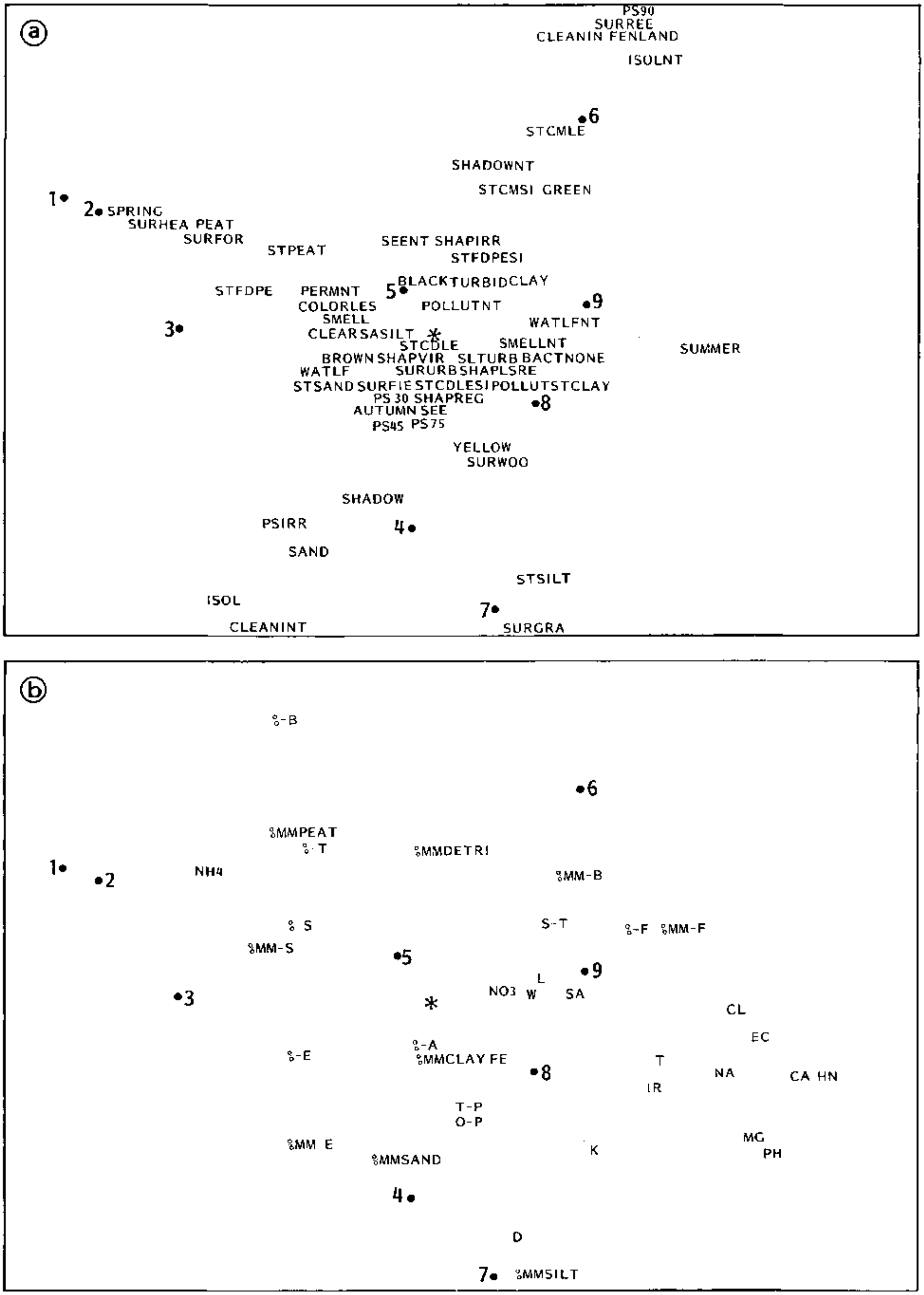

Figure 9.1 Ponds and small lakes; ordination (PCA) diagram for axes 1 (horizontally) and 2 (vertically) for nominal (A) and quantitative (B) environmental variables. For further explanation see Sections 3.4.2 and 9.2.3, and Figure 3.10. Abbreviations are explained in Table 10.5.

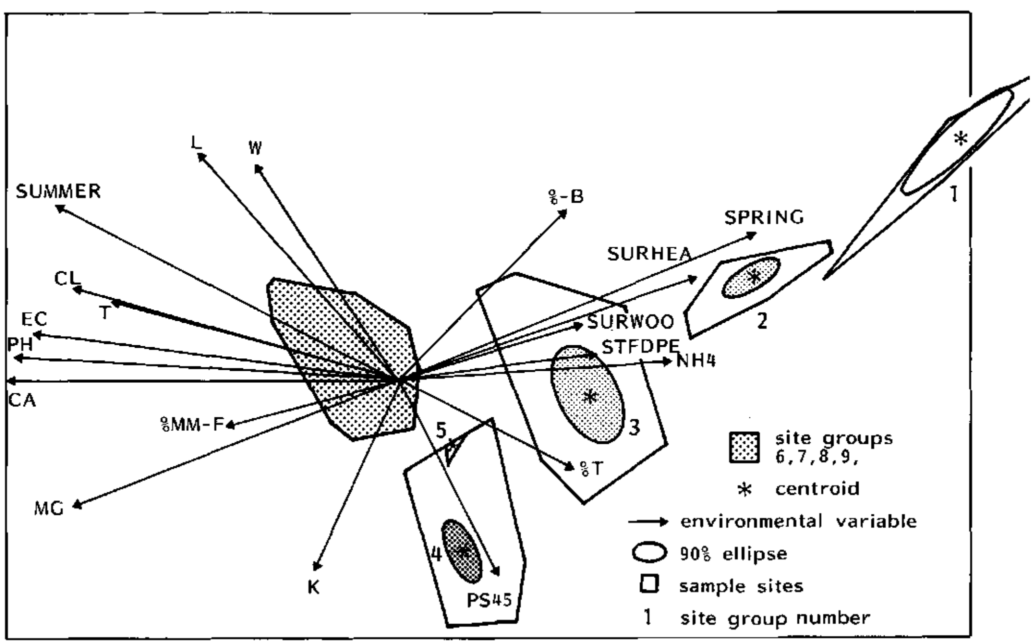

Figure 9.2 Ponds and small lakes; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically). Only environmental variables with an interset correlation greater than 0.4 are shown (arrows). For further explanation see Sections 3.4.2 and 9.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

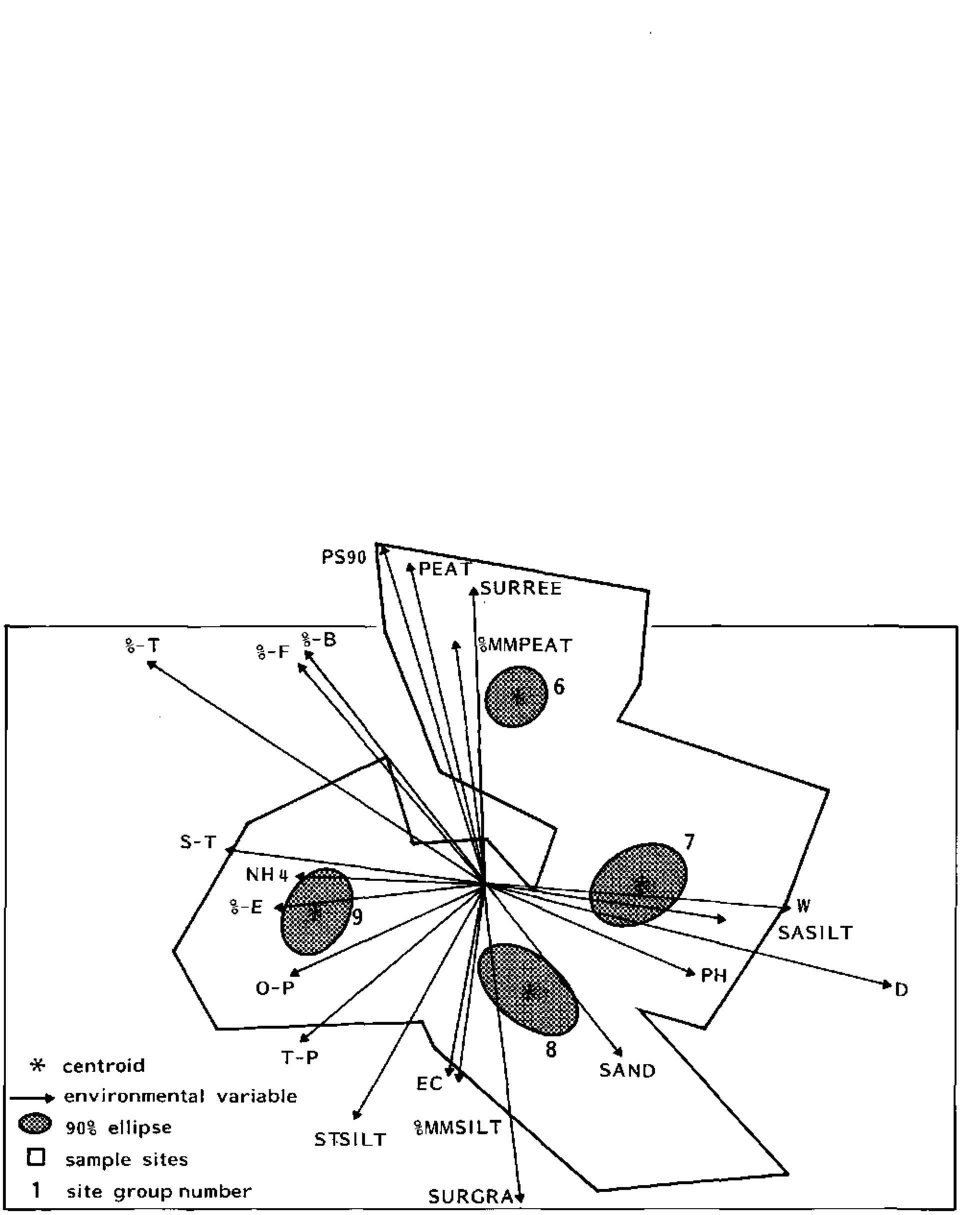

Figure 9.3 Ponds and small lakes; ordination (DCCA) diagram of the site groups 6, 7, 8 and 9 for axes 1 (horizontally) and 2 (vertically). Only environmental variables with an interset correlation greater than 0.4 are shown (arrows). For further explanation see Sections 3.4.2 and 9.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

0.16, 0.14, 0.12, and 0.08 for the first four DCCA ordination axes) indicate that there is a weak environmental gradient along the first three axes. The important environmental variables are the same as those relating to the third and fourth axes of the ordination of the total data set. The site projection is comparable but less compressed. This result justifies the steps of separated ordination.

The relations presented by the site groups will first be described with respect to the important environmental variables (Table 9.1) and the ordination results (Figures 9.2 and 9.3). Afterwards a validation of these relations will be based on knowledge present about the autecology of the typifying taxa.

The most important environmental gradient in Figure 9.2 runs from site group 1 (upper right hand corner) to site group 4 (below the centre). This gradient is comparable to the first pattern illustrated in Figure 9.1. Site group 1 represents one extreme of this pattern. Sites in group 1 are characterized by low concentrations of major ions, nitrate, phosphate and a low pH. Vegetation cover is high (mostly Sphagnum spp. and Juncus bulbosus) and the water level fluctuates greatly; a number of sites are, in fact, temporary. The high sulphate concentrations are a result of acid deposition in these temporary waters with a low buffer capacity. Sites are surrounded by heath or woods. They were sampled in spring. The average values of major ions and nutrients increase along the gradient from the groups 1, 2, 3 to 4, except for sulphate and ammonium which decrease. Those last two variables cause a different pattern of electrical conductivity, which is lowest in site group 3 and increases slightly towards groups 1 and 2 and, separately, towards 4. Sites in site group 2 are much like those of group 1 although all sites in group 2 are permanent, mostly with a bare sand and/or peat bottom. Sites in site group 3 have a slightly higher pH, are often shaded and situated in woods. Sites in group 4 have a small surface area, the water is neutral and especially the potassium and phosphate concentrations are high while the sulphate concentration is low. The substrate consists of silt on a sand or clay bottom. The sites are mostly situated in grassland. They were sampled in autumn.

Site group 5 consists of three sites, their average depth of 0.05 m indicates the swampy character. The calcium concentration is high but the phosphate concentration is low.

The differences between groups 1 to 4 and 6 to 9 have already been discussed with respect to the PCA-diagram. The difference can also be seen in Figure 9.2 where variables like length, width and season separate both groups. Table 9.1 shows the higher concentrations of major ions, the neutral character and the higher temperature due to summer sampling of groups 6 to 9 versus groups 1 to 4.

Figure 9.3 illustrates the differences within the groups 6 to 9. Sites in site group 6 are situated in fenland, indicated by the minerotrophic peat bottom, the steep profile and the surrounding reedland. Most sites are in open connection with ditches or canals and so are part of one water system. Most sites are well vegetated and have relatively low average concentrations of major ions and nutrients except for nitrate.

The sites in group 7 have the lowest major ion and nutrient (especially ammonium) concentrations, but the pH is slightly higher;

the sites are deep, with a medium-sized surface area, and they are less vegetated than sites in group 6. The sites are often partly shaded (due to the greater surface area). The bottom consists of sand, sometimes with a thin silt layer in the shallow littoral zone; in the deeper parts the silt layer is always thick.

The sites of group 8 have high concentrations of nutrients and major ions. These smaller and more shallow waters have a thick silt layer on a peat, sand or clay bottom. The average percentage of emergent vegetation is relatively high.

The sites of group 9 also have high concentrations of nutrients and major ions, although lower than in group 8. The sites are larger and deeper than those of group 8. Some of the sites are in open connection with ditches and canals. The sites occur on all bottom types and have a fairly thick silt layer. Vegetation is relatively sparse, especially the submerged part. The water colour is green at most sites.

The position of the four groups in relation to the environmental variables indicated in Figure 9.3 illustrates the combination of variables of morphometry, bottom/substrate and nutrient/major ion load dominating each of these groups. Despite the abiotic differences given for groups 6, 7, 8 and 9, the many transitions between these groups and therefore the varying combination of the dominant abiotic factors produce a relatively homogeneous biological set (illustrated by the low eigenvalue).

Macrofaunal relations

For a biological verification of the gradients indicated above, the typifying taxa (resulting from NODES) of each site group will be discussed with respect to data from the literature.

Site group 1

Site group 1 is typified by a number of coleopteran larvae (e.g. Dytiscus sp., Graphoderus sp., Rhantus sp.) and adults. They indicate acid, oligotrophic, temporary waters (e.g. Bidessus unistriatus, Berosus luridus, Berosus signaticollis; Burmeister 1981). Typifying midges for this habitat are Polypedilum cf. uncinatum (Moller Pillot 1984) and Telmatopelopia nemorum (Fittkau 1962). Temporary waters are further characterized by Aedes sp. and Culiseta sp. (culicids which deposit their eggs in temporary, acid environments; Mohrig 1969), which are also found in group 1. Other typifying taxa are Limnophyes sp., an inhabitant of semi-aquatic environments (Schleuter 1986), Hydroporus obscurus, H. erythrocephalus, and H. umbrosus, which all prefer acid moorland pools (Freude et al. 1971).

The macrofauna of site group 1 indicates a temporary, acid, mesotrophic environment.

Site group 2

Sites of group 2 are typified by taxa described in the literature as inhabitants of permanent, acid, oligotrophic and/or dystrophic waters (e.g. Cymatia bonsdorffi, Nieser 1982; Leucorrhinia rubicunda, Libellula quadrimaculata (sometimes also occurring in eutrophic ponds), Geijskes & van Tol 1983; Psectrocladius psilopterus, Moller Pillot 1984; Hydroporus umbrosus, Galewski 1971). Taxa typifying this group and more commonly collected in stagnant and sometimes slowly flowing waters are Holocentropus stagnalis (Edington & Hildrew 1981), Libellula depressa (Gardner 1954), Ablabemyia monilis/phatta (Fittkau 1962), Cymatia coleoptrata (Macan 1965), Lepthophlebia vespertina (Elliott & Humpesch 1983), Gerris odontogaster (Dethier 1985), Phalacrocera replicata (Johannsen 1969), Enallagma cyathigerum (Geijskes & van Tol 1983), and Argyroneta aquatica. Most of these taxa prefer, or are more abundant in, acid, oligotrophic environments. The typifying taxon Brillia longifurca (Moller Pillot 1984) is more often described as an inhabitant of flowing water. Taxa like Tipula sp. and Limnophyes sp. occur at the banks of these waters.

The macrofauna of group 2 indicates a permanent, acid, mesotrophic environment.

Site group 3

Sites of group 3 are typified by taxa generally found in shallow, stagnant water like Chaoborus obscurus (Parma 1969), Nais communis (Timm 1970), Agrypnia varia (Sedlak 1985), and Ablabesmyia monilis/phatta, or preferring acid (even temporary) waters such as Hydroporus erythrocephalus (Galewski 1971), Psectrocladius platypus (Kreuzer 1940), Enallagma cyathigerum, Libellula quadrimaculata (Geijskes & van Tol 1983), and Sigara semistriata (Bernhardt 1985). More common in oligo- and mesotrophic waters is the typifying taxon Notonecta obliqua (Bernhardt 1985). Arrenurus albator is a parasite of Chaoboridae (Stechmann 1980). Hesperocorixa sahlbergi is common in detritus-rich, stagnant, shallow waters (Macan 1965). Also typifying but generally considered common taxa are Polypedilum nubeculosum (Moller Pillot 1984), Procladius sp. (Fittkau & Murray 1986), Tanytarsus sp. (Pinder & Reiss 1983), Corynoneura sp. (Coffmann et al. 1986) and Psectrocladius gr. sordidellus (Langton 1980).

The macrofauna of group 3 indicates an acid, mesotrophic, slightly organically enriched environment.

Site group 4

Typifying taxa of group 4 are Armiger cristata (Beedham 1972), Phyrrhosoma nymphula (Geijskes & van Tol 1983), Cloeon dipterum (Macan 1979), Hyphydrus ovatus (Galewski 1971), Plea minutissima (Verstraete 1978), Dero digitata (Learner et al. 1978), according to the literature all common in vegetated, stagnant or slowly flowing waters. The waters can be acid or neutral (Dixella aestivalis, Disney 1975); permanent or temporary (Rhantus suturalis, Anacaena limbata; Klausnitzer 1984, Jackson 1973); small, shallow, eutrophic ponds (e.g. Chaoborus crystallinus, Parma 1969; Hydrobius fuscipes, Jackson 1973; Piona carnea, Arrenurus buccinator, A. mulleri (especially in woods), Kreuzer 1940; Cataclysta lemnata, Dethier 1985), and with a dense vegetation (e.g. Hydroporus planus, Agabus bipustulatus, Galewski 1971; Helocharus lividus, Cuppen 1986; Hydroporus palustris, Jackson 1973; Callicorixa praeusta, Corixa punctata, Macan 1965). If some organic enrichment is present taxa like Psectrotanypus varius (Fittkau 1962), Erpobdella testacea, Helobdella stagnalis (Mann 1961), and

Tubificidae (Brinkhurst & Jamieson 1971) occur. Ponds with a detritus-rich bottom are inhabited by Xenopelopia nigricans (Moller Pillot 1984) and Acilius sulcatus (Freude et al. 1971). Further typifying taxa from disturbed acid pools are Sigara lateralis (Nieser 1982), Laccobius minutus (Freude et al. 1971), Notonecta viridis (sandy bottom) (Nieser 1982), Hydroglyphus pusillus (sandy bottom), and a number of commonly distributed taxa (e.g. Hygrotus inaequalis, Noterus clavicornis, Colymbetes fuscus, Freude et al. 1971; Notonecta glauca, Macan 1965; Lumbriculus variegatus, Brinkhurst& Jamieson 1971; Coenagrion sp., Geijskes & van Tol 1983; Haliplus heydeni (especially in shallow water), Seeger 1971; Metriocnemus sp., Cranston et al. 1983; Anopheles sp., Mohrig 1969).

The macrofauna of group 4 indicates a small, shallow, slightly acid to neutral, eutrophic environment rich in vegetation.

Site group 5

Group 5 is typified, among others, by fifteen coleopteran taxa which generally occur in small, shallow permanent and/or temporary, acid pools and swamps (e.g. Hydroporus erythrocephalus and H. pubescens, Galewski 1971; Bidessus unistriatus, Enochrus coarctus, Hygrotus decoratus, Klausnitzer 1984; Dryops sp., Olmi 1972; Enochrus ochropterus, Hydroporus angustatus, Freude et al. 1971) or are more widely distributed in shallow ponds (e.g. Anacaena limbata, Jackson 1973; Enochrus melanocephalus, Helophorus obscurus, Klausnitzer 1984; Agabus strumi, Galewski 1971; Helocharus obscurus, Cuppen 1986; Haliplus ruficollis, Freude et al. 1971). Arrenurus mediorotundatus (in woods) (Kreuzer 1940) and Culex sp. (Mohrig 1969) are also typifying for shallow ponds. Other typifying taxa occurring in swamps are Odontomyia sp., Tabanus sp. (Johannsen 1969), and Dixella amphibica (Disney 1975). Bathyomphalus contortus, Radix peregra, Planorbis planorbis, Gyraulis laevis (especially in clear water)(Beedham 1972), Elgiva rufa (Johannsen 1969), and Paratanytarsus sp. (Pinder & Reiss 1983) are common taxa. Brachytron pratense is found in stagnant water in peaty areas (Geijskes & van Tol 1983).

The macrofauna of group 5 indicates a small, shallow or swampy, acid to neutral environment.

Site group 6

Sites of group 6 are typified by Anodonta anatina, a clam which prefers flowing water (Ellis 1978). The larvae of Sisyra sp. lives on and inside sponges inhabiting lakes, canals, rivers and streams (Elliott 1977). Sponges generally need clear, well oxygenated water, which is also true for Cryptocladopelma gr. lateralis (Lenz 1962), Gyrinus sp. (Sladecek 1963), and Tricholeiochiton fagesii (in plant thickets, Lepneva 1970). Typifying taxa, in this group, restricted to stagnant, vegetated water are Cyrnus insolutus and C. flavidus (Edington & Hildrew 1981), and Erythromma najas (Geijskes & van Tol 1983).

The macrofauna of group 6 indicates a stagnant, clear, well oxygenated environment rich in vegetation.

Site group 7

Most taxa typifying group 7 inhabit well oxygenated, clear, vegetated stagnant or slowly flowing waters (e.g. Hygrobatis longipalpis, Limnesia maculata, Davids 1979; Laccophilus sp., Moller Pillot 1971; Ranatra linearis, Bernhardt 1985; Athripsodes aterrimus and Mystacides nigra, Lepneva 1971; Endochironomus albipennis and Polypedilum sordens live on vegetation, Moller Pillot 1984; Caenis luctuosa (prefers sand/detritus substrate) and C. horaria, Malzacher 1986; Cyrnus trimaculatus, Hickin 1967; Limnesia maculata, Böttger 1972; Sialis lutaria (prefers silt substrate), Elliott 1977). A typifying taxon of this group which occurs especially in stagnant, well vegetated waters is Mesovelia furcata (Bernhardt 1985). Stictochironomus sp. (in oligo- to mesotrophic conditions) (Pinder & Reiss 1983), Molanna angustata (Hickin 1967) and Nanocladius bicolor (Moller Pillot 1984) prefer sandy bottoms in larger water bodies. Dicrotendipes gr. nervosus (Reiss 1968) and Piscicola geometra are more numerous in larger water bodies. Stictochironomus sp. and Tribelos intextus (Buskens 1987) occur in the littoral zone of these large waters with wave action. Commonly distributed mites typifying this group are Arrenurus globator, A. crassicaudatus, Limnesia sp., Brachypoda versicolor, Hydrachna globosa, Hydrodroma despiciens, Piona variabilis, P. conglobata and Mideopsis orbicularis. Cryptochironomus sp. (Moller Pillot 1984), Cladotanytarsus sp. (Pinder & Reiss 1983), Haliplus immaculatus (Klausnitzer 1984), Ilyocoris cimicoides (in vegetation, Macan 1965), Stagnicola palustris (littoral zone, Beedham 1972) and Stylaria lacustris are also common.

The macrofauna of group 7 indicates a stagnant, medium-sized, deep, clear, well oxygenated environment rich in vegetation.

Site group 8

Group 8 is typified by some commonly distributed gastropods which are abundant in dense vegetation e.g. Bathyomphalus contortus, Planorbarius corneus, Anisus vortex, Physa fontinalis, Bithynia leachi, B. tentaculata (especially in larger waters), Valvata piscinalis, and Planorbis carinatus (especially in larger waters, Beedham 1972). The same habitat supports Haliplus ruficollis, Dendrocoelum lacteum (Reynoldson 1978), Hesperocorixa linnei (Macan 1965), Holocentropus picicornis (Lepneva 1970), Hyphydrus ovatus, Acricotopus lucens (Cranston 1982), Glossiphonia heteroclita (Higler 1977), Haemonais waldvogeli (also on plants remains at the bottom, Chekanovskaya 1962), Hemiclepsis marginata (Mann 1955), and Tanypus kraatzi (in slightly larger ponds, Moller Pillot & Krebs 1981). Erpobdella testacea, E. octoculata, and Asellus aquaticus (Hynes 1960) are taxa which indicate organic enrichment. Common in sandy and silty substrates are Peloscolex ferox (less productive lakes, Brinkhurst 1964) and Dero dorsalis (Chekanovskaya 1962). Common taxa typifying this group are Arrenurus sinuator (Davids 1979), Pisidium sp. (especially in silty substrates, Kuiper 1965), Proasellus sp., Enochrus sp., Glossiphonia complanata (Dresscher & Higler 1982), and Piona alpicola/coccinea.

The macrofauna of group 8 indicates a densely vegetated, organically enriched environment.

Site group 9

Group 9 is inhabited by the typifying oligochaetes Limnodrilus claparedianus, L. hoffmeisteri and L. profundicola, all common and abundant in organic mud of hypertrophic waters (Pfannkuche 1977). Sigara falleni (Macan 1976), Gammarus tigrinus (in larger water bodies, Pinkster & Platvoet 1986), and Radix peregra (Beedham 1972) are also known to tolerate organic pollution. Piscicola geometra also occurs in larger water bodies. Hemiclepsis marginata and Valvata piscinalis are more closely related to the presence of vegetation.

The macrofauna of group 9 indicates a large, organically enriched environment.

9.3 Discussion of data

Compiling and interpreting the results of ordening sites according to their abiotic characteristics (ORDIFLEX), their macrofauna composition (FLEXCLUS, NODES) and their mutual relations (CANOCO) leads to the following conclusions. The abiotic descriptions of groups 1, 2, 3 and 4, which resulted from PCA, correspond with the descriptions from clustering and canonical correspondence analysis. The most important relations between the site groups are given in Figure 9.4.

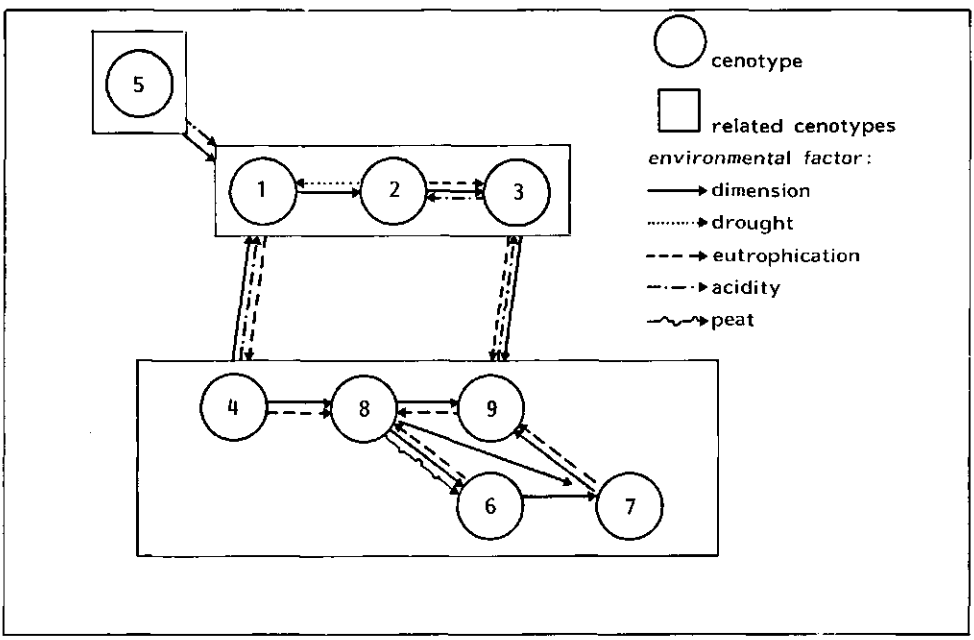

Figure 9.4 Ponds and small lakes; cenotypological relations. The arrows indicate the direction of increase of the respective variables.

Both environmental and macrofauna data indicate that the sites comprising group 1 are temporary, acid and mesotrophic waters. When a moorland pool has dried up during a dry summer reduced sulphur and nitrogen compounds derived from atmospheric deposition are stored in the sediment (van Dam 1987). As the pool is refilled these compounds are oxidized and the pH drops rapidly. This acidification after drought impoverishes the fauna (Leuven et al. 1986). Wiggins et al. (1980) concluded that temporary waters represent discrete types of freshwater habitats in which the dry phase imposes such rigorous environmental conditions that only a limited number of species can colonize and survive in them. A large proportion of temporary water species are members of groups which evolved on land, so adaptation problems to water loss may not be difficult and diversity of species can be high. Temporary water bodies support only species which are adapted to recurrent dry phases of varying duration. This drought period is a crucial factor for the inhabiting fauna. Williams (1987) stated that the best criteria to classify temporary waters are the length and intensity of the dry period as these are most relevant to the biology of this habitat. Such a division could not be made in this study. The average number of taxa (S) in group 1 is twenty-three which indicates the severe environmental conditions of low pH and drought.

The results indicate that the sites comprising group 2 are permanent, acid and mesotrophic. Permanency is the most important abiotic difference between groups 1 and 2. Sites of group 2 are also acidified. Acidity has long been recognized as a factor which impoverishes the taxa composition; a decrease in diversity is related to an increase in acidity (Harnisch 1951). Skadowsky (1923) made the first classification of waters according to their pH. The physiological mechanisms functioning in a macro-invertebrate in relation to an increase in concentration of hydrogen-ions were fully described by Havas (1981). The lethal pH range for a number of taxa lies between 5-6. Not only the hydrogen ions are directly lethal, death can also depend on a deficiency of calcium (Brehm & Meijering 1982). Furthermore, death can depend on lethal dissolved substances (e.g. aluminium; Herrmann 1987), or food relations (Hall et al. 1980). Taxa which are restricted to, or more abundant in, acid water have a low competitive force (Otto & Svensson 1983), or are physiologically well adapted (Havas 1981). The low diversity (S = 32) of group 2 corresponds with the harshness of the acid environment.

The sites combined in group 3 are less acid, meso- to eutrophic, permanent, and both shaded and unshaded. Two kinds of sites occur in this site group. The first group are shaded; they receive input of leaves. The second group is composed of unshaded sites which are situated in agricultural areas; they receive some input of nutrients through spill of fertilizers or subsurface runoff (therefore potassium concentrations are also high). Both groups are, to some extent, buffered against acidification. This abiotic condition is reflected in the taxa typifying group 3 and the higher diversity (S = 48). In autumn, a shaded pond receives a large quantity of decaying leaf matter causing a reduction in oxygen and an increase in carbon dioxide. The oxygen reduction causes anaerobic conditions, with the formation of H_2S and NH_4 (NH_3) which are lethal to many taxa (Bick 1958). To some extent this input of organic matter, termed saprobity by Sladecek (1973), can be compared to an anthropogenic increase of organic matter.

The unshaded pools are subject to eutrophication. Trophy is the most important factor used for lake classification. Most classifications are based on the division of the trophy continuum into the states: oligo-, meso-, eu-, and hypertrophy. The criteria used are based on nutrient loading (e.g. Ehrlich 1961, Carlson 1977) or nutrient concentration (e.g. Nauman 1932, Forsberg & Ryding 1980, Rodhe 1969). The trophic state is a useful parameter in applied ecology. Eutrophication means an increase in primary production and decomposition rate. Caspers & Karbe (1967) concluded that saprobity (e.g. input of leaves) and trophy (e.g. input of nutrients) are interdependent processess and that between these effects some parallelism can be seen. This corresponds with the clustering of both groups of sites within group 3.

Biotic and abiotic data indicate that group 4 consists of sites which are small, shallow, neutral and eutrophicated. All sites are situated in cultivated grasslands and therefore receive artificial fertilizers and organic dung. The relatively low concentration of ions (most sites are probably fed by groundwater) and an indication by several typifying taxa, both point to a former, more mesotrophic, slightly acid condition. The higher productivity also results in a higher diversity (S = 60). The sites of this group have two sources of water input, the groundwater flow and the precipitation (and overland flow). Water chemistry is basically dependent on the quality and quantity of rain or groundwater input in relation to the evaporation rate, as the sandy soil is poor in minerals. The groundwater supply (which is most probably higher than in sites of group 3) is sufficient to maintain a certain water level in summer which results in the neutral state. An extra increase in pH is caused by eutrophication, through the input of fertilizers (Schwoerbel 1974). There seems to be a seasonal difference (spring versus summer) between groups 1, 2, 3 and 4 and all the other ones but this is due to chance because firstly, group 3 consists of spring and autumn samples and still looks most like group 2, and group 4 consists of almost entirely autumn samples; secondly, 10-15% of groups 1 and 2 are summer samples; and thirdly, the taxa collected do not indicate a specific seasonal occurrence.

Site group 5 consists of only three sites situated in the oligo-mesotrophic, slightly acid, swamps in the fenland area. The macrofauna composition reflects this abiotic characteristic.

The low eigenvalue of the second DCCA-run indicates the minor differences between the following four groups. The sites of group 6 are well defined by their abiotic features, namely the complex of environmental factors occurring in the fenland area (e.g. surrounded by reedland, a minerotrophic peaty substrate, a steep profile, in open connection with ditches or canals) in combination with the neutral, mesotrophic nature of the water and a well developed (often submerged) vegetation. Still the macrofauna, though diverse (S = 68), is not typical of the "fenland" character of this environment, although the clear, well oxygenated water and richness in vegetation is well indicated. A number of taxa, comparable to the macrofauna-coenoses found by Higler (1977) on Stratiotes plants in the same region, are present but at a frequency too low to be typifying.

Site group 7 is best characterized as medium-sized, deep ponds with a silty substrate and the water is neutral and mesotrophic. The typifying macrofauna composition corresponds with the abiotic characterization. Smaller water bodies are more directly influenced by atmospheric conditions, so there is a gradient of decreasing environmental stress from shallow to deep water, at least in the sea (Sanders 1968). But also in freshwater, the daily differences of wind, rain and temperature cause motion of the water, dilution, ice formation, changes of water level or desiccation. These daily atmospheric conditions also act upon the processess of growth of plants, causing, e.g. oxygen levels to fluctuate. This fluctuation in relation to temperature causes stratification in the water column of even very shallow waters (Kuhlmann 1960, Kersting 1983). The oxygen level in relation to depth was used by Pichler (1939) to define puddles, pools and small ponds. Besides daily fluctuations seasonal processes can also be severe. In our temperate region oxygenating processes are predominant in spring and summer and reducing processes in winter (Kuhlmann 1960). Not only oxygen fluctuates but also variables like macro-ions, iron, pH and others can fluctuate strongly. Von Brandt (1935) stated that the daily temperature regime of a shallow pond corresponds with the yearly regime of a large lake and of course shading will make a great difference in small waters. The retention time of the water will generally decrease with a decreasing size of the water body. The most extreme condition is reached when the pond becomes temporary. In general, the range of fluctuation of a number of variables tends to increase as the water body decreases in size. To a certain extent sites of group 7 offer a more constant environment because of their greater depth, and diversity is therefore high (S = 77). The average transverse profile and the standard deviation of the site groups is illustrated in Figure 9.5. The relation between width and depth in relation to water volume is demonstrated.

Sites of group 8 are smaller, shallower ponds with a silt layer and the water is eutrophicated and densily vegetated. This corresponds with the many typifying gastropods and other common and widely distributed taxa. The eutrophicated and/or organically enriched state is also reflected by the presence of some leeches and high diversity (S = 82) is due to the large number of common taxa. There are more taxa despite the degree of eutrophication and the smaller dimensions. Probably diversity and stability do not run parallel in this environment.

Sites of group 9 have a large average surface area and are intermediate in depth. Water is eutrophicated (green colour) and sparsely vegetated. The large, open morphological character in combination with the silty substrate and organic enrichment corresponds with the presence of several typifying oligochaetes. The whole bottom area of large shallow lakes is influenced by wind-generated currents. A variety of dynamic conditions (e.g. washing away of organic material, instability of the substrate, and turbidity) limits the development of the bottom fauna (Raspopov et al. 1988). So the relation between abiotic stability and water volume, as described previously in relation to group 7, does not fully account for large but shallow lakes. The diversity of group 9 is relatively low (S = 59) which corresponds with the less stable, organically-enriched state and

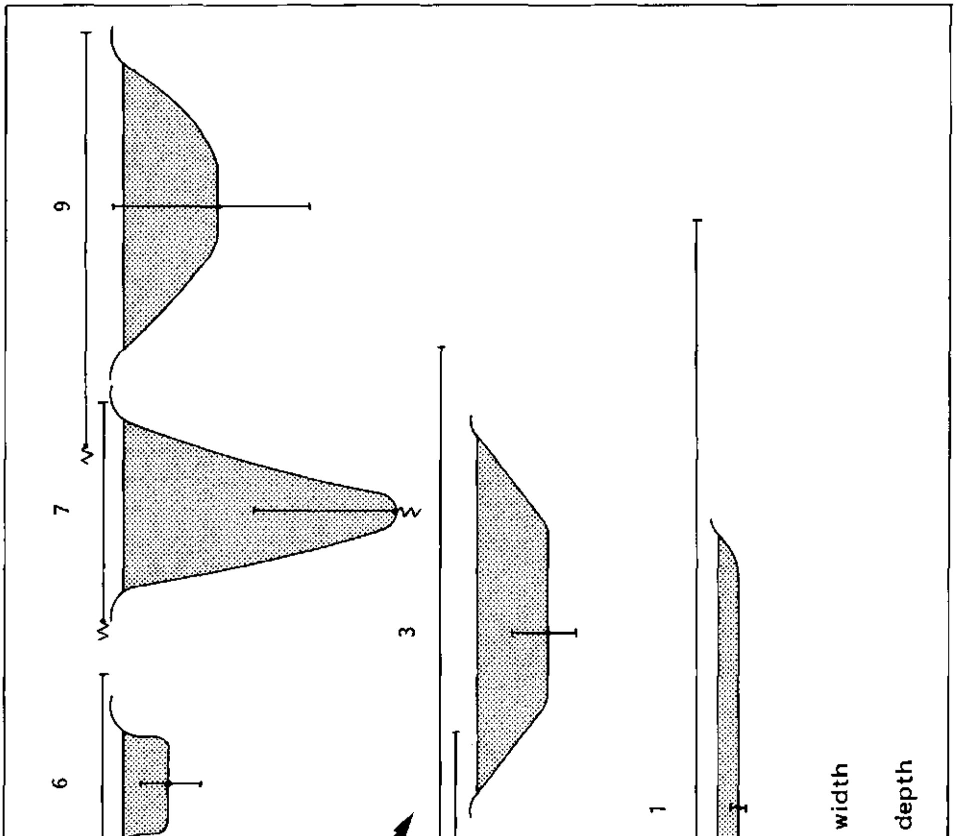

Figure 9.5 Scheme of the averages and the standard deviations of the transverse profiles per cenotype.

isopods. The the absence of vegetation.

In general, the biological differences between the last four groups are small and there are many transitions between the groups. The site groups represent a complex which can be separated into three groups of related cenotypes (Figure 9.4) namely; mesotrophic swamps (group 5), acid moorland pools (groups 1, 2 and 3), and stagnant, neutral ponds and lakes (groups 4, 6, 7, 8 and 9). The first cenotype consists of only three sites and is aberrant in this data set. The second group of cenotypes can be divided according to permanency and eutrophication (Figure 9.4). The third group of cenotypes represents a web of continua dominated by dimensions (Figure 9.5), eutrophication and bottom composition (the latter is specifically related to the complex of factors characteristic for the fenland region).

10. A REGIONAL TYPOLOGY OF SURFACE WATERS IN THE PROVINCE OF OVERIJSSEL

10.1 Introduction

In Chapter 1 it was stated that the five main physico-geographical water types, as described in Chapters 5-9, do not represent different ecological types. But only through an elaboration of all the collected data this statement and the intended typology can be justified. Therefore, all data were analysed together by the same multivariate analysis techniques as used before (see Chapter 3). A strategy based on the removal of sets of sites (site groups) along identified gradients, and a subsequent reordination (Peet 1980) is used. Simple, unidimensional environmental gradients can be easily recovered by using nonlinear ordination techniques. But as the complexity of a data set increases, the efficiency of information recovery decreases because the species-environment relations do not correspond to one consistent, geometric model (in casu the unimodal or Gaussian response model). This means that ordination results beyond two or three dimensions are difficult to interpret in terms of the underlying environmental variables. As Peet (1980) stated 'ordination can work well for the identification of the most important and conspicuous environmental trends in a data set with a simple underlying environmental structure but these would also have been deduced by a competent field ecologist'. Ordination works less effectively at resolving environmental relations in complex data sets. Peet (1980) referred to principal component analysis (PCA). These problems with PCA are partly solved within detrended (canonical) correspondence analysis (D(C)CA) (Hill & Gauch 1980, ter Braak 1986) because its response model is not linear but unimodal. However, because the technique of detrending used is not fully effective, higher axes remain partially dependent.

The basic methodology chosen was the progressive removal of groups of sites. After initial ordination in two dimensions using DCCA, the resulting diagram is examined for relations between site groups and environmental variables. Distinctive site groups are removed (or a continuum is partitioned) and the remaining sites are reordinated. Thereby, the impact of the originally observed variable(s) is greatly reduced.

10.2 Multivariate analysis

The results of clustering and ordination of sites (programs FLEXCLUS and CANOCO), arrangement of taxa (program NODES), and information on the autecology of taxa led to 42 site groups (see below). A list of all taxa with their typifying weight per site group (program NODES) is given (Appendix 1). Numbers of sites, averages and standard deviations of the quantitative environmental variables, and the relative frequency of the nominal variables per site group are given in Appendix 2. The final site groups were compared with the descriptions of the former site groups described for the five major water types, namely helocrene springs (Chapter 5), streams (Chapter 6), ditches (Chapter 7), rivers, canals and large lakes (Chapter 8), and ponds and small lakes (Chapter 9). A code was given to each new site group which corresponded to the most similar site group formerly presented for one of the five main water types. Hereby, the former site group number is combined with the first letter of the corresponding main water type as follows:

helocrene springs = H
streams = S
ditches = D
rivers, canals and large lakes = R
ponds and small lakes = P

A comparison of site groups within the former and the new arrangement is given in Table 10.1. Status and the number of sites which were replaced between the former and the new site groups are given (Table 10.1).

Table 10.1 The changes in site composition between the former site groups described for the main physico-geomorphological water types and the new site groups distinguished within the total data set.

cluster number	old number sites	number of removed sites	to	number of received sites	from	r r s
H1	13	1	S1(1)	2	S1(2)	1
H2	6	0	-	0	-	
H3	14	0	-	0	-	1
H4	3	1	H6(1)	0	-	
H5	4	0	-	0	-	
H6	3	0	-	2	H8(1),H4(1)	
H7	1	0	-	0	-	
H8	1	1	H6(1)	0	-	
S1	19	2	H1(2)	1	H1(1)	1
S2	5	0	-	0	-	
S3	5	0	-	0	-	
S4	21	0	-	0	-	2
S5	12	1	R9(1)	0	-	1
S6	16	4	S7(3),R9(1)	0	-	1
S7	21	7	R9(5),D3(2)	5	S6(3),R3(2)	1
S8	16	16	D3(6),R4(5),R9(5)	0	-	
S9	9	1	D8(1)	0	-	
S10	15	0	-	10	D3(1),D7(5),S11(4)	2
S11	4	4	S10(4)	0	-	
S12	3	0	-	4	D10(2),D9(2)	
S13	11	0	-	0	-	1
S14	1	0	-	0	-	
D1	17	17	R2(14),R4(3)	0	-	
D2A	14	5	D3(2),R2(1),P5(2)	0	-	

D2B	15	15	P8(8),R4(6)	0	-	0
D3	42	2	S10(1),P5(1)	13	S8(6),S7(2),D2A(2), P8(2),D4(1)	53
D4	3	3	P5(2),D3(1)	0	-	0
D5	4	4	P3(2),P5(2)	0	-	0
D6	4	0	-	0	-	4
D7	5	5	S10(5)	0	-	0
D8	8	0	-	2	S9(1),R4(1)	10
D9	2	2	S12(2)	0	-	0
D10	2	2	S12(2)	0	-	0
D11	1	0	-	0	-	1
D12	1	1	P5(1)	0	-	0
D13	1	0	-	0	-	1
D14	1	1	R9(1)	0	-	0
D15	1	0	-	0	-	1
D16	1	0	-	0	-	1
D17	1	0	-	0	-	1
D18	1	0	-	0	-	1
D19	1	0	-	0	-	1
D20	1	0	-	0	-	1
R1	26	11	R3(1),R4(2), R9(3),R12(5)	1	P9(1)	16
R2	35	0	-	17	D1(14),D2A(1), R4(1),P8(1)	52
R3	12	3	S7(2),R4(1)	1	R1(1)	10
R4	46	20	D8(1),R2(1),R9(1), R12(13),P11(4)	23	S8(5),D2B(6),D1(3),R1(2), R3(1),R9(1),P7(4),P8(1)	49
R5	6	1	R13(1)	0	-	5
R6	1	1	R9(1)	0	-	0
R7	4	0	-	0	-	4
R8	9	0	-	0	-	9
R9	28	2	R4(1),P7(1)	19	S5(1),S6(1),S7(5),S8(5),D2B(1 D14(1),R1(3),R4(1),R6(1)	45
R10	1	0	-	0	-	1
R11	10	0	-	0	-	10
R12	0	0	-	22	R1(5),R4(13),P7(3),P9(1)	22
R13	0	0	-	1	R5(1)	1
P1	9	0	-	0	-	9
P2	13	0	-	2	P3(2)	15
P3	14	5	P2(2),P4(1),P7(2)	2	D5(2)	11
P4	21	1	P10(1)	1	P3(1)	21
P5	3	0	-	8	D2A(2),D3(1),D4(2), D5(2),D12(1)	11
P6	26	0	-	2	P7(2)	28
P7	21	17	R4(4),R12(3),P6(2), P9(1),P11(7)	3	R9(1),P3(2)	7
P8	24	4	D3(2),R2(1),R4(1)	8	D2B(8)	28
P9	26	3	R1(1),R4(1),R12(1)	1	P7(1)	24
P10	0	0	-	1	P4(1)	1
P11	0	0	-	12	R4(4),P7(8)	12
	---	---		---		---
Total	664	163		163		664

The new site groups will be described with respect to:
- the ordination results (Figure 10.1 - 10.5),
- the changes in site composition (Table 10.1),
- the homogeneity of each site group (Table 10.2) which is defined as the average resemblance of the members of this site group to its centroid. A homogeneity of one means that the group is completely homogeneous (the sites have an identical taxon composition) and when it is zero, the group is completely heterogeneous (the sites have no taxa in common).
- the taxonomical and environmental description given for the former, most comparable, site group (Chapters 5 - 9),
- the important environmental variables within the total data set (Appendix 2 and Table 10.3), and
- the changes in the list of typifying taxa (Appendix 1).

In total five ordination (DCCA) runs were executed to analyse the most important relations present within the total data set. From each run only the axes 1 and 2 were taken into account. Site groups with less than four members are not represented in the figures.

For the interpretation of the ordination results the overall ordination characteristics are given in Table 10.4.

The eigenvalue is a number between zero and one; the higher the value, the more important the ordination axis. In DCCA, the eigenvalue is a measure of separation of the distributions of taxa along the ordination axis (between-site variability) (Jongman et al. 1987). In other words, it indicates the importance of each axis. Eigenvalues of about 0.3 and higher are quite common in ecological applications (ter Braak 1987). The eigenvalue of DCCA-run 1 is large for the first axis and much lower for the second axis. This indicates

Table 10.2 The average resemblance (homogeneity) of the sites in the site groups.

S	AR	S	AR	S	AR	S	AR	S	AR
H1	0.6719	S1	0.6055	D2A	0.5351	R1	0.5578	P1	0.585
H2	0.5234	S2	0.5132	D3	0.5230	R2	0.5510	P2	0.645
H3	0.5874	S3	0.4520	D6	0.4750	R3	0.5260	P3	0.496
H4	0.4892	S4	0.5460	D8	0.4971	R4	0.5654	P4	0.481
H5	0.5694	S5	0.5393			R5	0.4392	P5	0.344
H6	0.3912	S6	0.5495			R7	0.5058	P6	0.550
		S7	0.4471			R8	0.6447	P8	0.513
		S9	0.4458			R9	0.5003	P9	0.601
		S10	0.4735			R11	0.5829	P11	0.511
		S12	0.3853			R12	0.5813		
		S13	0.4687						

S = Site group, AR = Average resemblance

Table 10.3 Forward selection executed at each run. (a) Per variable included is given its contribution (e) to the sum of all eigenvalues of the CCA of environmental variables previously selected. (b) The results of the significance test of a variable at its point of inclusion.

(a)

RUN 1 variable	e	RUN 2 variable	e	RUN 3 variable	e	RUN 4 variable	e	RUN 5 variable	e
FALL	.33	W	.13	D	.12	D	.09	SHAPLSRE	.07
NO3	.21	FALL	.11	W	.11	NO3	.08	SPRING	.07
T	.18	D	.11	REGULNT	.08	W	.07	REGULNT	.06
W	.18	NO3	.11	%-T	.07	%-T	.07	REGUL	.06
WINTER	.17	TEMPOR	.10	REGUL	.07	STSAND	.06	W	.06
MEAND	.16	T	.10	O2	.07	SAND	.06	D	.06
STCDLE	.15	SAND	.08	NO3	.07	T	.06	SUMMER	.06
MEANDNT	.15	S	.08	SHAPLSRE	.07	%-B	.06	T	.06
%MMGRAVE	.15	%-T	.08	O2%	.06	%-F	.06	PSIRR	.05
D	.14	STSAND	.07	AUTUMN	.06	SPRING	.06	ISOL	.05
SHAPLSIR	.14	SUMMER	.07	STSAND	.06	PS90	.06	NO3	.05
%MMDETR	.14	%-F	.07	SPRING	.06	REGULNT	.06	SHAPREG	.05
S	.13	%MM-F	.07	EC	.06	%MMSAND	.05	SURREE	.05
PH	.13	FENLAND	.07	%-S	.06	FENLAND	.05	%-S	.05
EC	.13	NH4	.06	%MMSAND	.06	SUMMER	.05	SHAPIRR	.04
TEMPOR	.12	%MMSAND	.07	SAND	.05	PS30	.05	%-T	.04
%MMSAND	.11	REGULNT	.06	ISOL	.05	REGUL	.05	STSAND	.04
%-F	.11	SPRING	.06	SHAPREG	.05	MEANDNT	.05	EC	.04
%MM-F	.10	O2	.06	FENLAND	.05	SURREE	.05	O2	.04
STSAND	.10	REGUL	.06	PH	.05	SHAPLSRE	.05	S-T	.04
SUMMER	.10	O2%	.06	PROCON	.05	%MMSTONE	.04	SAND	.04
SAND	.10	SHAPLSRE	.06	%-F	.05	PROCON	.04	S	.04
SURWOO	.09	AUTUMN	.05	%MM-S	.05	S-T	.04	%MMSAND	.04
REGULNT	.09	MEANDNT	.06	SURREE	.04	%MM-F	.04	PS45	.04
%-T	.09	SHAPREG	.05	%-B	.04	ISOL	.04	%-B	.04
SURHEA	.09	ISOL	.05	SURGRA	.04	%-S	.04	NH4	.04
REGUL	.09	PS90	.05	MEANDNT	.04	PSIRR	.04	%MM-S	.04
ISOL	.09	SURREE	.05	%MMSTONE	.04	S	.04	COLORLES	.04
SHAPLSRE	.08	PH	.05	CL	.04	SHAPREG	.04	FENLAND	.04
CL	.08	O-P	.05	PS30	.04	FALL	.04	SEE	.03
STCM	.08	%-S	.05	%MM-F	.04	SHAPIRR	.03	GREEN	.03
FENLAND	.08	PROCON	.05	NH4	.03	CA	.03	PS75	.03
SEE	.07	EC	.05	%MMPEAT	.03	%MM-S	.03	PS90	.03
SHAPREG	.07	T-P	.05	PS75	.03	EC	.03	%MMSTONE	.03
PS90	.07	%MM-S	.04	FALL	.03	CL	.03	%MM-F	.03
CA	.07	%MMSILT	.04	%-E	.03	SURGRA	.03	O2%	.03
STCMDLPE	.06	%-B	.04	SHAPIRR	.03	O2	.03	CLEAR	.03
NH4	.06	%MMPEAT	.04	%MMSILT	.03	%MMPEAT	.03	SURGRA	.03
%-S	.06	%-E	.04	S	.03	CLEAR	.03	CLAY	.03
O2%	.06	STCDLESI	.04	CA	.03	PS75	.03	PROCON	.03
%-E	.06	SEE	.03	PSIRR	.03	PH	.03	%-A	.03

SPRING	.06	WATLF	.03	S-T	.03	WATLF	.03	YELLOW	.03
PEAT	.06	PS75	.03	CLEAR	.03	CLEANIN	.02	FALL	.03
AUTUMN	.06	PS30	.03	CLEANIN	.03	GREEN	.02	PH	.03
SURREE	.06	%MMSTONE	.03	COLORLES	.02	PS45	.02	%-F	.03
O2	.06	MEANDSL	.03	GREEN	.02	SHADOW	.02	CA	.03
SURGRA	.05	MEAND	.03	%-A	.02	SURWOB	.02	%MMDETR	.03
%MM-S	.05	CA	.03	%MM-B	.02	STFDPESI	.02	SLTURB	.03
%MMPEAT	.05	CLEAR	.03	SEE	.02	%MM-E	.02	SHADOW	.03
%-B	.05	PS45	.02	STSILT	.02	SHAPVIR	.02	%MMSILT	.02
SHAPIRR	.05	STSILT	.02	STFDPE	.02	COLORLES	.02	%MM-B	.02
SHADOW	.05	%MM-E	.02	%MMDETR	.02	AUTUMN	.02	STCDLESI	.02
O-P	.05	BLACK	.02	T-P	.02	O2%	.02	%MMPEAT	.02
COLORLES	.05	STCM	.02	%MM-E	.02	CLAY	.02	BROWN	.02
PROCON	.04	SURWOB	.02	SLTURB	.02	%MMDETR	.02	SURWOO	.02
%MM-E	.04	CLEANIN	.02	YELLOW	.02	SLTURB	.02	WINTER	.02
STCDLESI	.04	SHAPLSIR	.02	STCM	.02	SURWOO	.02	T-P	.02
T-P	.04	SURFIE	.02	POLLUT	.01	MEANDSL	.02	%MM-E	.02
CLEAR	.04	STFDPESI	.02	SURWOO	.02	%-E	.02	WATLF	.02
%MMSTONE	.04	STFDPE	.02	TEMPOR	.01	STCM	.02	STFDPESI	.02
MEANDNT	.04	%MMGRAVE	.02	SASILT	.01	TURBID	.02	STCM	.02
STSILT	.04	CLAY	.02	BLACK	.01	%-A	.02	MEANDNT	.02
STFDEPE	.04	SURWOO	.02			T-P	.01	TURBID	.02
CLEANIN	.03	SHADOW	.02			POLLUT	.01	POLLUT	.02
CLAY	.03	STCDLE	.01			BLACK	.01	SHAPLSIR	.02
%MM-B	.03	SURURB	.01					%MMGRAVE	.02
STFDPESI	.02								
BLACK	.02								

(b)
significance test

RUN 1

variable	P=	cumulation of variance explained
FALL	.01	.33
W	.01	.45
EC	.01	.56
NO3	.01	.64

RUN 2

variable	P=	cumulation of variance explained
W	.01	.13
NO3	.01	.24

RUN 3

variable	P=	cumulation of variance explained
W	.01	.12
REGULNT	.01	.20
FENLAND	.01	.25
AUTUMN	.01	.29
SPRING	.01	.33
O2	.01	.36
EC	.01	.40
D	.01	.43
NO3	.01	.46

RUN 4

variable	P=	cumulation of variance explained
D	.01	.09
SPRING	.01	.15
T	.01	.21
NO3	.01	.25
SHAPLSRE	.01	.29
SURREE	.05	.32
CL	.01	.35

O2%	.01	.48
PSIRR	.01	.50
%-S	.04	.53
%-F	.01	.55
REGUL	.01	.56

RUN 5 variable	P=	cumulation of variance explained
SHAPLSRE	.05	.07
SPRING	.05	.13
D	.05	.18
T	.10	.22
O2	.10	.26
NO3	.05	.29

Table 10.4 The overall ordination characteristics for all five DCCA - runs.

DCCA run	1	2	3	4	5
eigenvalue					
axis 1	.41	.20	.18	.15	.11
axis 2	.18	.17	.10	.08	.08
percentage of variance of species abundance data explained by species-sample plot					
axis 1	6.9	4.8	5.4	5.7	4.7
axis 2	10.	8.7	8.4	8.5	8.2
percentage of variance of species-environment table explained by species-environment biplot					
axis 1	24	16	16	13	7.8
axis 2	35	30	25	20	13
sum of all eigenvalues	5.8	4.2	3.4	2.7	2.3
sum of all canonical eigenvalues	1.7	1.2	1.2	1.2	1.4
P=	.01	.01	.01	.01	.09

that there is a strong environmental gradient along the first axis and a much weaker one along the second axis. The same feature, though weaker, is present in runs three and four. In the other runs the dominance of both environmental gradients is more equal. The eigenvalues decrease from run 1 to run 5, indicating a weakening of the successive environmental gradients investigated. Thus the role of a master factor or set of master factors is taken over by several less dominant factors.

The biplot leads to approximate values of the species abundances alone and of the weighted averages of species with respect to the environmental variables. The percentage of variance of species-abundance data accounted for by the species-sample biplot indicates the goodness of fit (the degree of approximation) of the diagram with respect to the distribution of species abundances. The percentage of variance of species-environment data in the species-environment biplot indicates the goodness of fit of the diagram with respect to the relation between species abundances and environmental variables. Both percentages are very low for all axes in all runs. The total is never a 100% because of noise in the data (see Chapter 1) and because it depends on the large number of variables elaborated (ter Braak 1986). A reference figure for these percentages cannot be given yet.

The sum of all eigenvalues of correspondence analysis (CA) is a measure of all biological variation present on all axes. For example, in run 1 this sum is 5.8 of which 0.41 is decribed by the first axis. The sum of all canonical eigenvalues (eigenvalues of CCA) is that part of the sum of all CA-eigenvalues which is decribed by the environmental variables investigated.

The significance of the sum of all canonical eigenvalues is tested (Monte Carlo permutation test). In the first four runs this test is significant at the 1% significance level. Thus the environmental variables are related to the distribution of species abundances, despite the relatively low percentages of variance explained by all environmental variables. The fifth run is only significant at the 9% significance level indicating only a vague relation between variables and species.

In the option 'forward selection' of CANOCO (version 3.0), the program indicates how well each individual environmental variable can explain the species data. The measure given is the (canonical) eigenvalue that would be obtained if the environmental variable would be the single predictor variable. The program selects the best variable and continues to produce a list of how much each variable would contribute if that variable would be added to the one previously selected. The measure listed is the increment in the sum of all (canonical) eigenvalues. The program again selects the best variable, and so on. At each step the significance of the contribution of the variable to be selected is tested by a Monte Carlo test. The selection process is stopped when the variable to be selected is no longer significant ($P < 0.10$). The increase in the sum of the eigenvalues and the results of the tests are given for each run in Table 10.3.

10.2.1 DCCA - RUN 1

The results of ordination of sites and environmental variables are shown in Figure 10.1. The first and most important environmental gradient in Figure 10.1 runs along the horizontal axis and is due to several sites situated in helocrene spring areas and small streams (site groups H1, H2, H3, H5, H6, S1, S2, S3 and S12). The most important variables that significantly describe the ordination are fall, width, electrical conductivity, and nitrate concentration (Table 10.3). In general, the environment of these site groups, as appears also from the arrows indicated in Figure 10.1, can be characterized by the following variables. The current velocity is high at most sites (10 - 33 cm/s) and more than 50% of all sites are shaded, are part of a meandering water course, and have an irregular profile and a substrate of coarse detritus, leaves, sand and sometimes gravel. The temperature is relatively low (3 - 11 °C) (autumn and spring samples). The chemical variables indicate a high concentration of nitrate (6.3 - 14.3 mg/l) and a relatively low electrical conductivity (175 - 302 μS). The sites are mostly oligosaprobic while the trophic condition fluctuates considerably. With respect to some physical variables, there is a difference between site groups S2, S3, S4 and S12 versus all the others. Within the last group, the sites are narrow (0.2 - 0.8 m), shallow (6 - 14 cm), and the fall is high (16 - 75 m/km) while in the first four site groups, sites are wider (1.0 - 2.2 m), deeper (19 - 44 cm), and the fall is relatively low (1 - 4 m/km).

Within the following description of the new site groups, this general characterization should be taken into account. One should further remember that remarks on the former site groups were made with respect to the water type under consideration. For example, a remark on eutrophication for a former stream site group (Chapter 6) was made only within the range of the phosphate concentrations measured for the stream sites, not for all sites. It should now be considered within the general environmental characterization given for this DCCA run. These notes apply to all the DCCA runs made.

Site group H1

The environmental description given for spring site group 1 (Chapter 5) also applies to this group despite the small changes in composition of sites (Table 10.1). The average resemblance of sites in group H1 is high, compared to all other groups. Group H1 has the most homogeneous composition of sites (Table 10.2). The taxa indicated as indifferent in spring site group 1, all become typifying within the total data set (Appendix 1). Furthermore, Plectrocnemia conspersa, Beraea maurus, Brillia modesta, and Thaumasoptera sp. (all inhabiting springs and/or hygropetric zones; Illies 1952, Hickin 1967, Lehmann 1971), among others, were added to the list of typifying taxa for group H1.

Site group H1 represents oligo- to β-mesosaprobic helocrene springs.

Site group H3

The composition of sites in this group did not change compared with spring site group 3. The average resemblance of sites in group H3 is high. The intermediate position with respect to the environmental

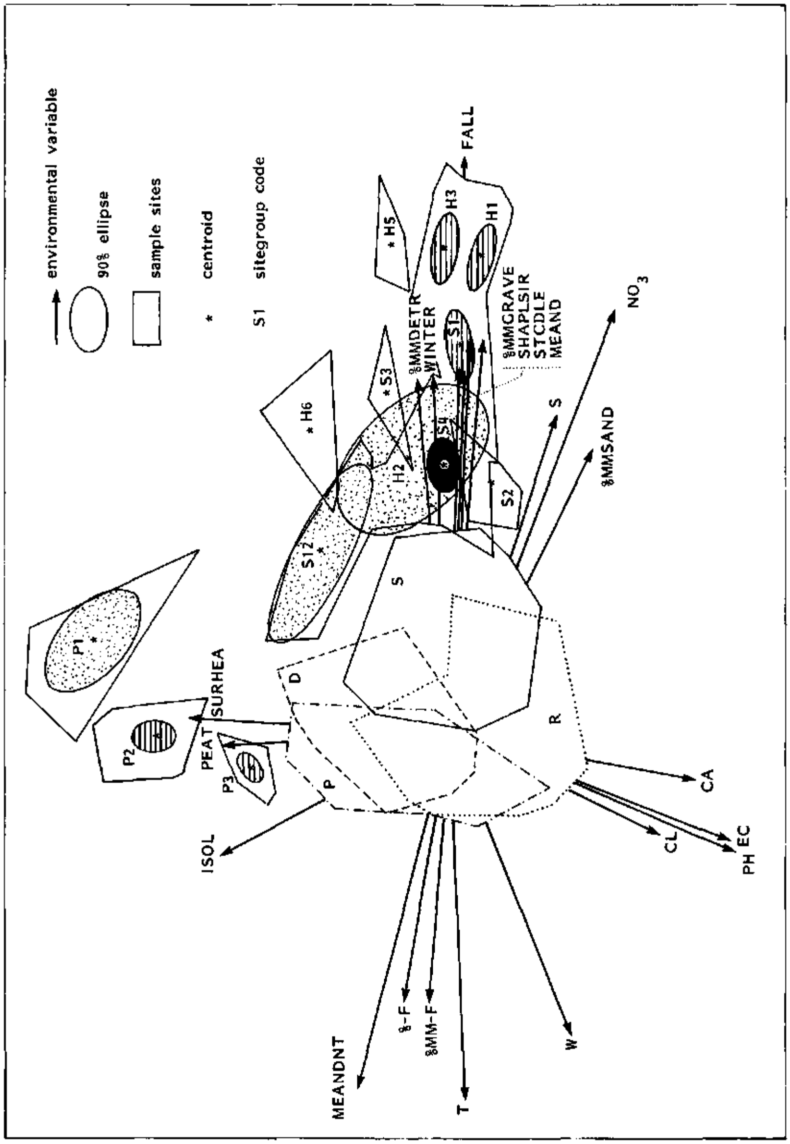

Figure 10.1 Run 1; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically). The selected site groups of the total data set are shown. The contour line describes the total variation of site scores. Within this contour line the site groups not indicated by a centroid and a confidence ellipse are indicated by their main physico-geomorphological water type; D = ditches, S = streams, R = rivers and canals, P = ponds and lakes. Only environmental variables with an interset correlation greater than 0.4 are shown (arrows). For further explanation see Sections 3.4.2 and 10.2.1, and Figure 3.9. Abbreviations are explained in Table 10.5.

variables remained and even the potassium and magnesium concentrations do not differ. The pH indicates slightly acid water, and phosphate and ammonium concentrations are slightly lower than in group H1. About one third of all the sites dry up temporarily. The indifferent taxa of helocrene spring site group 3 become typifying for group H3 within the total data set. Nine other taxa are added to the list of typifying taxa of this group, among which Dicranota bimaculata, Dixa maculata, and Gammarus pulex also typify group H1, and Nemurella picteti group H5. This underlines the intermediate position of group H3 between group H1 and H5.

Site group H3 represents neutral to slightly acid, oligo- to β-mesosaprobic helocrene springs.

Site group H5

Site group H5 did not change in site composition compared to spring site group 5 and the environmental description of the latter is applicable. The average resemblance of sites in group H5 is high. All sites are shaded and situated in woods with a sandy bottom. The current velocity is relatively high. The indifferent taxa of spring site group 5 together with nine other taxa are added to the list of typifying taxa of group H5, among which Krenopelopia sp., Macropelopia sp., Limnophyes sp., and Pedicia rivosa also typify group H3. Agabus guttatus, another typifying taxon, is often collected from springs and streams (Klausnitzer 1984). The typifying taxon Sialis fuliginosa is limited in its distribution to fast streams and upper reaches (Elliott 1977).

Site group H5 represents slightly acid, oligo- to β-mesosaprobic, oligo-ionic helocrene springs.

Site group S1

The exchange of some sites between groups S1 and H1 indicates a mutual resemblance (Table 10.1). The description of stream site group 1 (Chapter 6) also fits group S1 although in the latter the orthophosphate concentration is relatively high and the sulphate concentration is relatively low but higher than in the helocrene springs. Of all the stream site groups group S1 has a slightly higher fall but it is not comparable to that of the spring sites. The site composition of group S1 is homogeneous (Table 10.2). Fifteen taxa typify both groups H1 and S1, again indicating their similarity. Another fifteen taxa solely typify group S1. Most of the typifying taxa have already been described for stream site group 1 except, for example, Glyphotaelius pellucides which inhabits leaf packets in woodland pools and lowland streams (Hiley 1976), Rhyacodrilus coccineus which occurs in silty and silty sand substrata (Chekanovskaya 1962), Eukiefferiella sp. which primarily inhabits flowing waters (Cranston et al. 1983), and Conchapelopia sp. which is a poly-oxybiontic, more or less cold stenothermic inhabitant of flowing waters and lakes (Fittkau & Roback 1983). Two taxa have lost their typifying character (Odagmia ornata and Halesus digitatta/radiatus).

Site group S1 represents oligo- to β-mesosaprobic spring streams.

Site group S2

Site group S2 is identical, in site composition and description, to stream site group 2. The fall is much lower compared to the groups previously described. The electrical conductivity and the sulphate concentration are relatively high. All typifying taxa of stream site group 2 have kept their typifying weight, except for Brillia modesta which is also abundant in springs. Some new typifying taxa are Potamophylax sp., a genus inhabiting clean, well aerated, flowing waters (Hiley 1976) and Polypedilum breviantennatum, an inhabitant of flowing waters (Lindegaard-Petersen 1972).

Site group S2 represents permanent, rainwater-fed, β-mesosaprobic upper reaches of natural streams.

Site group S4

Stream site group 4 did not change in site composition and description within the total data set (Table 10.1). Within this DCCA-run the concentrations of bicarbonate and chloride of group S4 are high. The current velocity and electrical conductivity are also high. However, the ammonium concentration is low compared to other stream groups but higher than in the helocrene springs. Some of the sites are temporary (57%). The indifferent taxa of stream site group 4 also prove to be typifying for group S4 within the whole data set, except for the common Tubificidae. The new typifying taxa are Stenophylax sp. (an inhabitant of fast flowing streams which can diminish or dry up in summer, Hiley 1976) and Stictochironomus sp. (an inhabitant of soft or sandy sediments in stream and lakes, Pinder & Reiss 1983). The more common taxa, Rhantus sp. and Micropsectra sp., are removed from the list of typifying taxa.

Site group S4 represents temporary, β-mesosaprobic upper reaches of natural streams.

Site group H2

This group H2 completely corresponds with the composition and description of spring site group 2. Despite its large confidence ellipse (Figure 10.1), the average resemblance is intermediate (Table 10.2). Several new typifying taxa of group H2 also typify group H3, such as Ptychoptera sp. and Krenopelopia sp. Several common taxa, like Tubifex tubifex, Limnodrilus udekemianus, Polycelis sp., and Chironomus sp. prove not to be typifying of group H2 within the whole data set.

Site group H2 represents temporary or desiccating, neutral to slightly acid, β-mesosaprobic seepage marshes.

Site group S3

Site group S3 is identical, in site composition and description, to stream site group 3. Formerly indifferent taxa like Nemoura cinerea and Diplocladius cultriger (both bound to water flow, Hynes 1977, Cranston et al. 1983) together with Natarsia sp. (an inhabitant of streams, springs and the littoral zone of lakes, Fittkau & Roback 1983) are added to the list of typifying taxa of group S3.

Site group S3 represents temporary, α-mesosaprobic, small upper reaches of natural streams.

Site group H6

Site group H6 is a combination of sites (spring site groups 4, 6 and 8), all situated on the western hill ridge (Figure 1.6). The average resemblance of sites in group H6 is low, indicating that it is a heterogeneous group. The average temperature is low because the sites of group H6 are fed by a small groundwater aquifer with a small and seasonal (only in winter) discharge. The ionic concentrations are low, except for sulphate. This indicates a low retention time for rainwater in the aquifer. The isolated sites are surrounded by woods (60%) or heath (40%), and are situated on a sandy bottom. None of the sites discharges in a true stream. Some common coleopterans, like Anacaena globulus and Helophorus aquaticus/grandis, are removed from the list of typifying taxa and the formerly indifferent larvae of Hydroporinae have become typifying group H6. In general, taxa composition is poor.

Site group H6 represents temporary, acid, oligo-ionic, oligo- to β-mesosaprobic seepage marshes.

Site group S12

Site group S12 is a combination of stream site group 12 and both ditch site groups 9 and 10. Most sites of group S12 may become desiccated (71%), are slightly acid, and occur in regulated, and relatively small streams. The environmental description, given for stream site group 12, still holds. The calcium, chloride, and sodium concentrations are low but as for all other major ions, concentrations are higher compared with helocrene springs. The sulphate concentration is higher compared with all other stream site groups. The phosphate and nitrogen concentrations are high, indicating eutrophication. The sites of group S12 occur in very slowly flowing streams covered with filamentous algae (22%) and situated in an agricultural landscape (grassland 71%, woods 29%). They were sampled in spring. The ditch site groups were added due to their current flow and slightly acid character. They were responsible for the low average resemblance of sites in group S12. Several taxa typifying stream site group 12 prove not to be typifying of group S12 within the whole data set (e.g. Limnophyes sp., Limnephilus bipunctatus, Hydroporus nigrita, Sigara striata, and larvae of Hydroporinae). On the other hand, Polypedilum uncinatum (an inhabitant of oligotrophic water, Moller Pillot 1984), and Limnephilus vittatus (an inhabitant of sandy or silty pools, Hiley 1976) are added to the list of typifying taxa along with several taxa formerly typifying of ditch site groups 9 and 10, such as Stylodrilus heringianus, Hydroporus pubescens, and Limnephilus centralis.

Site group S12 represents temporary, slightly acid, α-mesosaprobic upper reaches of regulated streams or ditches.

The second environmental gradient in Figure 10.1 runs along the vertical axis and is due to a number of sites which are oligo-ionic, oligotrophic, and acid. The most important environmental character of the three distinguished site groups are the low concentrations of major ions, a low electrical conductivity (72 - 122 μS), a low pH (4 - 5), and low concentrations of phosphate (t-P: 0.06 - 0.13 mg/l) and nitrate (0.1 - 0.2 mg/l). Most sites are well vegetated (65 - 97%), especially in the submerged part (20 - 40%). The water level fluctuates (33 - 67%), the sites are mostly isolated (82 - 100%), often shaded (33 - 55%), and situated on an ombrotrophic peat (33 - 53%) or a sand (56 - 73%) bottom. The sites are surrounded by heath (27 - 67%) or woods (55 - 89%). They were often sampled in spring (36 - 89%).

Site group P1

Site group P1 represents the former pond site group 1 and did not change in site composition and description (Table 10.1). The average resemblance of sites in group P1 is high, indicating a homogeneous site group composition (Table 10.2). The high average ammonium concentration is the highest in the total data set. All taxa typifying pond site group 1 remain typifying of group P1. Psectrocladius sp., an eurytopic genus (Cranston et al. 1983) is added.

Site group P1 represents temporary, acidified, oligo-ionic, α-meso- to polysaprobic, mesotrophic moorland pools.

Site group P2

The small changes in composition of site group P2 compared with pond site group 2 did not alter its environmental character. The exchange of two sites of pond site group 3 indicates the resemblance to site group P3. Group P2 has a homogeneous site composition. Limnophyes sp. proved not to be typifying of this group within the whole data set. Some taxa were added to the list of typifying taxa of group P2, like Telmatopelopia nemorum (an inhabitant of temporary, acid, oligotrophic water; Fittkau 1962), Holocentropus dubius (an inhabitant of still water, Edington & Hildrew 1981), Nais communis and Agrypnia varia (both inhabitants of shallow, stagnant water; Timm 1970, Sedlak 1985), and Hydroporus erythrocephalus (an inhabitant of acid moorland pools, Freude et al. 1971).

Site group P2 represents permanent, acid to acidified, oligo-ionic, α-mesosaprobic to polysaprobic, mesotrophic moorland pools.

Site group P3

The composition of site group P3, compared with pond site group 3, shows only minor changes. It should be noted that the sites have, on average, a thick layer of organic material. The list of typifying taxa of group P3 is long compared with pond site group 3 (Appendix 1). Several taxa which also typify group P1 and/or P2, were added to this list. There are some interesting new typifying taxa of group P3, e.g. Corixa punctata (a widely distributed corixid also occurring in dystrophic water, Bernhardt 1985), Rhantus suturalis (an inhabitant of stagnant, vegetated waters; Freude et al. 1971), Dixella aestivalis (an eurytopic species also recorded from acid, oligotrophic peat pools; Disney 1975), and Notonecta viridis (collected in small, temporary moorland pools; Bernhardt 1985).

Site group P3 represents permanent, slightly acid to acid, oligo-ionic, α-mesosaprobic pools.

10.2.2 DCCA - RUN 2

The results of ordination of sites and environmental variables of the second DCCA-run (in which, the site groups discussed for run 1 were skipped from the analysis) are illustrated in Figure 10.2. Firstly, the aberrant site group D6, situated in the lower middle of this figure, is discussed.

Site group D6

Site group D6 did not change in site composition compared to ditch site group 6. Despite the slightly acid condition and the lower electrical conductivity, the average concentrations of most major ions and iron are high compared with all other groups. Within this run, the phosphate concentration is not high and the nitrate concentration is relatively low. The average cover percentage of filamentous algae is high (30%) compared with all other groups. Several taxa, formerly typifying ditch site group 6, are removed (e.g. Ptychoptera sp., Chaetocladius sp., Culiseta sp., and Chaoborus crystallinus) but widespread taxa (e.g. Agabus sturmi, Haliplus heydeni, and Limnephilus marmoratus) become typifying of group D6, including Hydroporus angustatus (an acidophilic inhabitant of shaded woodland pools; Freude et al. 1971), Agrypnia pagetana (an inhabitant of slowly flowing waters and lake shores, Tobias & Tobias 1981), and Hebrus pusillus (often collected from Sphagnum vegetation, Nieser 1982).

Site group D6 represents acid, oligo-ionic, α-mesosaprobic to polysaprobic small ditches.

The differences between the first and second environmental gradients, as judged by the eigenvalues (Table 10.4), are small and divide Figure 10.2 into four main parts. The lower right corner of the figure consists of small, shallow, temporary waters (groups D8, S9, S10 and S13). The upper right corner consists of streams with an increase in current velocity and fall, going from group R9, S7, S6 to S5. The upper middle section of the figure shows a group of large, very slightly flowing to stagnant waters. Finally, the remaining sites are all situated in the middle and left of the figure. Width and nitrate concentration appear to be significantly describing the ordination (Table 10.3). In general, the electrical conductivity is high for all sites (400-533 μS) which is also the case for the concentrations of ammonium (1.6-2.5 mg/l), total phosphate (0.45-2.53 mg/l) and major ions. The nitrate concentrations are lower than those in the helocrene springs and the upper reaches of streams but higher than in most other groups. The dimensions are larger than in the helocrene springs and the upper reaches of streams. Several groups have a medium current velocity due to a slight fall. The bottom consists of sand (80%) and is partially covered with silt (>50%). Often sites are

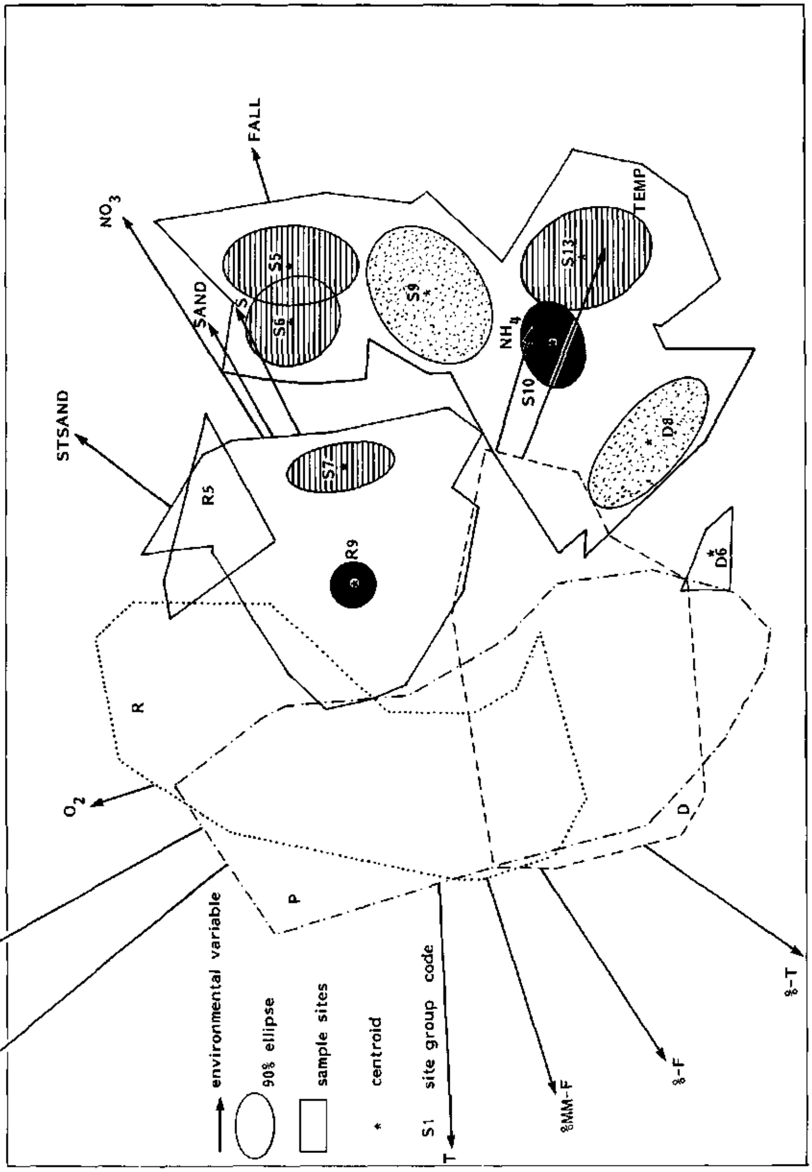

Figure 10.2 Run 2; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically). The selected site groups of the reduced data set are shown. The contour line describes the total variation of site scores. Within this contour line the site groups not indicated by a centroid and a confidence ellipse are indicated by their main physico-geomorphological water type; D = ditches, R = rivers and canals, P = ponds and lakes. Only environmental variables with an interset correlation greater than 0.4 are shown (arrows). For further explanation see Sections 3.4.2 and 10.2.2, and Figure 3.9. Abbreviations are explained in Table 10.5.

surrounded by grasslands (>40%) and have a steep profile (25-64%). The arrows pointing to the upper left and lower right corners are associated with variations present within the remaining groups.

Site group D8

Site group D8 is comparable to ditch site group 8, although most of the percentages given earlier differ by about 10%. The present high total phosphate concentration (Appendix 2) is due to only one aberrant site (there is a high standard deviation). The average temperature is high (indicating summer samples). Several taxa, like Micropsectra sp., Hydroporus striola, Colymbetes fuscus, and Chaetocladius sp. prove not to be typifying of group D8 within the total data set. The new typifying taxa of group D8 are Hydroporus umbrosus and Rhantus sp., both also typifying of group P1. Haliplus lineatocollis, although widely distributed (Freude et al. 1971) also typifies this group.

Site group D8 represents temporary, very slightly flowing, α-meso-ionic, α-mesosaprobic small ditches.

Site group S13

Site group S13 represents stream site group 13 within the total data set. The environmental description is still appropriate. Besides the already mentioned typifying taxa of stream site group 13, Aplexa hypnorum (an inhabitant of temporary waters, den Hartog & de Wolf 1962) and Laccobius biguttatus are added to the list of typifying taxa of group S13. Only the genus Culex is removed from the list of typifying taxa compared to stream site group 13.

Site group S13 represents the summer aspect with α-mesosaprobic conditions of temporary, small upper reaches of natural streams.

Site group S10

Site group S10 is a combination of stream site groups 10 and 11, and ditch site group 7. All three former descriptions resemble each other. The sites occur in regulated waters (88%), are temporary (76%) and have a sandy bottom (96%) with a silty substrate (80%). The phosphate and nitrogen concentrations are average within the whole data set. Most sites are situated in grassland (72%). The total vegetation cover is relatively high (41%), partly due to the presence of filamentous algae (19%). The samples were taken mainly in spring (88%). Several typifying taxa of stream site group 10 prove not to be typifying of group S10 within the whole data set (e.g. Stylodrilus heringianus, Hydrobius fuscipes, and Laccobius minutus). Almost none of the taxa typifying stream site group 11 or ditch site group 7 are typifying of group S10. The new typifying taxa are Macropelopia sp. (an inhabitant of fine sediments of cool water bodies, Fittkau & Roback 1983), Hydryphantus sp. (an inhabitant of small, still or slowly flowing waters; Davids 1979), and Tubifex tubifex (an inhabitant of extreme, often organically enriched environments; Verdonschot 1987).

Site group S10 represents temporary, α-mesosaprobic, flowing upper reaches of regulated streams or ditches.

Site group S9

The environmental description of group S9 corresponds to that of stream site group 9. The site composition of group S9 is quite heterogeneous (Table 10.2). The new typifying taxa of group S9 are Agabus didymus (a commonly distributed taxon which prefers small ditches, Freude et al. 1971), Velia caprai (a common inhabitant of shaded upper and middle reaches of streams, Bernhardt 1985), Smittia sp. (a mostly terrestrial living genus, Cranston et al. 1983), and the semi-aquatic genus Tipula (Theowald 1967).

Site group S9 represents the summer aspect with α-meso- to polysaprobic conditions of temporary upper reaches of natural streams or temporary, α-meso- to polysaprobic regulated streams.

Site group S5

The environmental description of group S5 corresponds to that of stream site group 5. Note the high average current velocity (26 cm/s) and the profile consolidation (63%) which is often found. To the list of typifying taxa of stream site group 5, the following taxa are added; Dicrotendipes gr. notatus (a common inhabitant of stagnant waters, Fittkau & Reiss 1978), Conchapelopia sp. (a more or less cold stenothermic inhabitant of flowing waters and lakes, Fittkau & Roback 1983), and Tubificidae. Limnodrilus profundicola proved not to be typifying of group S5.

Site group S5 represents polysaprobic upper and middle reaches of natural and regulated streams.

Site group S6

The description of stream site group 6 corresponds to the group S6. Group S6 has a lower average phosphate and nitrogen concentration compared with group S5 and the silt layer is much thinner. Additional typifying taxa of group S6 are Micropsectra sp. (an inhabitant of muddy desposits in streams and small rivers, Pinder & Reiss 1983), Dicranota bimaculata (an inhabitant of streams, Tolkamp 1980), and Hygrobatus longipalpus (an inhabitant of flowing waters, Viets 1936), Limnodrilus hoffmeisteri and Tubifex tubifex (both associated with organic enrichment, Kennedy 1965), and Anabolia nervosa (an inhabitant of slowly flowing, clear water or sunlit streams; Lepneva 1971) among others.

Site group S6 represents α-mesosaprobic middle reaches of semi-natural streams.

Site group S7

Due to the changes in site composition of stream site group 7 compared to group S7, the averages of some environmental variables have changed. This group S7 has a heterogeneous site composition. The ammonium, nitrate, calcium and bicarbonate concentrations are higher and the phosphate concentration lower, compared with group S6. Width and depth are slightly larger than in group S6. Most sites are part of regulated streams (84%) and the current velocity is moderate (22 cm/s). The new typifying taxa of group S7 are Paratendipes gr.

albimanus, Limnephilus lunatus, and Anabolia nervosa (all three taxa also typifying group S6), Hydropsyche angustipennis (a taxon which is quite common in streams and tolerates high temperatures, low oxygen concentrations and low water velocities; Edington & Hildrew 1981), and Sigara distincta (which is common in vegetated waters; Bernhardt 1985). The widely distributed taxa, formerly typifying stream site group 7, Bathyomphalus contortus, Planorbarius corneus, Physa fontinalis, Erpobdella octoculata, Sigara striata, and Cloeon dipterum prove not to be typifying group S7.

Site group S7 represents α-mesosaprobic middle reaches of regulated streams.

Site group R5

In site composition and description, site group R5 is comparable to river site group 5 (Chapter 7) although its composition in sites is fairly heterogeneous (Table 10.2). The large dimensions of sites in this group contrast with those in the other groups within this DCCA-run. Note that there is no relation to a bare sandy substrate (0%; Table 10.2) although suggested by the arrow in Figure 10.2. The ammonium and phosphate concentrations are low within this run and there is no current. Both taxa indifferent in river site group 5 become typifying of group R5 within the whole data set.

Site group R5 represents α-mesosaprobic, fairly large regulated rivers or stagnant canals.

Site group R9

There are many more sites in group R9 than in river site group 9. Most of the sites added formerly belonged to stream site groups 7 and 8. Although river site group 9 is small compared to other river site groups, group R9, with comparable dimensions as river site group 9, is much larger than group S7. The samples were taken in spring (44%) and autumn (53%). The nutrient concentrations are mostly high and the current velocity is moderate despite the relatively minor fall. The formerly typifying but widely distributed taxa of river site group 9 (e.g. Cloeon dipterum, Procladius sp., and Neumania deltoides) and taxa more abundant in upper and middle reaches of streams (e.g. Micropsectra sp., Baetis sp., Centroptilum luteolum, Conchapelopia sp., and Aulodrilus pluriseta) are removed from the list of typifying taxa of group R9. Formerly indifferent taxa become typifying of group R9 within the whole data set (e.g. Cryptochironomus sp., Limnodrilus claparedianus, Hygrobates longipalpis (all three taxa also typifying group S6), Polypedilum gr. bicrenatum (an inhabitant of lakes, Brundin 1949), and Valvata piscinalis (a common inhabitant of slowly running waters of all kinds, Macan 1977).

Site group R9 represents α-meso-ionic, α-mesosaprobic lower reaches of regulated streams or slightly flowing very small rivers.

10.2.3 DCCA - RUN 3

The results of ordination of sites and environmental variables of the third DCCA-run (for which the site groups discussed for runs 1 and 2 were removed from the analysis) are illustrated in Figure 10.3. In general, the site groups distinguished within this DCCA-run have low average nitrate concentrations (0.1-2.0 mg/l) and high bicarbonate concentrations (80-197 mg/l) due to a rich vegetation (>50%) at the moment of sampling. The samples were taken mainly in summer, which also explains the higher temperatures. One site group (R7) is aberrant. A high number of variables describes significantly the ordination (Table 10.3). Most arrows in the diagram are explained in the descriptions of the different site groups, such as the increase in dimensions and decrease in vegetation cover going from group P5 to D2A to D3 or the low electrical conductivity of group P4 or the high pH of group R7.

Site group R7

Site group R7 completely replaces river site group 7. The environmental characterization of the latter also applies to group R7. Limnophyes sp. and Stictotarsus duodecimpustulatus proved not to be typifying of group R7 within the whole data set. The new typifying taxa of group R7 are Potamothrix moldaviensis (see group R5), Arrenurus sp., Eylais sp., Limnesia sp., Dreissena polymorpha (an inhabitant of large slowly flowing or stagnant waters, Ellis 1978), Piona alpicola/coccinea, and Oulimnius sp.

Site group R7 represents oligo- to β-mesosaprobic, medium to fairly large stagnant canals.

Site group P5

Site group P5 is a compilation of pond site group 5 and several sites from ditch site groups 4 and 5. Group P5 has the most heterogeneous composition of sites of all the groups (Table 10.2). Both the environmental characterization and list of typifying taxa of pond site group 5 markedly changed for group P5. The sites of group P5 are small and very shallow with a dense vegetation (57%), especially the submerged part (46%). The bicarbonate concentration is high and the oxygen, potassium and phosphate concentrations are slightly lower compared to other groups within this run. Most sites have a linear shape (73%) and a thick silt layer or are swampy. The typifying taxa of group P5 are Dixella amphibia (an inhabitant of sedge and reed swamps, hydroseres and emergent beds of vegetation; Disney 1975), Agabus sturmii, Helophorus minutus, Haliplus flavicollis, Enochrus testaceus, Helophorus sp., and Hydroporus palustris (all six taxa are widely distributed coleopterans, Freude et al. 1971), Xenopelopia nigricans (an inhabitant of small water bodies and the littoral zone of lakes, Fittkau & Roback 1983), Arrenurus fimbriatus, Segmentina nitida (an inhabitant of drainage ditches in marshes and occasionally in ponds, Macan 1977), Planorbarius corneus, and the taxa already discussed: Haliplus ruficollis, Odontomyia sp., Enochrus melanocephalus, Enochrus coarctus, Bathyomphalus contortus, Cyphonidae, and Planorbis planorbis.

Site group P5 represents permanent, α-mesosaprobic, eutrophic, very shallow (swampy), small ditches.

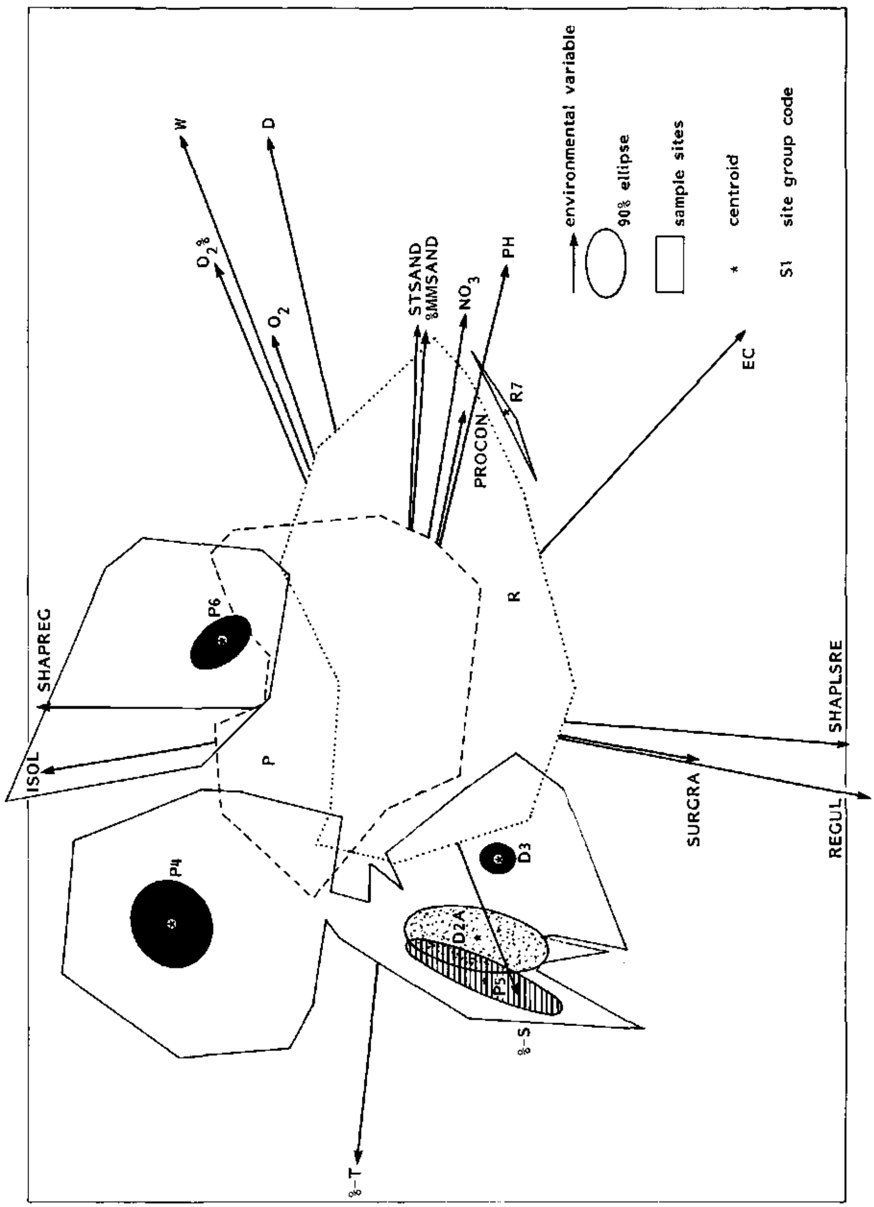

Figure 10.3 Run 3; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically). The selected site groups of the reduced data set are shown. Within this contour line the site groups not indicated by a centroid and a confidence ellipse are indicated by their main physico-geomorphological water type; R = rivers and canals, P = ponds and lakes. Only environmental variables with an interset correlation greater than 0.35 are shown (arrows). For further explanation see Sections 3.4.2 and 10.2.3, and Figure 3.9. Abbreviations are explained in Table 10.5.

Site group D2A

Despite the loss of five sites (Table 10.1), the environmental description of ditch site group 2A applies to group D2A. Compared with group P5, sites are wider and deeper with much floating vegetation (77%). The average concentrations of major ions, nitrate and ammonium are rather low. The substrate often consists of fine detritus and minerotrophic peat (89%). The new typifying taxa of group D2A are, among others, Argyroneta aquatica and Hydroporus erythrocephalus (both taxa also typify group P1 and P3), Hydroporus angustatus (an acidophilic taxon inhabiting Sphagnum and woodland pools, Freude et al. 1971), Agabus undulatus, Xenopelopia nigricans (see group D6), Dicrotendipes gr. lobiger, and several widespread molluscs and coleopterans. Odontomyia sp. and Colymbetes sp. are removed from the list of typifying taxa compared to ditch site group 2A.

Site group D2A represents permanent, β-meso- to α-mesosaprobic, small, shallow ditches.

Site group D3

The changes in site composition of ditch site group 3 compared to group D3 did not affect the environmental characterization. Several sites of stream site groups 7 and especially 8 are included. Most sites have a rather steep profile (53%) and are situated in grassland (94%). The dimensions are comparable to those of sites in group D2A but the standard deviations are much larger indicating a wider range. The nitrate concentration is low, the sites are less vegetated and the oxygen content is lower compared to group D2A, but the concentrations of nutrients and electrical conductivity are higher. This indicates a greater eutrophication compared to group D2A. Some new typifying taxa of group D3 (e.g. Xenopelopia nigricans, Haliplus ruficollis, Arrenurus globator, Bathyomphalus contortus, Planorbarius corneus, Noterus crassicornis, and Stagnicola palustris) also typify group D2A. Other new typifying taxa are, e.g. Polycelis sp., Hydroporus palustris, Lymnaea stagnalis, Bithynia leachi, Planorbis planorbis, Sphaerium sp., Erpobdella octoculata, and Glossiphonia complanata (all common inhabitants of vegetated, stagnant waters; Freude et al. 1971, Macan 1977, Reynoldson 1978, Dresscher & Higler 1982).

Site group D3 represents permanent, α-mesosaprobic, shallow, small ditches or stagnant regulated streams.

Site group P4

Site group P4 is comparable, in site group composition, to pond site group 4. The presented environmental description strongly depends on the comparison with pond site groups P1, P2 and P3. In general, the electrical conductivity and the concentrations of nitrate, oxygen and sulphate are low and phosphate concentrations are high in these small, isolated pools. The new typifying taxa of group P4 are Chaoborus obscurus, Chaoborus flavicans, Notonecta obliqua (all three also typify group P3), Oligotricha striata (an inhabitant of stagnant and slowly running waters, usually swampy, with brown peaty water, often in peat deposits and draining ditches; Lepneva 1970), Acroloxus lacustris (a commonly found taxon attached to vegetation in hard water, Macan 1977), and juvenile Coenagrionidae and their parasite Arrenurus cuspidator (Stechmann 1978). The Cyphonidae and Tubificidae were removed from the list of typifying taxa of group P4 within the total data set.

Site group P4 represents slightly acid to neutral, α-mesosaprobic, vegetation-rich, small, shallow pools.

Site group P6

The sites of group P6 have a relatively low phosphate and nitrogen concentration, and a high oxygen concentration, although they are still eutrophic. The environmental description of pond site group 6 is applicable to group P6. The composition of sites of group P6 is reasonably homogeneous. The sites have a thick organic or silty substrate and a regular shape. The new typifying taxa are, among others, Holocentropus dubius (a trichopteran restricted to stagnant waters, Edington & Hildrew 1981), Gyrinus marinus (a common taxon, Freude at el. 1971), Agrypnia pagetana (a characteristic inhabitant of lakes, Lepneva 1970), Parachironomus gr. arcuatus (an inhabitant of all kinds of water, locally abundant in small peaty lakes on Stratiotes; Higler 1977), Ecnomus tenellus (an inhabitant of stagnant and slowly flowing waters, in plant thickets; Lepneva 1970), Ablabesmyia longistyla (an inhabitant of ditches, streams and peat pits; Moller Pillot 1984), Endochironomus tendens, Polypedilum gr. sordens, and Chaoborus flavicans (all three taxa also typify group P3). Neumania limosa is removed from the list of typifying taxa of pond site group 6 compared to group P6.

Site group P6 represents clear, well oxygenated, β-mesosapobic, meso- to eutrophic waters (peat pits) with a rich vegetation on a minerotrophic peat bottom.

10.2.4 DCCA - RUN 4

The results of ordination of sites and environmental variables of DCCA-run four (in which the site groups discussed for runs 1, 2 and 3 were removed from the analysis) are illustrated in Figure 10.4. The important environmental variables which describe the ordination significantly are given in Table 10.3. The first and most important environmental gradient runs along the horizontal axis and is due to two sets of site groups. On the right side of the figure, three groups occur (R3, R8 and R11). Most sites in these groups have a high electrical conductivity, and high concentrations of total phosphate, nitrate and major ions. The ammonium concentrations are low. The sites are wide, deep and almost free of vegetation. They have a sandy bottom with a silty substrate. The sites were mainly sampled in spring, the water is slightly turbid to turbid, and there is some current. On the left side of the figure, the groups P8 and R2 occur. In comparison with the groups already discussed above, the electrical conductivity and the concentration of phosphate are lower, and the bicarbonate concentration and the cover percentage of vegetation is higher (about 50%), especially the floating part (27%). Group P7, above the middle in Figure 10.4, differs in biotic and abiotic characteristics from both above-mentioned set of groups.

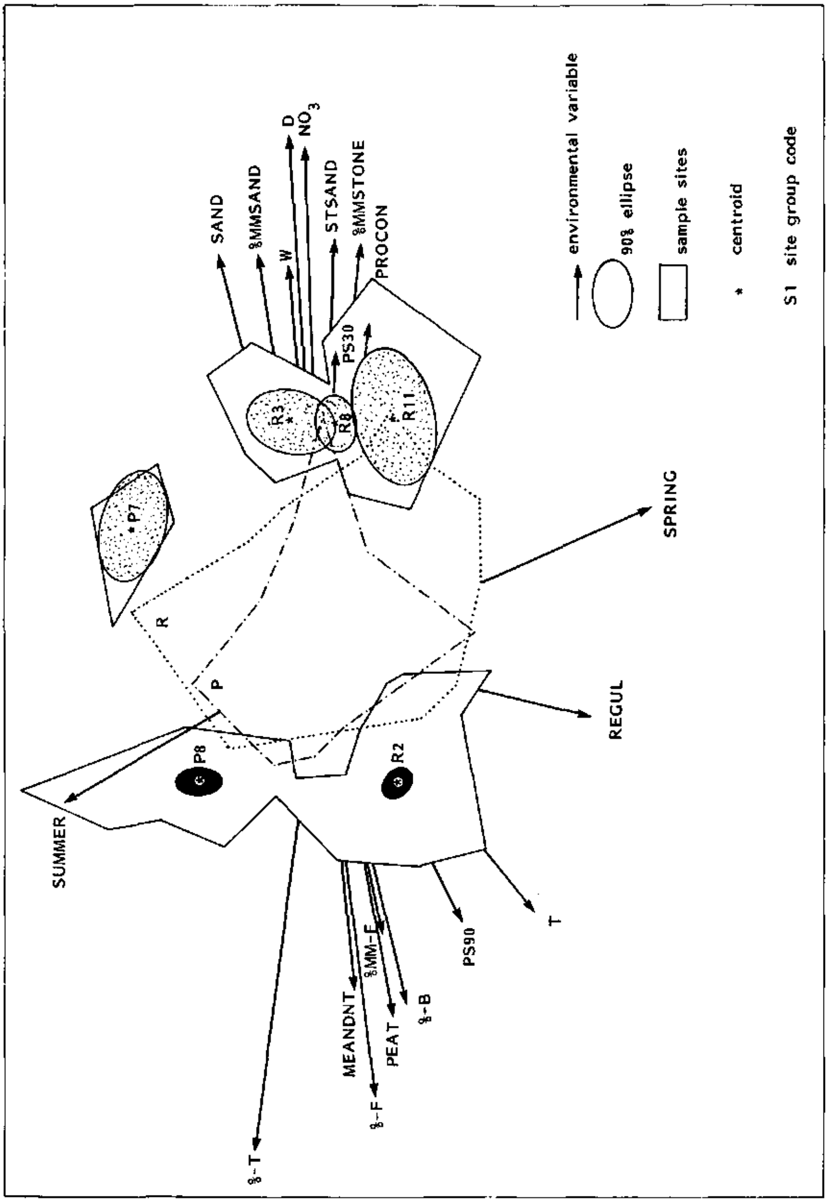

Figure 10.4 Run 4; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically). The selected site groups of the reduced data set are shown. Within this contour line the site groups not indicated by a centroid and a confidence ellipse are indicated by their main physico-geomorphological water type; R = rivers and canals, P = ponds and lakes. Only environmental variables with an interset correlation greater than 0.35 are shown (arrows). For further explanation see Sections 3.4.2 and 10.2.4, and Figure 3.9. Abbreviations are explained in Table 10.5.

Site group R11

Site group R11 completely replaces the river site group 11. The composition of sites of group R11 is slightly heterogeneous (Table 10.2). The environmental description of river site group 11 is also valid for group R11. The new typifying taxa are Potamothrix moldaviensis (see group R5) and Piscicola geometra (an inhabitant of clean, fairly large to large waters with a sparse vegetation due to its relation to fish; Garms 1961).

Site group R11 represents β-meso- to α-mesosaprobic, α-meso-ionic, mesotrophic, large, linear, slightly flowing rivers or stagnant waters.

Site group R8

Site group R8 completely replaces river site group 8 within the whole data set and the environmental characterization of river site group 8 is still applicable. The composition of sites of group R8 is homogeneous. The taxa Nais elinguis and Limnophyes sp., typifying river site group 8, are removed while some widespread taxa in stagnant waters, like Hygrobates nigromaculatus, Midea orbiculata, Sigara falleni, Psammoryctides barbatus (see group R11), Oecetis lacustris (an inhabitant of solid bottoms in small, eutrophic lakes, mouths of slow rivers, and ponds; Lepneva 1970), and Polypedilum gr. bicrenatum (see group R9) are added to the list of typifying taxa of group R8.

Site group R8 represents β-mesosaprobic, α-meso-ionic, very large, round to irregularly shaped lakes.

Site group R3

Site group R3 resembles river site group 3 in site composition and description. The environmental description of the latter also applies to group R3. All major ion concentrations are relatively low. The samples were mostly taken in the vegetation of the littoral zone or from the bare sandy bottom. Several taxa are removed from the list of typifying taxa of group R3 compared to river site group 3 (e.g. Zavrelimyia sp., Nemoura cinerea, Nais elinguis, Conchapelopia sp., Uncinais uncinata, and Rheotanytarsus sp.). The new typifying taxa of group R3 are Cladotanytarsus sp., Cryptochironomus sp., Oecetis lacustris, and Potamothrix moldaviensis (for details of all four taxa see group R8), Anodonta anatina (an inhabitant of flowing waters and a sandy bottom, Ellis 1978), Nais barbata (an inhabitant of middle and lower reaches of streams, Learner et al. 1978), Unio pictorum (an inhabitant of slow rivers, canals, lakes and large ponds; Ellis 1978) and Thienemaniella sp. (an inhabitant of lotic habitats, Cranston et al. 1983).

Site group R3 represents ααmesosaprobic, medium-sized, slightly meandering, slowly flowing small rivers.

Site group P7

Site group P7 is almost completely different in site composition and description compared with pond site group 7 (Table 10.1). The important environmental variables which describe the ordination significantly are given in Table 10.3. Most sites were sampled in summer (71%). The electrical conductivity and the nutrient and major ion concentrations are relatively low. The sites are deep and the surface area is fairly large. There is a moderate vegetation development, the water is clear (86%), shaded (86%), and surrounded by woods or wooded banks (86%). The profile shape is often irregular (86%), the sites are isolated (86%) and the bottom consists of sand. The water level can fluctuate (57%). The typifying taxa of group P7 are Psectrocladius sp. (an eurytopic taxon, Cranston et al. 1983), Ablabesmyia monilis/phatta (an inhabitant of stagnant waters, Fittkau 1962), Cladotanytarsus sp. (common, Pinder & Reiss 1983), Cyrnus flavidus (an inhabitant of still waters, Edington & Hildrew 1981), Erythromma najas (an inhabitant of vegetation-rich, stagnant waters; Gardner 1954), Mideopsis orbicularis (common), Cryptochironomus sp. (common, Moller Pillot 1984), Caenis luctuosa (an inhabitant of larger streams, rivers, and meso- to slightly eutrophic, stagnant waters; Malzacher 1986), Centroptilum luteolum (a taxon found on stony shores of lakes and in slowly flowing sections of streams and rivers, especially amongst vegetation and on sandy bottoms; Elliott & Humpesh 1983), Cloeon simile (an inhabitant of slowly flowing sections of streams and rivers, small ponds and amongst vegetation in deeper parts of ponds and lakes (Elliott & Humpesh 1983), Demicryptochironomus vulneratus (found in lakes and rivers, Lehmann 1971), Gerris argentatus (common, especially in vegetation; Nieser 1982), Hydrodroma despiciens (an inhabitant of lakes on a sandy substrate, Davids 1981), Pseudochironomus sp., Stictochironomus sp., and Tribelos intextus (all three chironomids preferring sandy bottoms in larger, oligo- to mesotrophic water bodies or the littoral zone with wave action; Pinder & Reiss 1983, Buskens 1987), Molanna angustata, Mesovelia furcata, Mystacides sp., Ranatra linearis (common in stagnant, well vegetated waters; Bernhardt 1985), and Ablabesmyia longistyla (an inhabitant of well oxygenated, vegetated waters; Fittkau 1962).

Site group P7 represents β-mesosaprobic, clear, well oxygenated, meso- to eutrophic, medium-sized, deep stagnant waters rich in vegetation.

Site group R2

Site group R2 is a combination of river site group 2 and ditch site group 1. The average resemblance of sites in group R2 is reasonably high. The sites are medium-sized, have a linear shape (90%) with a steep profile (83%) and are situated on a minerotrophic peat bottom (60%). The sites are surrounded by reed- (54%) or grassland (52%). They were sampled in spring (67%) or summer (33%). The environmental description given for river site group 2 also applies to group R2. The new typifying taxa of group R2 are, among others, Limnesia connata (an inhabitant of stagnant waters between vegetation, Besseling 1964), Tiphys ornatus (a species occurring in spring, Davids 1979), and Oecetis furva (an inhabitant of vegetated ponds, Tobias & Tobias 1981) compared to river site group 2. Only a few typifying taxa of ditch site group 1 are also typifying of group R2 (e.g. Endochironomus albipennis, Piona alpicola/coccinea). Argyroneta aquatica, Segmentina nitida, Bathyomphalus contortus, and Hippeutis complanata are removed from the list of typifying taxa of river site group 2 within the whole data set.

Site group R2 represents β-meso- to α-mesosaprobic, large ditches and small canals on a minerotrophic peat bottom.

Site group P8

Group P8 is mainly composed of sites formerly belonging to pond site group 8 and ditch site group 2B. The environmental description of both the latter site groups does not fit with that of group P8. The sites of group P8 were mainly sampled in summer (75%). They are sometimes shaded (46%) and situated in grassland (64%). The sites are smaller and shallower than the sites of group P7. The profile is irregular (54%) and the substrate consists of silt (61%) deposited on all kinds of bottom. The major ion and nutrient concentrations are comparable to group R2. Almost 50% of this group is hydrologically isolated compared to 6% in group R2. The new typifying taxa of group P8 are, among others, Holocentropus dubius, Cymatia coleoptrata, Gerris odontogaster (for details of all three taxa see group P2), Hippeutis complanata (common, particularly in closed ponds; Macan 1977), Notonecta glauca (common, Freude et al. 1971), Erythromma najas (see group P7), Anatopynia plumipes (an inhabitant of muddy, vegetated littoral zone of lakes; Fittkau 1962), Agrypnia pagetana (an inhabitant of lakes, Lepneva 1971), Theromyzon tessulatum (an inhabitant of shallow, stagnant and slowly flowing waters; Dresscher & Higler 1982), Sialis lutaria (an inhabitant of sluggish parts of streams and rivers, Elliott 1977), Paramerina cingulata (found in lakes and slowly flowing rivers, Fittkau 1962), Tanypus villipennis (an inhabitant of stagnant waters, Moller Pillot 1984), and Triaenodes bicolor (an inhabitant of vegetation-rich ponds, Tobias & Tobias 1981) compared to pond site group 8. However, Bathyomphalus contortus, Planorbarius corneus, Bithynia leachi, Physa fontinalis, Stagnicola palustris, Anisus vortex, and Piona alpicola/coccinea proved not to be typifying of group P8 within the whole data set.

Site group P8 represents β-meso- to α-mesosaprobic, medium-sized, stagnant shallow waters.

10.2.5 DCCA - RUN 5

The results of ordination of sites and environmental variables of the fifth DCCA-run (in which the site groups discussed for runs 1, 2, 3 and 4 were removed from the analysis) are illustrated in Figure 10.5. There is no clear environmental gradient present (see section 10.2). In general, sites of all groups in run five have high average temperatures, a fairly high electrical conductivity (390-501 μS), high concentrations of sodium and chloride, are well oxygenated (10-13 mg/l), oligo-β-mesosaprobic, and eutrophic to hypertrophic. All sites are wide and deep (176-358 cm) or have a fairly large surface area. The water is mostly yellow and slightly turbid. The bottom consists mainly of sand (42-78%) or clay (10-38%) with a silt layer (42-75%). The sites are often surrounded by grassland (50-96%).

Site group P9

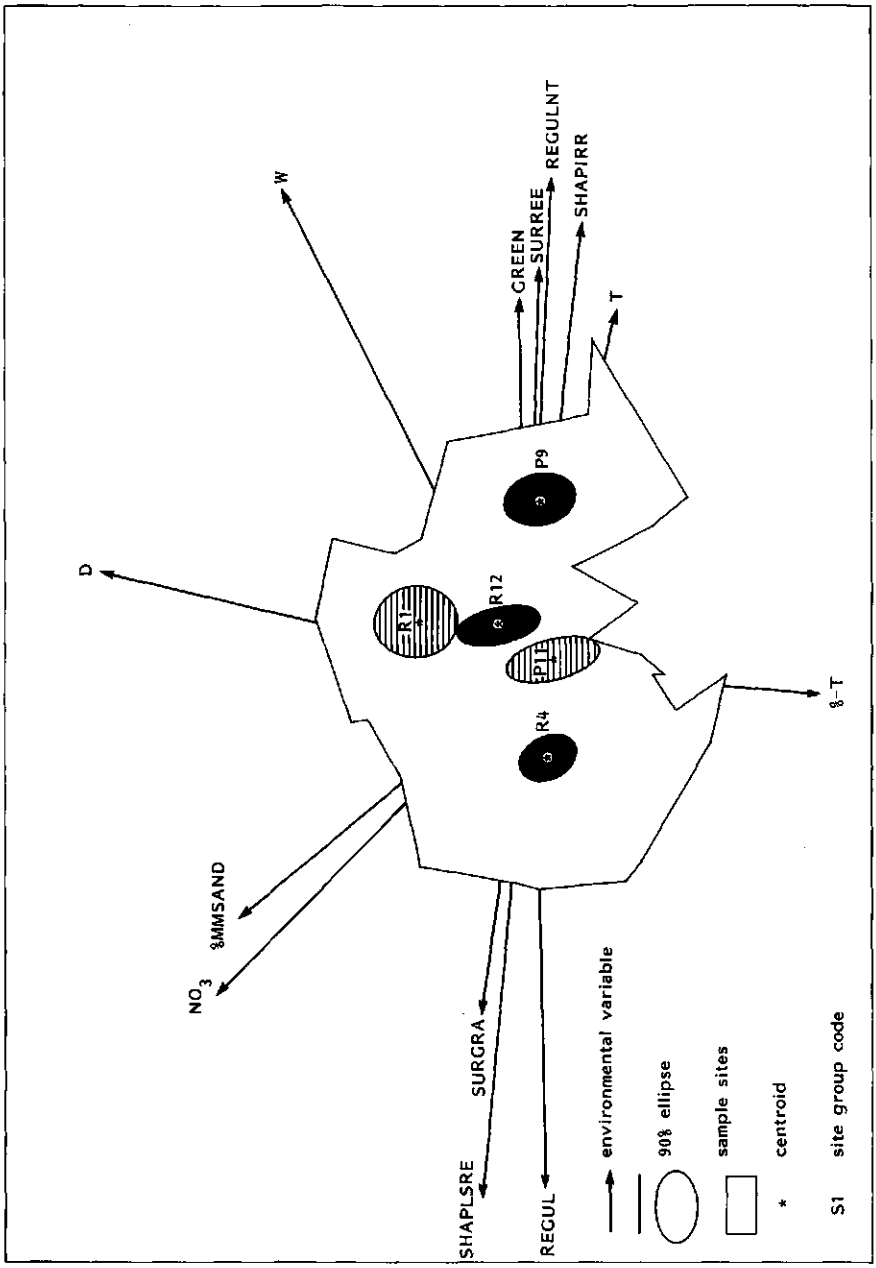

Figure 10.5 Run 5; ordination (DCCA) diagram for axes 1 (horizontally) and 2 (vertically). The selected site groups of the reduced data set are shown. Only environmental variables with an interset correlation greater than 0.35 are shown (arrows). For further explanation see Sections 3.4.2 and 10.2.5, and Figure 3.9. Abbreviations are explained in Table 10.5.

Site group P9 is strongly similar to pond group 9 in site composition and description. The environmental characterization of the latter fits group P9 reasonably well. The composition of sites of group P9 is homogeneous (Table 10.2). The surface area of most sites is large. Some of the sites are isolated (46%), some have an irregular profile (67%) and the water is sometimes green (42%). The bicarbonate concentration is high and the nitrate concentration low. The sites are sometimes situated in reedland (42%). Compared to pond group 9 the new typifying taxa of group P9 are, among others, Tanypus kraatzi, Theromyzon tessulatum (both taxa see group P8), Dero digitata, Polypedilum gr. sordens, Endochironomus albipennis (both the latter chironomids inhabit tubes in vegetation in ponds and lakes, Shilova 1968), Parachironomus gr. arcuatus (an inhabitant of lakes and rivers, Moller Pillot 1984), and Phryganea bipunctata (an inhabitant of vegetation-rich, stagnant waters; Tobias & Tobias 1981). All three species of the genus Limnodrilus and Valvata piscinalis were removed from the list of typifying taxa of group P9.

Site group P9 represents α-mesosaprobic, fairly large ponds or small lakes.

Site group R4

Site group R4 is compiled from some of the sites of river site group 4 and a number of other sites from different groups. Despite the changed site group composition compared to river site group 4, group R4 is a reasonably homogeneous group. The sites have a low current velocity, are relatively shallow (within this DCCA-run), have a linear shape (88%), and are surrounded by grassland (96%). The sites were mainly sampled in spring (47%) and summer (41%), and the bottom consists of sand with a silt layer (67%). The electrical conductivity is high. Compared to river site group 4 the new typifying taxa of group R4 are, among others, Cryptochironomus sp. (an inhabitant of lakes, streams and rivers; Pinder & Reiss 1983), Laccophilus hyalinus (common, Freude et al. 1971), Mystacides sp., Eylais extendens (both inhabitants of vegetation rich, stagnant waters; Hickin 1967, Besseling 1964), Oulimnius tuberculatus (found in unpolluted, stagnant waters with wave action or streams; Cuppen 1984), Parachironomus gr. vittiosus (an inhabitant of lakes and rivers, Reiss 1968), Bithynia leachi (common, Macan 1977) and several common mites. Haliplus ruficollis proved not to be typifying of group R4 within the whole data set.

Site group R4 represents α-meso-ionic, β-meso- to α-mesosaprobic, linear shaped small to medium-sized waters.

Site group P11

Site group P11 is a combination of sites formerly belonging to pond site group 7 and river site group 4. Besides the general environmental description applicable within this DCCA-run, group P11 itself has only a few environmental characteristics. Most sites are isolated (67%) and shaded (75%). The samples were mainly taken in summer (92%). The average nitrate concentration is low. The typifying taxa of group P11 are, among others, Gerris sp., Gerris odontogaster (an inhabitant of lakes, swamps, and temporary waters;

Bernhardt 1985), Arrenurus globator, Cyrnus flavidus (an inhabitant of stagnant or slowly flowing waters, Lepneva 1971), Piscicola geometra (an inhabitant of clean, larger, less weedy waters; Garms 1961), Unionicola aculeata, Dicrotendipes gr. nervosus (collected from lakes and rivers, Reiss 1968), Cryptochironomus sp. (an inhabitant of lakes and rivers, Pinder & Reiss 1983), Nanocladius sp. (common in lakes and rivers, Cranston et al. 1983), Oecetis lacustris (an inhabitant of ponds and small eutrophic lakes, Lepneva 1970), Polypedilum gr. sordens and Endochironomus albipennis (both chironomids living on the vegetation in stagnant, eutrophic waters; Moller Pillot 1984), several widespread taxa (e.g. Piona conglobata, Hydrachna globosa, Limnesia sp., Laccophilus sp., Enochrus sp., and Haliplus immaculatus), and several taxa also typifying group P7 (e.g. Hydrodroma despiciens, Mesovelia furcata, Mystacides sp., Ranatra linearis, Ilyocoris cimicoides, and Ablabesmyia longistyla).

Site group P11 represents β-mesosaprobic, medium-sized, deep stagnant waters.

Site group R12

Site group R12 is a combination of sites formerly belonging to river site groups 1, 4 and 12, and pond site groups 7 and 9. Group R12 is a fairly homogeneous group. Again, beside the general environmental characterization of all sites within this DCCA-run, group R12 itself has few characteristics. The phosphate concentrations are relatively low and the bottom is silty. The samples were mainly taken in spring (77%). Only a third of the sites is isolated from other water bodies. The sites are slightly deeper and larger than those of group P11. The typifying taxa of group R12 are Cladotanytarsus sp. (an eurytopic taxon, Pinder & Reiss 1983), Cryptocladopelma gr. laccophila (an inhabitant of well oxygenated lakes, Lenz 1962), Oecetis furva (an inhabitant of vegetated ponds, Tobias & Tobias 1981), Ophidonais serpentina (an inhabitant of stagnant, vegetated waters; Verdonschot 1984), and several taxa also typifying group R3 (e.g. Piona pusilla, Corynoneura sp., Caenis horaria, Ecnomus tenellus, Nais barbata, Psammoryctides barbatus, and Parachironomus gr. arcuatis), and group P11 (e.g. Piscicola geometra, Dicrotendipes gr. nervosa, Mystacides sp., Polypedilum gr. sordens, Unionicola crassipes, Endochironomus albipennis, Glyptotendipes sp., and Ablabesmyia longistyla).

Site group R12 represents β-meso- to α-mesosaprobic, meso- to eutrophic, large, less deep stagnant waters.

Site group R1

Site group R1 is comparable, in site composition and description, to river site group 1. The site group composition is reasonably homogeneous. The environmental description of river site group 1 fits group R1. In addition, the calcium and nitrate concentrations are high, the sites are linear (94%), the profile is often consolidated (56%) and there is some current. The sites were sampled in summer (63%). Compared to river site group 1 the new typifying taxa of group R1 are Gerris sp., Potamothrix moldaviensis (an inhabitant of lower reaches of rivers, Timm 1970), Glyptotendipes gr. caulicola, Branchiura sowerbyi (an inhabitant of silt in stagnant waters, Chekanovskaya 1962), Limnodrilus claparedianus (a saprobic inhabitant of lakes and rivers in mud and muddy sand, Dzwillo 1966), Cyrnus trimaculatus (an inhabitant of lower reaches of large rivers, Eddington & Hildrew 1981), taxa also typifying group R11 (e.g. Dreissena polymorpha, Dicrotendipes gr. nervosa, and Psammoryctides barbatus), and group P11 (e.g. Endochironomus albipennis and Glyptotendipes sp.).

Site group R1 represents β-meso- to α-mesosaprobic, medium-sized to large very slowly flowing lower courses of streams and rivers.

10.2.6 The environmental characterization of the site groups

In the environmental characterization of the site groups, the physical and chemical variables were weighed against each other but an evaluation is only possible by comparing them to other data.

The nutrient content is mostly expressed as the load and/or concentration of phosphate and nitrogen. Several trophic classifications based on nutrient concentrations were made but it should be borne in mind that the relation between nutrient balance and productivity is not a straightforward one (Elster 1962). For the present study only concentrations were available. Leentvaar (1979) introduced a trophic classification based on orthophosphate and nitrate concentrations. Within that classification, the groups P1, P2, P3 and P11 are classified as mesotrophic, group P6, P7 and R12 are meso- to eutrophic, and group P5 is eutrophic. Several other groups also have either a low orthophosphate or a low nitrate concentration indicating meso- or eutrophy, but the other variable then indicates hypertrophy. This trophic indication is given in the characterization of the site groups. One should consider that the nutrient concentrations are strongly related to the season, especially the orthophosphate concentration. Vollenweider (1968) published a trophic classification based on total phosphate concentration. In his classification most of the presented site groups prove to be polytrophic, except for groups H4, H5, H6, P1, P6 and P7 which are eutrophic to polytrophic. In fact, the inorganic nitrogen compound should also be considered (Vollenweider 1968). Looking at the nitrate concentration in combination with total phosphate concentration, only groups P1 and P7 prove not to be polytrophic. It can be concluded that there are almost no truly oligotrophic waters in the province of Overijssel nowadays. For most of the sites investigated, neither phosphate nor nitrate probably limits primary production. The nitrate concentrations were even excessively high in smaller waters in the Pleistocene part of the province (springs, streams and ditches).

The indication of saprobity, used for the characterization of the site group, is based on the ammonium concentration (Wegl 1983). The high saprobity of acid waters has already been discussed in Section 9.3.

The total ion concentration is classified by Olsen (1950). Most of our groups are β-meso-ionic, except for those indicated in the characterization of the site groups. According to Olsen (1950), all the groups have soft to medium-hard water, except for group R12 which has hard water. The alkalinity is slightly below or above average, except for groups S12, P1, P2, P3, R1, and R3 in which it is low.

The physical variables (such as width, depth and shape) have already been discussed in the site group descriptions. The indication of the physico-geographical water type (Table 1.2) is related to a combination of important physical variables and is used in that sense for the characterization of the site groups. Note that not all waters which correspond to a physico-geographical water type belong to the same site group. On the contrary, the indication of a physico-geographical type is only one of the components contributing to the characterization of a site group.

The typifying taxa of each site group within the whole data set change when compared with the analyses within one of the main water types. The following changes occurred:

- Former typifying taxa became indifferent or their typifying weight decreased. This concerns taxa which were typifying a certain group within a main water type but for which the environment of this group is less than optimal. Their optimal environment is present in another (main) water type. For example, taxa common in streams (e.g. Micropsectra sp., Conchapelopia sp., and Baetis sp.) typified river site group 9 within the main water type "rivers and canals" but their occurrence in these sites is limited and suboptimal. Due to their wide distribution range within streams they were removed from the list of typifying taxa for group R9. Another example concerns taxa which are widely distributed but locally abundant (e.g. Chironomus sp. and Tubificidae). Their typifying character in several groups within the main water types is coincidental.
- Former indifferent taxa became typifying or their typifying weight increased. This concerns taxa which were widely distributed within a main water type and were less abundant or lacking in all other main water types. For example, several taxa typically inhabiting small streams (e.g. Dicranota bimaculata, Prodiamesa olivacea, and Brillia modesta) are common within the stream site groups and typify them within the whole data set.

10.3 The biological similarity between the site groups

A hierarchical dendrogram of site groups based on the total data set reflects the biological similarity between the groups (Figure 10.6). This dendrogram is based on agglomerative clustering of site groups. Each site group is compared to all others and its resemblance (a measure of distance between the centroids of two groups) to the most similar site group is calculated (centroid clustering; van Tongeren 1986). The two most similar groups (i.e. those with the highest resemblance) are fused and a new centroid is calculated for this new group. Again, a new fusion is executed and this process is repeated until all the groups are fused. In Figure 10.6 the resemblances between (combinations) of groups were plotted on the vertical axis. The site groups are plotted on the horizontal axis. The groups R1, R4, P11, R12, R2 and R8 are quite similar to each other while they differ markedly from groups H5 and H6, which are also completely different from each other (Figure 10.6). In this way the similarity between all the site groups can be seen. In the dendrogram, at the different divisions, the most important variables or complexes of variables related to that division are indicated.

The two most aberrant site groups are S14 and D11. They are equal to stream site group 14 and ditch site group 11 respectively. They

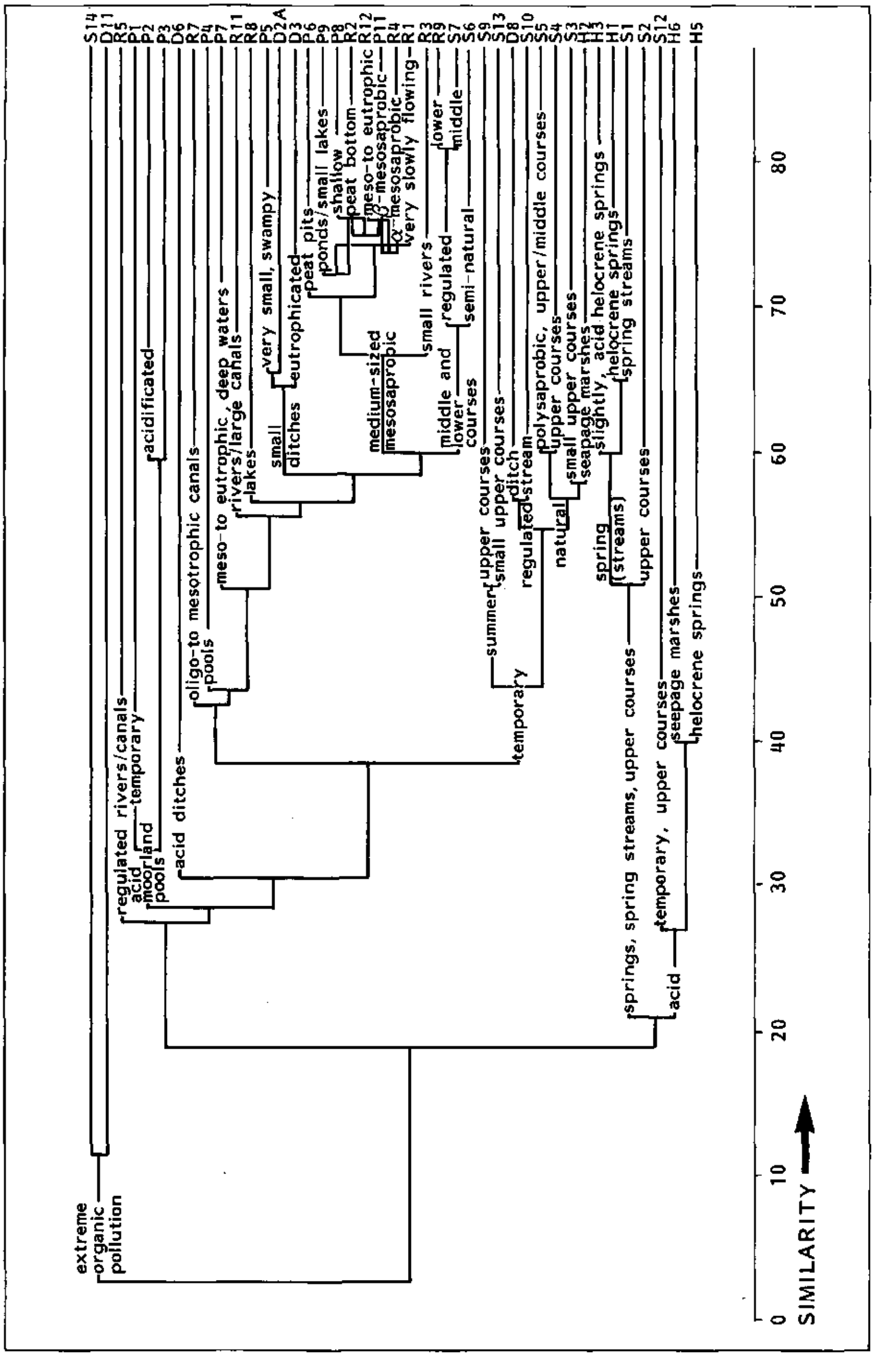

Figure 10.6 Hierarchical dendrogram of site groups indicating factors potentially responsible for the divisions.

have not been discussed yet. The two groups consist of only one, extremely organically polluted site each, which is reflected in the absence of almost all taxa. The few taxa present differ between the two groups which explains their dissimilarity. The second most dissimilar set of site groups concerns the seepage marshes, helocrene springs, and spring streams. They represent an environment inhabited by its own characteristic macrofauna, clearly distinct from that of the other waters. All these sites are situated on the steepest slopes of the hill ridges. Their characteristic fauna is probably preserved by this natural physical protection against disturbances of the environment by (mainly agricultural) human activities. Chapters 5 and 6 dealt with the characteristics of these sites. Next, still with a high dissimilarity ratio, several quite distinctive groups are separated stepwise. This concerns the slowly flowing rivers, the moorland pools, and the acid ditches. All the remaining groups are separated into temporary versus permanent waters, except for the polysaprobic upper and middle reaches of streams which appear to be biologically similar to temporary upper reaches. Both forms of stress, desiccation and extreme organic enrichment, have to a certain extent a comparable effect upon the fauna. The similarity between middle and lower reaches of regulated streams, small rivers, ditches and medium-sized, more or less stagnant waters (group R1 to P6) is striking. Apparently these stagnant, hypertrophic, mesosaprobic environments have a fair part of the macrofauna in common. This shows, firstly, the decreasing dominance of flow in running waters and secondly, the decreasing dominance of shape, depth and bottom type in stagnant waters. The decreasing dominance of thee masterfactors is due to disturbance and stress induced by human activity (e.g. by regulation of streams, discharge of wastes, agricultural activity in the watershed, etc.) and leads to an impoverishment of the macrofauna.

Table 10.5 Abbreviations of environmental variables. All chemical variables in mg/l unless otherwise indicated.

Quantitative environmental variable	Abbreviation
Temperature (^oC)	T
Acidity	PH
Electric conductivity (μS)	EC
Oxygen concentration	O2
Oxygen saturation	O2%
Ammonium	NH4
kjeldahl-Nitrogen	Kj-N
Nitrate	NO3
Nitrite	NO2
Ortho-phosphate	O-P
Total-phosphate	T-P
Chemical oxygen demand	COD
Biological oxygen demand	BOD
Total organic carbon	TOC
Chloride	CL
Sulphate	SO4
Sodium	NA
Potassium	K
Magnesium	MG
Calcium	CA
Bicarbonate	HCO3
Iron	FE
Ionic ratio	IR
Hardness	HN
Surface area (ha)	SA
Width (m)	W
Depth (m)	D
Length (m)	L
Stream velocity (cm/s)	S
Fall (m/km)	FALL
Distance to the source (km)	SOURDIST
Transparancy (m)	TRANSPAR
Silt thickness (m)	S-T
Percentage algae	%-A
Percentage floating	%-F
Percentage submerged	%-S
Percentage emergent	%-E
Percentage bank	%-B
Total percentage	%-T
Percentage sampled habitat:	
bank-littoral	%MM-B
emergent veg.	%MM-E
floating veg.	%MM-F
submerged veg.	%MM-S
silt substrate	%MMSILT
sand substrate	%MMSAND

peat substrate	%MMPEAT
clay substrate	%MMCLAY
detritus subst.	%MMDETR
gravel subst.	%MMGRAVE
stone substrate	%MMSTONE

Nominal environmental variable	Abbreviation
Sampling date	
	SPRING
	SUMMER
	AUTUMN
	WINTER
Profile shape	
line shaped regular	SHAPLSRE
line shaped irregular	SHAPLSIR
very irregular	SHAPVIR
irregular	SHAPIRR
regular	SHAPREG
Temporary	TEMPOR
Water level fluctuation	WATLF
Seepage	SEE
Watercolour	
	COLORLES
	YELLOW
	BROWN
	GREEN
	BLACK
Smell	SMELL
Transparancy	
clear	CLEAR
slightly turbid	SLTURB
turbid	TURBID
Visible bacteria	
none	BACTNONE
slight	BACTSL
abundant	BACTABUN
Pollution indication	POLLUT
Cleaning	CLEANIN
Bottom type	
sand	SAND
sandy-silt	SASILT
clay	CLAY
peat in fenland	FENLAND
peat	PEAT
Substrate type	
sand	STSAND
sandy-silt	STSASI
peat	STPEAT
clay	STCLAY
silt	STSILT
fine detritus/peat/silt	STFDPESI
detritus/peat	STFDEPE

coarse material	STCM
idem./leaves/peat	STCMDLPE
idem./detritus/leaves	STCMDELE
idem./silt	STCMSI
coarse detritus/leaves	STCDLE
idem./silt	STCDLESI
comb. organic material	STCOMB
Profile slope	
0-30	PS30
30-45	PS45
45-75	PS75
75-90	PS90
concave	PSCON
irregular	PSIRR
Meandering	
none	MEANDNT
slight	MEANDSL
strong	MEAND
Regulation	
none	REGULNT
slight	REGULSL
strong	REGUL
Profile consolidation	PROCON
Shadow	SHADOW
Surrounding	
urban	SURURB
woodland	SURFOR
wooded bank	SURWOB
field	SURFIE
grassland	SURGRA
reedland	SURREE
heath	SURHEA
Isolated	ISOL

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11. GENERAL APPLICATIONS IN WATER MANAGEMENT

11.1 The web of cenotypes

The typology of surface waters in the province of Overijssel resulted in the description of 42 site groups (Section 10.2). These site groups meet the concitons and criterion described in Section 2.5 and therefore will be called cenotypes. The most important environmental relations between these cenotypes are shown in Figure 11.1. The results of the first DCCA-run, axes 1 and 2 (Section 10.2.1), are used as a basis for the construction of this figure. The contour line indicates the variation, in macrofauna composition and environmental conditions, present at the 664 sampled sites. All sites together form a continuum except for three cenotypes in the left upper corner. The ecological entities recognized in the continuum are presented by the centroids of the respective cenotypes (circles). The centroids of the cenotypes are arranged along major environmental gradients. This is not only due to the two major gradients of acidity and fall (or more generally 'stream-character') discussed in Section 10.2.1. Other factors influence the pattern presented in this two-dimensional field as well. The inset in the upper right corner (Figure 11.1) shows the four most dominant factors, 'stream-character', acidity, duration of drought and dimensions. The spatial configuration of cenotypes more or less corresponds to their biological similarity shown in the hierarchical dendrogram (Figure 10.6). The cenotypes related to hypertrophic, mesosaprobic environments (Section 10.3), for example, are situated close together. The significant environmental relations between the cenotypes are taken from the environmental characterization of the cenotypes and are indicated by arrows (Figure 11.1). The web does not distinguish between natural and disturbed environmental conditions, it merely reflects the cenotypes present under the given environmental conditions. Still, the impoverishment of the macrofauna due to human induced environmental disturbance (Section 2.7 and Section 10.3) can be read from Figure 11.1, partly in the variables indicated and partly in the spatial arrangement of the cenotypes. Especially the cenotypes in the lower left corner (mostly large waters) have been changed due to human disturbance.

The web is the result of a descriptive study, but can it be used for future water management? For water management, two applications are important.

Firstly, the possibility should exist to predict the effects of the intended management. A comprehensive ecological survey of sites present in a certain region has a descriptive value. Potentially, the results can, with caution, be used to predict effects of management measures. Although May (1984) noted that "despite recent advances, both in the acquisition of data and its analysis, it is doubtful whether any multispecies community is sufficiently well understood for us to be able to make confident predictions about its response to particular disturbances, especially those caused by man. Probably many ecological concepts are limited explanations of the biological reality around us. This limitation is brought about through

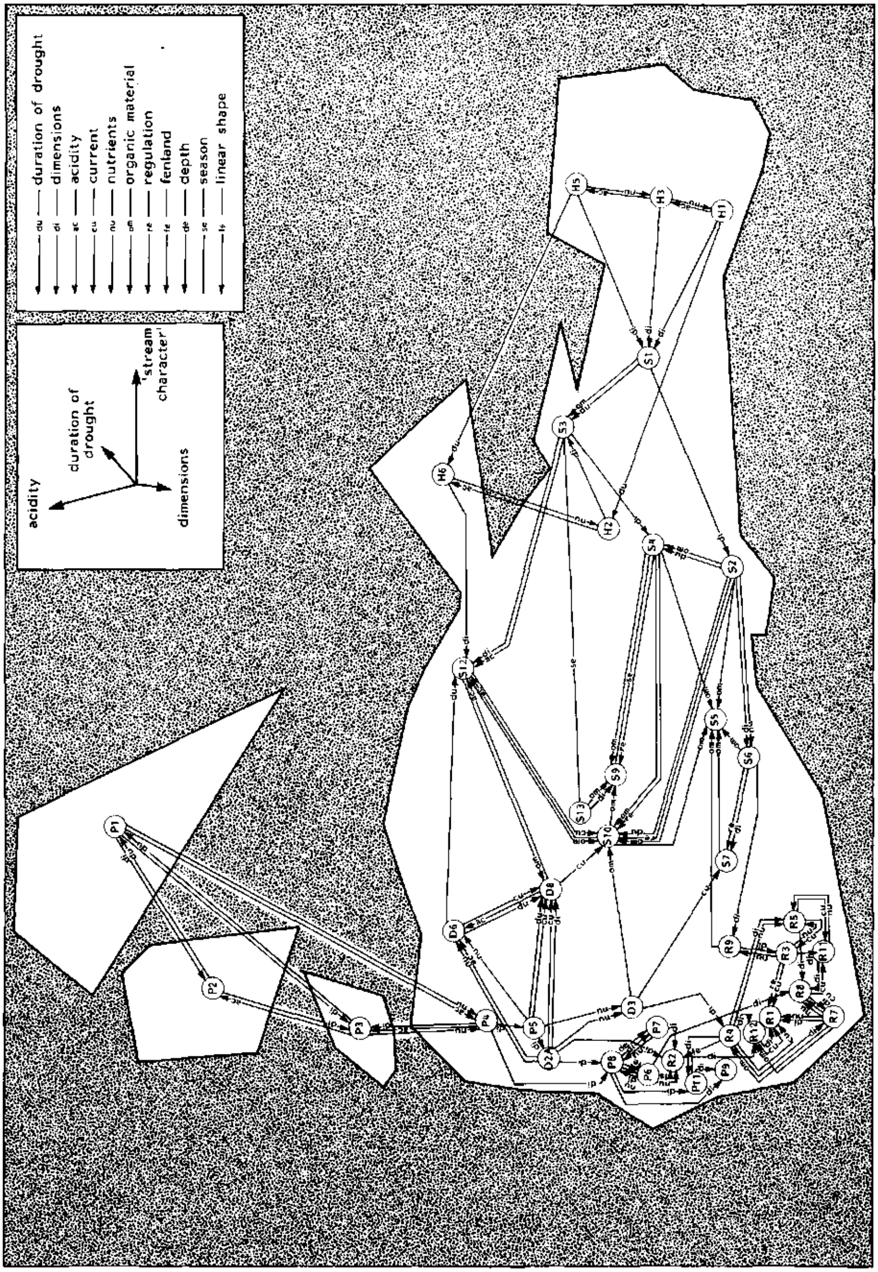

Figure 11.1 The web of cenotypes. The contour line describes the total variation present in all site scores. The centroid of each cenotype is indicated by a code (see Chapter 10). The arrows between cenotypes indicate the most important environmental relations. The inset represents the four most important environmental gradients (master factors) in the total data set.

dimensions of space and time and through the limitations of definitions." On the other hand, several authors (Hawkes 1975, Resh & Unzicker 1975, Maitland 1979, Persoone 1979) have stressed the predictive value of the results of an ecological survey despite the fact that it is based on conceptual ideas and correlation of data rather than on causal proof.

The second application of the web for water management is the possibility to evaluate the actual state of water bodies. In principle, each cenotype represents the optimal system functioning within the specific environmental conditions. But not every ecosystem equally adds to the existence of other systems. Although there is no objective criterion to evaluate a certain water, for management purposes an evaluation of the cenotypes present is necessary. As Rykiel (1985) argued, an ecologically significant characterization of environmental disturbance and, hence, an evaluation of an aquatic ecosystem, requires a specification of the reference conditions of the system under study. The reference conditions are the conditions to which the actual conditions can be compared to. An evaluation needs a scale and a reference condition which is not necessarily an endpoint of succession nor a pristine situation. To evaluate a given water body it is necessary to compare it with comparable but more and less undisturbed water bodies as well as with other different water bodies in a particular group.

None of the cenotypes distinguished in our study represents an original (pristine) state, in the sense that it is not affected at all by human activities. The most natural state is found in the helocrene springs and spring streams. Furthermore, some waters are artificial (dug by men e.g. ditches, canals) and would gradually fill in without regular human interference (cleaning, dredging). Their natural state would not be aquatic but more or less terrestrial. Therefore, the natural state cannot be the only evaluation criterion (see also Section 2.7) or reference condition. The reference condition should, at least, be a condition that can indicate a certain direction of improvement for the management aims chosen. This should be improvement on a scale according to the ecological concepts appropriate for the respective cenotype.

For water management, a decision must be made about the difference that is acceptable between the actual and reference condition. This greatly depends on the given political, economic and social possibilities. For example, in water management different kinds of human interference are distinguished. Regulation of streams, for example, is a human activity and so is discharge of organic waste. Regulation, often for drainage or navigation purposes, has become part of the economic system. Deregulation or restoration of running waters, especially of rivers, may sometimes demand great social and economic changes. Discharges of organic waste can be tackled with purification plants, which is much easier, since it mainly meets financial problems. At present for each individual water body one should determine its ecological characteristics and the scale towards the reference condition versus the political feasibility of arriving at this condition and not try to reach the ultimate reference condition. An ecologist has a great responsibility in this situation.

The presented web of environmental relations between cenotypes (Figure 11.1) does not solve the previously stated problems on ecological concepts nor will it serve to solve specific water management questions, but it can be used as a practical tool which indicates the directions in which the answers can be found. Typology can be used to advantage in solving water management problems if it is considered together with the appropriate ecological concepts.

11.2 Application of the web of cenotypes

The aim of this study with respect to water management is to provide a basis for the development of a water quality policy. In Section 1.1 the historic development in the water quality policy of The Netherlands from tackling point sources of mainly organic pollution towards an ecologically inspired policy for the complete management of surface waters was described. The need for a typological basis for this ecologically inspired water management is mainly a result of the following two developments:

Firstly, for monitoring purposes water management authorities are trying to obtain suitable biological methods to evaluate the water quality. As most assessment systems are restricted to one or a few water types, there is a need to distinguish types. Secondly, water management authorities need reference communities for assessment (each water type needs its own assessment system and scale) and management (important and managable environmental conditions in relation to the reference community of each water type should be known) work.

The differences between physico-chemical and biological assessment have been discussed by Hellawell (1978), Illies (1980), and others. For example Heckman (1982) studied two ponds and concluded; "Although physical and chemical factors are basically the same, the ecological characteristics of the water body subjected to regular maintenance by the city authorities are fundamentally different from those in the undisturbed pond". In general, physical and chemical samples merely provide a transient picture of a water body, unless derived from an extensive array of automatic physico-chemical samplers. Biological samples can provide evidence of the recent environmental history; they show an integrated response to all the varying environmental parameters (Hellawall 1978).

Several different methods of biological water assessment were developed: methods based on indicator indices, on community indices, and on community composition (Warren 1971). Indicator indices are based on only a few taxa which are uniquely dependent, within relatively narrow tolerance limits, of specific environmental conditions, and thus they are coupled to the autecology of these taxa. So, indicator indices are related to only one complex of environmental parameters, but not to a water type. Community indices use the distribution of individuals of all taxa of the whole community; they describe certain community phenomena (e.g. diversity, eveness, redundancy). The approach based on community composition includes knowledge of the environmental requirements of all taxa composing the whole community, which is a synecological approach. If one is interested in only one important aspect of a water body, like organic material, an indicator index (e.g. the "Saprobien System" of Kolkwitz & Marsson 1908, Sladecek 1973) is sufficient. But if one is interested in the quality of the system the whole community composition must be studied. Each approach has its own advantages according to one's aims.

This study shows that each cenotype is a result of its specific environmental complex and that communities of different waters more or less overlap. It has become evident that it is less significant to classify waters within strict boundaries. So, in water management one should neither try to classify each water body within a type nor try to develop an assessment system for each recognized water type. Several tools may be needed to help solve the problems. Hynes (1960) concluded that it is a mistake to try to develop methods of assessment which are too formal; natural systems are not simple and straightforward, and a rigid classification system only leads to rigidity of thought and approach. The use of tables with species and numbers of individuals give the most complete information. Although this is true from a biological point of view, society still needs methods which are readily usable by nonbiologists.

For the assessment of the overall water quality one should preferably use the whole community composition. The presented typological approach offers a method that combines the advantages of using complete tables with a relatively simple diagram presentation. However, this too is only a tool to help solve pollution problems.

The need for reference communities in water management for the evaluation of the actual state of a water body has already been indicated in the foregoing section. Originally, a natural stream and certain stagnant waters (e.g. a moorland pool or an old meander cut off from a river) must have had characteristic taxa assemblages. Later, a number of artificial waters were created in our study area by human activity. So the natural state cannot be the evaluation criterion for all types of waters. The choice of the reference community for these artificial waters cannot be objective. However, there are several ecological aspects which can be helpful in making this choice (e.g. diversity, stability, maturity, scale). A major aspect of this choice will always be the comparison made with the communities present in other waters under the same major environmental conditions (master factors). Therefore, the altered (artificial) running waters must often be compared with the natural running streams, and the artificial stagnant waters with the oligotrophic moorland pools or the mesotrophic old meanders which were cut off from streams or rivers.

The management of waters always depends on the form of the human activity causing a change in the original (reference) situation and on the water quality one is trying to achieve. Therefore, water management should aim at reduction or reversal of changes in a water body with respect to the reference cenotype assigned to that water body. The presented regional ecological typology (Figure 10.6) offers a basis for establishing the reference community and for assigning this community to a water body. The groups of related cenotypes, described in Chapters 5 to 9, will be helpful for comparison.

In water management one uses easily recognizable characters as simple and practical criteria to distinguish water types (like our five main physico-geomorphological water types). Thereby only some of the characteristics of the ecological system are taken into account. This study shows the importance of combining abiotic and biotic parameters in ecological typology.

The most important rule in the application of the presented typology is to measure, think, plan and act by starting with the methods and thoughts which lead to the web of interrelations between the cenotypes. Each individual water is a result of the interactions between environmental factors. One must be aware of this uniqueness. After analysing the biological composition of a certain water body, firstly the master factors should be distinguished and then the other important environmental factors. All these factors are responsible for the actual state of the system. This can be determined by projecting the results (executing DCCA-run 1 whereby the new sites (samples) are added as passive sites) of the studied site on the web of cenotypes. Secondly, if desired, a direction of improvement should be chosen. Thirdly, one should distinguish those factors which are responsible for potential improvement and are manageable. Note that the factors presented in the web of cenotypes are a result of a descriptive study and therefore cannot be used as an absolute predictive tool (see Section 11.1); they merely indicate possibilities (an indicative tool).

Some potential water management activities will be indicated below to illustrate the application of typology. In the discussion (Chapter 10) it was concluded that, in most cases, natural conditions are absent. For example, in the sequence from cenotype H3, S1, S2, S6, R9, R3 to R11, the course of a river is followed from spring towards mouth. But most of these cenotypes are more or less changed with respect to the original situation and the original reference condition is also often unknown. An exception is found in the helocrene springs. The northeastern hill ridge was more acid and more oligotrophic than the southeastern ridge (Chapter 5). Cenotype H5, on the northeastern ridge, probably represents only a slightly impoverished reference condition. This also accounts for the occurrence of cenotype H3 on the southeastern ridge.

It is important to realize that each cenotype presented does not consist of a homogeneous set of sites. So each individual site can differ slightly from the described cenotype. The following lists of potential water management measurements illustrates one of the uses of the web of cenotypes (Section 11.1). For each potential measurement an example is given of how a cenotype thereby can change towards another cenotype. In general, changes in the physical and hydraulic conditions will be dominant in running waters.

Some specific examples of potential water management activities for running waters are:

(a) the restructuring or restoration of the profile by
- planting trees/shrubs on the banks and thereby also introducing natural shading (e.g. 40% of the sites of cenotype S2 are not shaded),
- removing the consolidation of the banks (e.g. 38% of the sites of cenotype R9 have a profile consolidation),
- allowing or creating micromeandering in a larger streambed (e.g. sites belonging to cenotype S7 can change towards cenotype S6);

(b) smoothing the discharge pattern by
- retention of rain water by reducing the number of drainage systems/trenches in the catchment area (e.g. sites belonging to cenotype S3 can change towards cenotype S1),

-reduction of the number of weirs in combination with a reduction of the size of the transverse profile or by creating a smaller transverse profile in a larger streambed (e.g. sites belonging to cenotype S4 can change towards cenotype S2);

(c) the reduction of eutrophication or organic enrichment by
 -stopping the input of organic wastes and toxic pollutants by tackling point sources of pollution by building purification plants (or improving their discharge through a greater removal of P and N compounds)
 or by tightening legal water quality standards on discharges
 or even forbidding certain discharges,
 or by also purifying the input by biological means (e.g. by using the filter function of a reedbed, swamp and/or marsh) (e.g. sites belonging to cenotype S5 can change towards cenotypes S2, S6, or S7),
 -reducing the use of fertilizers and pesticides in the catchment area (e.g. 21% of the sites belonging to cenotype S7 are not regulated but their fauna is impoverished, possibly due to pesticides, change can lead towards S6),
 -reducing surface runoff, for example by constructing a slight embankment along a wooded bank (e.g. sites belonging to cenotype S3 can change towards cenotype S1).

In stagnant waters, succession will lead, in general, towards a terrestrial stage. From an aquatic point of view an aquatic reference condition (e.g. a mature aquatic system) should be chosen. This will automatically ask for regular human interference. The succession stages are often comparable to situations resulting from certain human activities (e.g. cleaning, pollution)(Chapter 7). The consequences of both succession and human activity should be taken into account in the process of planning water quality goals. The following environmental measures can be derived from the presented results and considered in management:

(a) the reduction of eutrophication or organic enrichment by the possibilities already given for running waters (e.g. sites belonging to cenotypes R4 or R12 can change towards R7),
 -the reduction of the use of fertilizers or pesticides in the catchment area (e.g. sites belonging to cenotype D11 can change towards D3 and sites belonging to cenotype D3 can change towards D2A),
 -enlarging the filter function of the bank vegetation against direct spill of fertilizers or overland runoff (e.g. smaller-sized sites belonging to cenotype P8 can change towards P4),
 -the reduction of surface runoff by the construction of a slight embankment (e.g. sites belonging to cenotype D3 can change towards D2A),
 -reducing the necessity of inlet of polluted water by increasing the buffer capacity and thereby increasing the retention time of the original water (e.g. sites belonging to cenotype D3 can change towards D2A),
 -conservation of rainwater by decreasing the output (e.g. sites belonging to cenotype D2A can change towards D6), and
 -regulation of (polluted) water inlet (e.g. sites belonging to cenotype R4 can change towards R7).

(b) the restructuring of the profile by
- reducing the gradient of the slope and/or enlarging the littoral zone of a water body (e.g. 47% of the sites of cenotype P8 have a steep profile slope),
- creating an irregular slope (e.g. only 24% of the sites of cenotype P4 have an irregular slope),
- deepening the middle part (e.g. sites belonging to cenotype P8 can change towards P7), and
- making the length profile irregular (e.g. sites belonging to cenotype D3 can change towards P5).

(c) the reduction of water level fluctuations by
- reducing the amount of ground water extraction (e.g. sites belonging to cenotype P1 can change towards P3),
- reducing the drainage system (e.g. sites belonging to cenotype D8 can change towards D6 or P5), and
- removal of a wooded zone, especially for moorland pools (e.g. shaded sites belonging to cenotype P3 can change towards P2 (see Section 9.3)).

(d) improvement of the biological management by
- a balanced scheme of cleaning/dredging (in a catchment area once in four or five years per water body or undertaking cleaning/dredging only in a quarter of the area of the pond or lake per year) (e.g. sites belonging to cenotype D3 can change towards D2A), or
- removing of both the aquatic vegetation and the vegetation of the littoral zone once a year in autumn after the vegetation has, at least partially, died or removing this vegetation partly in spring and partly in autumn (e.g. sites belonging to cenotype D3 can change towards P5), in order to maintain the carrying capacity of the water course and
- no chemical treatment (e.g. smaller-sized sites belonging to cenotype P11 can change towards P8).

The examples of potential water management measurements given above illustrates one of the uses of the web of cenotypes. Other applications will be developed in the near future. But the examples above show the possibility of using the web of cenotypes as a basis for the development of policies, particularly for water management, nature management and nature conservation.

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Appendix 1 The typifying weight of the taxa per site group. The coleopterans, heteropterans, and mites indicated as genus refer to the life stage larvae or nymph.

Site group Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Dicranota bimaculata	11	7	0	12	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	4	1
Beraea maurus	11	12	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brillia modesta	12	12	1	8	3	2	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Dixa maculata	12	11	0	7	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elodes minuta	12	12	1	12	3	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0
Ptychoptera sp	12	1	0	12	0	1	8	1	0	0	0	0	0	1	1	0	1	1	0	0	1
Sericostoma personatum	12	1	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Stenophylax sp	11	12	0	11	0	7	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Thaumastoptera sp	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macropelopia sp	1	12	8	5	1	8	1	0	1	2	0	1	0	0	12	0	5	1	1	12	3
Micropsectra sp	3	12	1	12	1	1	1	1	0	0	0	0	0	0	1	0	1	1	2	5	1
Psychoda sp	1	11	0	4	2	11	2	2	0	0	0	0	0	0	0	7	1	7	2	1	1
Telmatoscopus sp	1	12	0	0	0	1	1	0	0	0	0	0	0	7	1	0	1	0	0	0	0
Limnophyes sp	1	12	8	1	0	1	2	0	12	1	5	2	1	1	1	0	1	1	1	0	1
Eriopterinae	1	11	0	1	1	10	10	0	0	0	0	0	1	0	1	0	1	2	2	0	0
Empididae	0	10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Krenopelopia sp	1	12	12	1	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nemurella pictetii	2	10	12	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parametriocnemus stylatus	1	12	0	10	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pedicia sp	1	12	12	7	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plectrocnemia conspersa	5	12	12	12	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sperchon squamosus	1	12	0	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Zavrelimyia sp	0	12	0	0	0	1	1	0	0	0	0	0	0	0	2	0	11	0	1	1	1
Chaetocladius sp	1	12	1	2	2	5	1	1	2	1	0	0	0	1	1	0	1	0	1	2	1
Dicranomyia sp	1	10	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Dixa dilatata	1	12	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ochthebius sp	0	10	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pericoma sp	0	10	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0
Hexatominae	5	12	1	12	1	9	9	11	1	1	1	1	1	0	1	1	2	1	1	5	2
Muscidae	0	1	10	0	0	0	1	0	0	0	0	0	0	0	0	0	0	10	0	0	0
Agabus guttatus	0	0	10	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Sialis fuliginosa	1	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyphotaelius pellucidus	1	1	0	10	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1
Nemoura cinerea	1	1	0	12	1	12	3	9	0	1	1	0	0	0	1	0	3	0	1	1	1
Polypedilum breviantennatum	2	0	0	12	11	1	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0
Prodiamesa olivacea	2	1	0	12	1	2	0	1	0	0	0	0	0	0	0	0	1	1	12	12	1
Rheocricotopus gr fuscipes	1	0	0	12	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
Rhyacodrilus coccineus	0	0	0	10	1	11	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1
Amphinemura standfussi/sulcicollis	1	0	0	10	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Chaetopteryx villosa	1	0	0	11	12	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
Polypedilum laetum agg	1	0	0	12	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sperchon glandulosus	0	1	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beraeodes minutus	0	0	0	0	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Eiseniella tetraedra	1	5	1	3	12	8	12	12	0	0	1	0	1	0	0	1	1	0	2	2	1
Hygrobates nigromaculatus	0	0	0	1	12	1	0	0	0	0	0	0	0	0	0	1	0	0	1	12	4
Lebertia inaequalis	0	0	0	1	12	2	0	0	0	0	0	0	0	0	0	0	1	0	0	12	11
Tabanidae	1	0	0	1	12	8	1	0	0	0	1	1	1	0	1	2	1	2	2	12	8
Tipula sp	3	5	3	8	12	5	8	3	12	0	5	5	1	0	1	0	1	6	1	1	2
Baetis sp	0	0	0	1	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lumbricidae	0	0	0	0	11	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1
Paratrichocladius rufiventris	0	0	0	0	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potamophylax sp	0	0	0	1	11	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Diplocladius cultriger	0	1	0	1	2	12	1	12	0	0	0	0	0	0	0	0	1	0	0	0	1
Nais elinguis	0	0	0	1	0	12	0	1	0	0	0	0	0	0	0	0	1	1	11	1	1
Limnephilus bipunctatus	0	1	0	0	0	1	10	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Limnephilus coenosus	1	1	2	0	0	1	12	0	1	0	0	1	0	0	0	0	1	0	0	0	0
Limnephilus sparsus	0	0	0	1	0	0	10	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Ephydridae	0	0	0	1	0	0	0	11	0	0	0	0	1	0	1	0	1	0	0	1	1
Natarsia sp	0	0	0	1	0	1	0	11	0	1	0	0	1	7	1	0	12	0	1	0	0
Scatophagidae	0	0	0	1	0	0	0	11	0	1	0	0	0	0	0	0	0	0	0	0	0
Enchytraeidae	1	3	5	1	1	3	3	3	12	1	8	1	1	0	0	0	1	1	2	1	1
Hydroporus memnonius	0	1	0	0	0	0	1	0	11	0	0	0	0	0	1	10	1	0	0	0	0
Limnephilus centralis	1	0	0	1	0	1	0	1	0	12	0	0	0	0	0	0	1	0	0	0	0
Polypedilum uncinatum	0	0	0	0	0	0	0	0	0	11	12	2	11	0	1	0	1	0	0	0	0
Limnephilus auricula	0	0	0	0	0	1	0	0	0	10	0	0	0	0	0	0	1	0	0	1	1
Paralimnophyes hydrophilus	0	0	0	0	0	1	0	0	0	12	1	1	2	12	1	0	1	0	0	1	0
Stylodrilus heringianus	0	0	0	0	0	1	0	0	0	11	0	0	0	0	0	0	1	1	1	0	1
Hydroporus pubescens	0	0	0	0	0	0	0	0	0	12	0	0	1	0	1	0	0	0	0	0	0
Limnephilus vittatus	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	1	0	1	0	0

Site group / Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Aedes sp	0	0	0	0	0	0	0	0	0	10	12	2	1	12	0	0	1	0	0	0	0
Argyroneta aquatica	0	0	0	1	0	1	0	0	0	0	12	12	6	1	1	0	0	0	0	1	1
Hydroporus umbrosus	0	0	0	0	0	0	0	0	0	0	11	10	10	12	4	0	1	0	0	0	0
Rhantus sp	0	0	0	0	0	2	0	0	0	0	12	1	11	1	11	0	0	0	0	1	0
Dytiscus sp	0	0	0	0	0	0	0	0	0	0	11	10	1	0	1	1	0	0	0	0	0
Berosus signaticollis	0	0	0	0	0	1	0	0	0	0	11	0	1	0	0	0	0	0	0	0	1
Culiseta sp	0	0	0	0	0	0	1	0	0	1	12	1	0	1	0	0	0	0	0	0	0
Berosus luridus	0	0	0	0	0	0	0	0	0	0	12	1	1	0	0	0	1	0	0	0	0
Psectrocladius sp	0	0	0	0	0	0	0	0	0	0	12	11	12	1	2	0	1	0	1	0	1
Bidessus unistriatus	0	0	0	0	0	0	0	0	0	0	12	1	10	0	0	0	0	0	0	0	0
Graphoderus sp	0	0	0	0	0	0	0	0	0	0	10	1	1	0	0	0	0	0	0	0	0
Hydroporus obscurus	0	0	0	0	0	0	0	0	0	0	12	1	0	0	1	0	0	0	0	0	0
Telmatopelopia nemorum	0	0	0	0	0	0	0	0	0	0	12	11	1	0	0	0	0	0	0	0	0
Brillia longifurca	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	1	0	0
Enochrus ochropterus	0	0	0	0	0	0	0	0	0	0	1	10	0	0	0	0	0	0	0	0	0
Holocentropus dubius	0	0	0	0	0	0	0	0	0	0	0	11	7	0	0	0	0	0	0	0	0
Nais communis	0	0	0	0	0	0	0	0	0	0	1	11	7	0	0	0	0	0	0	1	0
Holocentropus stagnalis	0	0	0	0	0	0	0	0	0	0	1	12	1	0	0	0	1	0	0	0	0
Cymatia coleoptrata	0	0	0	0	0	0	0	0	0	0	0	11	1	0	0	0	0	0	0	0	0
Gerris odontogaster	0	0	0	0	0	0	0	0	0	0	1	11	10	0	1	0	0	0	0	0	0
Leptophlebia vespertina	0	0	0	0	0	0	0	0	0	0	0	11	1	0	0	0	0	0	0	0	0
Cymatia bonsdorffi	0	0	0	0	0	0	0	0	0	0	0	12	1	0	0	0	0	0	0	0	0
Phalacrocera replicata	0	0	0	0	0	0	0	0	0	0	0	12	10	0	0	0	0	0	0	0	0
Agrypnia varia	0	0	0	0	0	0	0	0	0	0	0	11	10	0	0	0	0	0	0	0	0
Enallagma cyathigerum	0	0	0	0	0	0	0	0	0	0	0	12	12	0	0	0	0	0	0	0	0
Leucorrhinia sp	0	0	0	0	0	0	0	0	0	0	0	12	1	0	0	0	0	0	0	0	0
Libellula depressa	0	0	0	0	0	0	0	0	0	0	1	11	1	0	0	0	1	0	0	0	0
Libellula quadrimaculata	0	0	0	0	0	0	0	0	0	0	1	12	1	0	0	0	0	0	0	0	0
Ablabesmyia monilis/phatta	0	0	0	0	0	0	0	0	0	0	1	12	12	0	1	0	0	0	0	0	0
Corixa punctata	0	0	0	0	0	1	0	0	0	1	1	1	11	2	1	0	1	0	0	0	1
Gerris sp	0	0	0	0	0	0	0	0	0	0	0	1	11	0	1	0	0	0	0	0	0
Hydroporus erythrocephalus	0	0	0	0	0	0	0	0	0	1	8	5	12	7	1	0	1	0	1	0	0
Hygrotus inaequalis	0	0	0	0	0	0	0	0	0	0	1	1	12	1	2	0	1	0	0	0	1
Pyrrhosoma nymphula	0	0	0	0	0	1	0	0	0	0	0	1	10	0	0	0	0	0	1	0	2
Rhantus suturalis	0	0	0	0	0	0	0	0	0	0	0	0	10	0	4	0	0	0	0	0	1
Colymbetes fuscus	0	0	0	0	0	0	0	0	0	0	0	1	10	0	1	1	1	0	0	0	0
Hydroglyphus pusillus	0	0	0	0	0	0	0	0	0	0	0	0	11	0	10	1	1	0	0	0	0
Hesperocorixa sahlbergi	0	0	0	0	0	1	0	0	0	1	0	1	12	0	2	1	1	1	0	1	1
Sigara semistriata	0	0	0	0	0	1	0	0	0	0	1	1	12	0	1	1	1	0	0	0	1
Callicorixa praeusta	0	0	0	0	0	0	0	0	0	0	1	1	10	1	1	0	1	0	0	1	1
Enochrus affinis	0	0	0	0	0	0	0	0	0	0	1	1	10	0	1	0	0	0	0	0	0
Microvelia reticulata	0	0	0	0	0	0	0	0	0	0	0	1	10	1	0	0	0	0	0	0	0
Helochares punctatus	0	0	0	0	0	0	0	0	0	0	0	0	10	0	1	0	0	0	0	0	0
Chaoborus crystallinus	0	0	0	0	0	0	0	0	0	0	0	0	10	3	0	0	1	0	0	0	0
Chaoborus obscuripes	0	0	0	0	0	0	0	0	0	0	1	1	12	0	0	0	0	0	0	0	0
Dixella aestivalis	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
Notonecta obliqua	0	0	0	0	0	0	0	0	0	0	0	1	10	0	0	0	0	0	0	0	0
Notonecta viridis	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
Dixella amphibica	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0
Hydrobius fuscipes	1	0	0	1	1	1	0	0	0	1	0	0	1	11	12	12	3	0	0	1	1
Agabus sturmii	0	0	0	0	0	1	0	1	0	0	0	0	1	10	1	1	1	0	0	0	1
Hydroporus angustatus	0	0	0	1	0	0	0	0	0	0	1	0	0	10	0	0	0	0	0	0	0
Agabus undulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1	0	1	0	0	0	0
Haliplus heydeni	0	0	0	0	0	0	0	0	0	0	0	0	1	10	1	0	1	0	0	0	1
Agrypnia obsoleta	0	0	0	0	0	0	0	0	0	0	0	1	0	10	0	0	0	0	0	0	0
Ceriagrion tenellum	0	0	0	0	0	0	0	0	0	0	0	0	1	10	0	0	0	0	1	0	1
Acilius canaliculatus	0	0	0	0	0	0	0	0	0	0	0	1	1	10	1	0	0	0	0	0	1
Xenopelopia nigricans	0	0	0	0	0	1	0	0	0	0	0	1	0	12	1	0	5	1	0	0	1
Hebrus pusillus	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0
Limnephilus marmoratus	0	0	0	0	0	0	0	0	0	0	0	0	1	10	0	0	0	0	0	0	0
Arrenurus batillifer	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0
Gerris lacustris	0	0	0	0	1	1	0	0	0	0	0	1	4	0	11	1	0	0	0	0	1
Psectrotanypus varius	0	0	0	1	0	1	1	0	0	0	0	0	1	3	12	1	9	5	1	2	1
Agabus bipustulatus	0	1	0	0	0	1	1	0	0	1	0	0	1	0	11	12	1	2	1	0	0
Anacaena globulus	1	1	0	1	1	1	0	1	1	1	1	0	0	1	12	2	2	0	1	1	1
Hydroporus nigrita	0	0	2	0	0	1	0	0	1	1	0	0	0	0	10	1	10	0	0	0	0
Hydroporus planus	0	0	0	0	0	0	0	0	0	8	0	0	1	0	10	2	1	0	0	0	1
Helophorus brevipalpis	0	1	0	0	0	0	0	0	1	0	0	1	1	1	12	0	1	0	0	0	0
Acricotopus lucens	0	0	0	0	0	1	0	0	0	0	0	0	0	0	12	0	1	0	0	0	0
Helophorus minutus	0	0	0	0	0	0	0	0	0	2	0	0	1	0	12	0	1	0	0	0	0
Anisus leucostoma/spirorbis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	11	0	12	0	1	1	1
Helophorus aquaticus/grandis	0	1	0	0	0	1	0	0	1	0	0	1	1	1	12	1	1	0	0	0	0

Site group / Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Helophorus flavipes/obscurus	1	0	0	1	1	2	0	1	0	0	0	0	0	0	5	12	1	2	0	1	0
Agabus chalconatus	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	11	0	0	0	0	0
Agabus didymus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	10	1	10	1	1	1
Agabus paludosus	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	11	0	0	0	0	1
Aplexa hypnorum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	10	11	0	1	0	1
Gyrinus marinus	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	11	0	0	0	0	1
Hydroporus discretus	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	11	1	0	0	0	0
Laccobius biguttatus	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	10	1	0	0	0	1
Limnebius crinifer	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	11	0	0	0	0	1
Nepa cinerea	1	0	0	2	1	1	0	0	0	0	0	1	1	0	1	12	1	1	0	1	1
Velia caprai	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	10	0	1	1
Haliplus lineatocollis	0	0	0	1	1	1	0	0	0	1	0	0	1	3	8	5	11	1	0	1	2
Dina lineata	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	11	0	0	0	0
Haemopis sanguisuga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	10	0	0	0	0
Hydryphantes sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	1
Hydryphantes dispar/ruber	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	11	0	0	0	1
Paratendipes gr albimanus	0	0	0	1	2	1	0	0	0	0	0	0	0	0	1	2	1	12	1	12	7
Smittia sp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	10	0	0	0
Paratendipes gr nudisquama	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	10	0	1	0
Dicrotendipes gr notatus	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	10	4	1
Limnodrilus udekemianus	1	0	0	1	0	1	2	1	0	0	0	0	0	0	1	0	0	0	12	0	1
Phaenopsectra sp	0	0	0	1	5	2	0	0	0	0	0	0	0	0	1	1	0	2	12	11	2
Tubifex tubifex	1	1	0	3	3	9	3	1	0	1	0	0	1	0	1	1	9	1	12	5	2
Cladotanytarsus sp	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	12	2
Conchapelopia sp	1	3	1	5	3	6	6	1	0	0	0	0	0	0	2	1	1	1	9	12	12
Dicrotendipes gr lobiger	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	11	1
Forelia variegator	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	11	1
Limnesia koenikei	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	10	12
Mideopsis crassipes	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	1
Limnephilus lunatus	0	0	0	2	0	3	0	0	0	2	0	0	0	0	0	0	2	1	2	12	8
Paracladopelma nigritula	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	10	0
Athripsodes aterrimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	12
Aulodrilus pluriseta	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	0	1	0	1	3	12
Hydropsyche angustipennis	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	10
Haliplus flavicollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	10
Limnephilus decipiens	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	2	11
Potamothrix moldaviensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus rhombicus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
Haliplus ruficollis	0	0	0	0	0	0	0	0	0	0	1	0	1	1	2	0	1	1	0	0	1
Odontomyia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus fimbriatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Segmentina nitida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochrus melanocephalus	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0
Enochrus coarctatus	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Arrenurus globator	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Bathyomphalus contortus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1
Cyphon sp/Hydrocyphon sp/Scirtes sp	1	1	0	0	0	1	2	1	1	1	1	2	2	9	1	0	1	0	1	0	1
Gyraulus riparius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperocorixa sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hippeutis complanatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Holocentropus picicornis	1	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1
Notonecta glauca	0	0	0	0	0	1	0	0	0	0	0	1	9	1	0	0	1	0	0	0	1
Paroecetis struckii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona nodata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sciomyzidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Guttipelopia guttipennis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Hygrotus decoratus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1
Anisus vorticulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus integrator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochrus testaceus	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Limnesia connata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Helochares obscurus	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Midea orbiculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiphys ornatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Arrenurus bifidicodulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyptotendipes caulicola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus cuspidator	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0
Eylais tantilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrochara caraboides	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Porhydrus lineatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Succineidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Limnesia fulgida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Site group Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Lymnaea stagnalis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Planorbarius corneus	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	2	0	0	1	1
Viviparus contectus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Anopheles sp	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Armiger crista	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
Arrenurus buccinator	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0	2	1
Cataclysta lemnata	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0
Dero digitata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Noterus clavicornis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sigara lateralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Acilius sulcatus	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0
Laccobius minutus	0	0	0	0	0	1	0	0	0	0	0	0	1	1	2	1	1	0	0	1	1
Metriocnemus sp	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	1	0
Helochares lividus	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0
Arrenurus mulleri	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Oligotricha striata	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0
Piona carnea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodonta anatina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrnus flavidus	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
Erythromma najas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptocladopelma gr lateralis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Helius sp	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0
Ripistes parasita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sisyra sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tricholeiochiton fagesi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cyrnus insolutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyrinus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Arrenurus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Branchiura sowerbyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forelia liliacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mideopsis orbicularis	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1
Nais variabilis	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0
Piona pusilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Piscicola geometra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nais pardalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Tinodes waeneri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Glyptotendipes gr signatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nais barbata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Eylais sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forelia brevipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionicola aculeata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicrotendipes gr nervosus	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1
Dreissena polymorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psammoryctides barbatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Uncinais uncinata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unio pictorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Parachironomus sp Kampen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydropsyche contubernalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptochironomus sp	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	1	1	2	9	5
Limnodrilus claparedeianus	0	0	0	1	5	1	0	0	0	0	0	0	0	0	1	0	2	0	1	9	2
Limnodrilus profundicola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	1	1
Lithoglyphus naticoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gammarus tigrinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microchironomus tener	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Einfeldia gr insolita	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1
Potamopyrgus jenkinsi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyraulus laevis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Assiminea grayana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fleuria lacustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lipiniella arenicola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anabolia nervosa	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	5	8
Calopteryx splendens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cyrnus trimaculatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Laccophilus hyalinus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1
Micronecta sp	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Thienemanniella sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
Nanocladius sp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Arrenurus albator	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Arrenurus biscissus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus knauthei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caenis luctuosa	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Centroptilum luteolum	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

Site group Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Chaoborus flavicans	0	0	0	0	0	0	0	0	0	1	0	0	5	1	0	0	1	0	0	0	1
Cloeon simile	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Demicryptochironomus vulneratus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1
Gerris argentatus	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Hydrodroma despiciens	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1	0	0	0	0	0	1
Hygrobates trigonicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesovelia furcata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Molanna angustata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Mystacides sp	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Stictochironomus sp	0	0	0	1	1	7	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0
Dicrotendipes gr tritomus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Ranatra linearis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tribelos intextus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pseudochironomus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona variabilis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Notonecta sp	0	0	0	0	0	0	0	0	0	0	0	1	1	0	5	1	0	0	0	0	0
Tanypus kraatzi	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0
Spercheus emarginatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Anatopynia plumipes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Dendrocoelum lacteum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Dero dorsalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Theromyzon tessulatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Hesperocorixa linnei	0	0	0	0	0	0	0	0	0	0	0	1	5	0	1	1	1	0	0	0	1
Agrypnia pagetana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haemonais waldvogeli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemiclepsis marginata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sigara distincta/falleni/longipalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydrachna globosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocoris cimicoides	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	1
Laccophilus sp	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Limnesia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Oecetis lacustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Piona conglobata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Polypedilum gr sordens	0	0	0	1	0	1	0	0	0	0	0	1	6	0	0	0	0	0	0	0	1
Enochrus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cryptocladopelma gr laccophila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oecetis furva	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Parachironomus gr arcuatis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1
Eylais hamata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ecnomus tenellus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Haliplus fluviatilis	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2
Phryganea bipunctata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1
Eylais extendens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Limnesia maculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1
Limnesia undulata	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
Oulimnius tuberculatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Pionopsis lutescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Parachironomus gr vitiosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acercinae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0
Gammarus pulex	9	5	1	9	9	1	3	1	0	0	0	0	0	0	0	1	1	1	1	1	1
Agabus/Ilybius sp	0	1	1	1	3	3	1	6	1	6	9	1	3	5	9	1	3	1	1	1	1
Endochironomus tendens	0	0	0	0	0	0	0	0	0	0	0	3	9	1	0	0	1	0	1	0	1
Corynoneura sp	1	1	5	1	0	1	0	0	0	0	1	1	9	0	1	0	1	0	0	1	1
Proasellus meridianus	1	1	0	6	1	1	0	1	0	0	0	0	0	9	1	1	1	1	1	3	6
Anacaena limbata	0	1	0	1	1	1	0	0	0	1	1	1	1	0	8	2	5	0	0	0	1
Hydroporus palustris	0	0	0	0	0	1	0	0	0	1	0	0	1	6	8	5	8	1	0	1	1
Dugesia lugubris/polychroa	1	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	9	0	0	0	1
Polycelis sp	0	0	0	1	1	1	2	0	0	1	0	1	2	0	1	0	9	1	1	0	1
Caenis horaria	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	3	9
Hygrobates longipalpis	0	0	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	9
Sialis lutaria	0	0	0	1	0	1	1	0	0	0	0	1	1	1	2	1	1	1	0	2	9
Sigara distincta	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	7
Potamothrix hammoniensis	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Helochares sp	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
Anisus vortex	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1
Endochironomus gr dispar	0	1	0	0	0	0	0	0	0	0	0	1	2	1	0	0	1	1	0	0	1
Noterus crassicornis	0	0	0	0	0	0	0	0	0	0	0	2	2	3	0	0	1	0	0	0	0
Stagnicola palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1
Valvata cristata	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Planorbis carinatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Aeshna sp	0	0	0	0	1	0	0	0	0	0	0	2	2	0	1	1	1	1	0	1	1
Bithynia leachi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1

Site group Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Physa fontinalis	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1
Planorbis planorbis	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	0	0	1
Sphaerium sp	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	6
Acroloxus lacustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Coenagrion sp	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	1	0	0	1	1
Erpobdella testacea	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1
Unionicola crassipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Piona alpicola/coccinea	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1
Psammoryctides albicola	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Proasellus coxalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laccobius sp	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0
Tanytarsus sp	0	1	1	0	0	1	0	0	2	1	1	3	2	0	3	1	1	1	1	6	3
Caenis robusta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Stylaria lacustris	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1
Paramerina cingulata	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0
Tanypus vilipennis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigara falleni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Sigara striata	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Arrenurus crassicaudatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Endochironomus albipennis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
Graptodytes pictus	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	5
Ophidonais serpentina	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1
Polypedilum gr bicrenatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Microtendipes sp	6	1	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1
Pisidium sp	1	6	0	1	1	1	6	1	0	0	0	0	0	1	6	1	6	0	1	3	3
Eukiefferiella sp	1	1	0	4	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Erpobdella octoculata	1	0	0	1	5	1	0	0	0	0	0	0	1	1	1	1	1	0	1	3	3
Limnodrilus hoffmeisteri	0	1	0	1	6	6	1	1	0	0	0	0	0	1	1	1	3	1	3	6	3
Lumbriculus variegatus	1	1	1	3	1	3	6	6	1	6	1	1	3	3	1	1	6	0	1	3	1
Hydroporinae	0	1	0	0	0	1	2	0	5	2	5	1	2	1	3	0	1	0	0	1	1
Ceratopogonidae	1	1	1	1	1	1	1	1	1	1	6	6	6	1	1	1	3	1	1	3	1
Chironomus sp	1	1	0	1	1	1	1	1	1	1	1	3	6	1	6	1	1	3	6	1	1
Cloeon dipterum	0	0	0	1	0	1	0	0	0	0	1	1	6	1	1	1	1	1	1	1	1
Glyptotendipes sp	1	0	0	1	0	1	0	0	0	0	1	1	6	0	1	0	1	0	1	1	1
Polypedilum gr nubeculosum	1	1	0	1	1	1	0	0	0	1	0	1	6	1	1	1	1	1	1	1	1
Procladius sp	0	0	0	1	1	1	0	0	0	1	1	3	6	1	1	1	1	1	1	6	3
Radix peregra	1	1	0	1	1	1	1	1	0	1	0	0	0	0	1	3	6	1	1	1	1
Tubificidae juv. without hair setae	0	1	0	1	1	3	1	1	0	0	1	1	1	0	1	1	6	1	1	3	3
Tubificidae juv. with hair setae	1	1	1	1	3	3	1	1	0	1	0	0	1	1	1	3	3	1	6	6	3
Paratanytarsus sp	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	6	2
Glossiphonia complanata	1	1	0	2	1	1	0	0	0	0	0	0	1	0	1	2	1	1	0	3	6
Valvata piscinalis	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1
Glossiphonia heteroclita	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Hyphydrus ovatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1
Asellus aquaticus	1	1	0	1	1	1	1	0	0	1	0	0	1	1	1	1	1	1	1	1	3
Bithynia tentaculata	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Clinotanypus nervosus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	2
Haliplus sp	0	0	0	1	1	1	0	0	0	1	0	0	1	1	3	1	1	1	1	1	2
Laccophilus minutus	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	0	0	0	1
Gyraulus albus	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	1
Helobdella stagnalis	1	0	0	1	1	1	1	0	0	0	1	1	1	1	1	0	1	1	1	1	1
Plea minutissima	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ablabesmyia longistyla	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1
Ischnura sp	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
Oulimnius sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Cricotopus sp	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	0	1	0	3	1	1
Peloscolex ferox	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Valvata macrostoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Neumania limosa	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2
Arrenurus sinuator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Triaenodes bicolor	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Radix auricularia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus immaculatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0
Hygrotus versicolor	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Proasellus sp	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	2	0	1	2	2
Odagmia ornata	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Notidobia ciliaris	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1
Dugesia gonocephala	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Halesus radiatus/digitatus	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lebertia glabra	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neoascia sp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Silo sp	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Site group Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Simulium morsitans	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sperchon setiger	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adicella sp	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rheocricotopus fuscipes	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simulium sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stagnicola glabra	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
Beraea pullata	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Galba truncatula	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0
Hydroporus gyllenhalii	0	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0
Apatania muliebris	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hydroporus longulus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lebertia duricoria	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paraphaenocladius pseudirritus agg	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rheocricotopus atripes	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sperchon sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Heterotanytarsus apicalis	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudorthocladius sp	0	0	10	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beris sp	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Dolichopodidae	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Elmis aenae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eusimulium aureum	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Limnephilus extricatus	0	0	0	1	1	1	1	1	0	1	0	0	0	0	1	0	0	0	0	1	1
Paraponyx sp	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Rheotanytarsus sp	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Coelostoma orbiculare	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
Limnebius truncatellus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Velia sp	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Apsectrotanypus trifascipennis	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
Crunoecia irrorata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dixa nebulosa	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enoicyla pusilla	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eusimulium angustipes	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Eusimulium latipes	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
Hydraena sp	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydraena riparia	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ironoquia dubia	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Lebertia sp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lype reducta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Osmylus fulvicephalus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Physa acuta	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Planaria torva	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prionocera sp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhagionidae	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Thyas pachystoma	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dryopidae	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0	1	1	1
Ephemera vulgata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephrotoma sp	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Eisena foetida	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sargus sp	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Orectochilus villosus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Platambus maculatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anacaena sp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
Sigara nigrolineata	0	0	0	0	0	1	0	0	0	0	0	1	1	0	2	1	1	0	0	1	1
Einfeldia gr pagana	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Eusimulium cryophilum	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Gerris najas	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heleniella sp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Helophorus sp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Heterotrissocladius marcidus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus incognitus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hydroporus melanarius	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Leptophlebia marginata	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Oulimnius troglodytes	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pachygaster sp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Paracladopelma laminata agg	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Rheocricotopus chalybeatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Zonitidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Camptocladius stercorarius	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copelatus sp	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tachytrechus sp	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyas barbigera	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Site group Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Parakiefferiela sp	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Agabus labiatus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Ochthebius minimus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0
Agabus uliginosus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Limnephilus flavicornis	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Coelambus impressopunctatus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	0	0
Laccobius bipunctatus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1
Lestes sponsa	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Lestes viridis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Monopelopia tenuicalcar	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0
Sympetrum flaveolum	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Hydroporus tristis	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0
Graphoderus zonatus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Rhantus suturellus	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Pogonocladius consobrinus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Copelatus haemorrhoidalis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Trichostegia minor	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Dolichopeza sp	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lestes dryas	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Arrenurus bicuspidator	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Rhantus exsoletus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1
Oecetis ochracea	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Rhantus latitans	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
Corixa dentipes	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Graphoderus cinereus	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Cymatia sp	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Notonecta lutea	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Arrenurus neumani	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Hesperocorixa castanea	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Sigara scotti	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Sympetrum danae	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Arrenurus stecki	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Arrenurus vietsi	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Limnephilus subcentralis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Paralimnophyes sp	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Haliplus confinis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Orthetrum cancellatum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Culex sp	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0	0	0	0
Dytiscus marginalis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0
Somatochlora metallica	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1
Ilybius quadriguttatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Hygrobia hermanni	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Nymphula nymphaeata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Tiphys scaurus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Acilius sp	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Arrenurus maculator	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Acentria nivea	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Anax imperator	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cybister lateralimarginalis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Chaoborus pallidus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ilybius aenescens	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Arrenurus affinis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Arrenurus compactus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Berosus sp	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Dytiscus circumflexus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hydrochus angustatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Notonecta maculata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sigara limitata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sigara semistriata/nigrolineata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Normandia nitens	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Panisopsis vigilans	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pionacercus norvegicus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Trissocladius brevipalpis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
Hydroporus scalesianus	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0
Oxyethira sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Gerris gibbifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
Ilybius fuliginosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
Hydryphantes planus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Hydroporus dorsalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Arrenurus latus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydaticus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydrochus elongatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Site group / Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Hydrochoreutes krameri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Polycentropus irroratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Eristalis sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydrometra sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Colymbetes sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ilybius ater	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dryops auriculatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Hydroporus rufifrons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydroporus striola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Gyrinus substriatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ochthebius pusillus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Agabus nebulosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Haliplus lineolatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Helophorus granularis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Limnebius truncatulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ilyodrilus templetoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	2
Limnochares aquatica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Lumbriculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
Peltodytes caesus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Slavina appendiculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Limnephilus affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Zavrelia pentatoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Oplodontha viridula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Gerris thoracicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Haliplus laminatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Helophorus avernicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Parathyas thoracata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Haliplus fulvus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Dixella autumnalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Coquillettidia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Agabus affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hydraena britteni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Nais pseudoptusa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Laccobius striatulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Odontomesa fulva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Athripsodes cinereus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Hygrobates fluviatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Neumania deltoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Potthastia longimanis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hydrobaenus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tinodes maculicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tiphys torris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hydrochus carinatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tubifex ignotus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Agabus conspersus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Agraylea multipunctata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chaetogaster diaphanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Dugesia tigrina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Haliplus wehnkei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hygrobates sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lebertia insignis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Potamonectes depressus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Stempellina sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Unionicola minor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Kiefferulus tendipediformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Limnebius papposus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Neumania vernalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Limnebius sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Haementeria costata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lebertia bracteata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gomphus vulgatissimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Heptagenia flava	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tinodes assimilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Wettina podagrica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hydropsyche exocellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Oxycera sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Siphlonurus armatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Orchestia cavimana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ancylus fluviatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus cylindratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus securiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baetis buceratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Site group Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Baetis fuscatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caenis pseudorivulorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrnus crenaticornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dero nivea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dero obtusa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gammarus roeselii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnesia pseudundulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neureclepsis bimaculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neumania sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phryganea grandis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona longipalpis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona rotundoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudanodonta complanata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Roederiodes juncta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stictotarsus duodecimpustulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sympecma sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syrocax sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionicola gracilipalpis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrobius sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trissopelopia longimanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potamothrix heuscheri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus inexploratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myxas glutinosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harnischia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanypus punctipennis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potamothrix bavaricus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eylais koenikei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hebrus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrometra stagnorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peloscolex speciosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plectrocnemia geniculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protzia eximia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boophtora erythrocephala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hygrobates longiporus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus octagonus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gomphidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachypoda versicolor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zavreliella marmorata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus mediorotundatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microvelia umbricola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhantus grapii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydaticus seminiger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna leegei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachytron pratense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochrus bicolor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lauterborniella agrayloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnebius atomus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxygastra curtisii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stratiomys sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus truncatellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viviparus viviparus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus politus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrovatus cuspidatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona obturbans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrometra gracilenta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus virens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus schreuderi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilus piceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus stigma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neumania spinipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orthotrichia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiphys sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilybius fenestratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona neumani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sympetrum sanguineum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxus ovalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna goldfeldi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corixa sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cordulia aenea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allolophora sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erythromma viridulum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus obliquus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Site group Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Tetanocera sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudosmittia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona clavicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetarthria seminulum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erpobdella nigricollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camptochironomus tentans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus binotatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiphys pistillifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus leuckarti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neumania imitata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sympetrum striolatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus cuspidifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulodrilus limnobius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agraylea sexmaculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus pugionifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelambus nigrolineatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colymbetes paykulli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochrus quadripunctatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna skorikowi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus elongatulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pristina menoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhantus frontalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigara fossarum/scotti nymphe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiphys bullatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus tubulator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dryops luridus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micronecta minutissima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nais simplex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Demeijerea rufipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenochironomus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona paucipora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus claviger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus forpicatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eylais discreta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxus oblongus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionicola intermedia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptotendipes sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cordulegaster sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atyaephyra desmarestii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potamothrix bedoti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nais bretscheri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodonta cygnea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceraclea sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetogaster diastrophus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trocheta bykowskii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parachironomus gr longiforceps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rheocricotopus effusus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synorthocladius semivirens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xenochironomus xenolabis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionicola sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna processifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eclipidrilus lacustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microchironomus deribae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracorixa concinna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paranais frici	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paranais litoralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubifex newaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Procloeon bifidum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micronecta meriodionalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anacaena bipustulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heptagenia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnebius nitidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pionacercus vatrax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vejdovskyella intermedia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus perforatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orconectus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forelia longipalpis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epitheca bimaculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pagastiella orophila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus tricuspidator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrochoreutes sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptocerus tineiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Site group / Taxon/	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Forelia curvipalpis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna cruenta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Noterus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marstoniopsis scholtzi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna conjecta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus variegatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus falciger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forelia koenikei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus fuscicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cybister sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plea sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigara fossarum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atractides ovalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microvelia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atractides sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Endochironomus sp Ubbergen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionicola figuralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Criorhina berberina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxus nodigerus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notonecta reuteri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dictenidia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyas palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus nigriceps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus bruzelii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus tetracyphus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eylais infundibulifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Frontipoda musculus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oecetis testacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peltodytes sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myathropa florea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psammoryctides moravicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionicola inusitata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atractides nodipalpis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracymus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus varius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyopsis cancellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forelia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetogaster cristallinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gomphus pulchellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unio tumidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydropsyche pellucidula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus nodosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydraena testacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mideopsis sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oligostomis reticulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Setodes sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelostoma sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platycnemis pennipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracladius conversus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona dispersa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stempellinella sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laccobius atrocephalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pristina amphibiotica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sympetrum vulgatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachycercus harrisella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnoporus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidostomatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Theodoxus fluviatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paraleptophlebia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna globosa/uniscutula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Site group Taxon/	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Dicranota bimaculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beraea maurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brillia modesta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dixa maculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elodes minuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptychoptera sp	0	1	1	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Sericostoma personatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenophylax sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thaumastoptera sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macropelopia sp	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Micropsectra sp	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	0
Psychoda sp	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0
Telmatoscopus sp	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnophyes sp	0	1	1	1	1	1	1	3	1	1	1	0	1	1	0	1	1	2	1	0	0
Eriopterinae	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	12	12
Empididae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0
Krenopelopia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemurella pictetii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parametriocnemus stylatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pedicia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plectrocnemia conspersa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sperchon squamosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zavrelimyia sp	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Chaetocladius sp	0	1	0	0	1	0	0	0	12	0	3	0	0	1	0	0	1	0	1	0	0
Dicranomyia sp	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Dixa dilatata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ochthebius sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pericoma sp	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Hexatominae	0	1	0	1	1	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0
Muscidae	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0
Agabus guttatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sialis fuliginosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyphotaelius pellucidus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemoura cinerea	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0
Polypedilum breviantennatum	0	1	0	0	1	0	0	0	1	1	4	0	0	0	0	0	1	0	1	0	0
Prodiamesa olivacea	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Rheocricotopus gr fuscipes	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhyacodrilus coccineus	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0
Amphinemura standfussi/sulcicollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetopteryx villosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polypedilum laetum agg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sperchon glandulosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beraeodes minutus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eiseniella tetraedra	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	0	0
Hygrobates nigromaculatus	0	1	0	0	0	1	0	12	1	5	0	0	0	0	1	0	1	1	1	0	0
Lebertia inaequalis	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0
Tabanidae	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	0	1	0	0
Tipula sp	0	1	1	0	1	1	0	0	1	1	1	1	1	0	0	1	1	1	1	5	0
Baetis sp	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Lumbricidae	0	0	1	0	1	0	1	2	0	0	1	0	0	0	1	1	1	0	1	0	0
Paratrichocladius rufiventris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potamophylax sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplocladius cultriger	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Nais elinguis	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	1	0	0
Limnephilus bipunctatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus coenosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus sparsus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ephydridae	0	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
Natarsia sp	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Scatophagidae	0	0	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0
Enchytraeidae	1	1	0	0	1	1	0	1	1	1	1	1	1	0	1	0	1	1	1	0	0
Hydroporus memnonius	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus centralis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polypedilum uncinatum	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0
Limnephilus auricula	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paralimnophyes hydrophilus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stylodrilus heringianus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Hydroporus pubescens	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus vittatus	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Aedes sp	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argyroneta aquatica	1	1	3	6	1	3	1	0	0	0	1	1	1	3	1	1	1	1	1	0	0
Hydroporus umbrosus	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0

Site group Taxon/	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Rhantus sp	0	1	0	1	1	1	0	0	0	0	1	0	1	1	0	1	0	0	1	0	0
Dytiscus sp	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
Berosus signaticollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Culiseta sp	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Berosus luridus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psectrocladius sp	0	1	2	1	1	1	1	1	1	1	1	5	1	2	1	1	1	0	1	0	0
Bidessus unistriatus	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Graphoderus sp	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Hydroporus obscurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Telmatopelopia nemorum	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Brillia longifurca	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochrus ochropterus	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Holocentropus dubius	0	1	0	1	1	0	11	0	0	0	1	0	0	10	0	1	0	1	1	0	0
Nais communis	0	1	1	0	1	1	1	1	1	0	1	2	1	1	0	0	1	0	1	0	0
Holocentropus stagnalis	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cymatia coleoptrata	0	0	0	1	1	0	2	0	0	0	0	1	2	7	1	1	1	0	1	0	0
Gerris odontogaster	0	0	0	0	1	1	1	0	0	0	0	1	1	4	2	4	0	2	1	0	0
Leptophlebia vespertina	0	1	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0
Cymatia bonsdorffi	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalacrocera replicata	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Agrypnia varia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enallagma cyathigerum	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Leucorrhinia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Libellula depressa	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Libellula quadrimaculata	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ablabesmyia monilis/phatta	0	1	0	1	1	1	1	0	0	0	1	5	1	1	1	0	0	1	1	0	0
Corixa punctata	0	1	1	0	1	12	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0
Gerris sp	0	1	0	0	1	1	2	0	0	0	1	1	1	1	1	12	0	7	1	0	0
Hydroporus erythrocephalus	0	1	2	5	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hygrotus inaequalis	0	1	8	12	5	12	1	0	0	0	1	1	1	1	1	1	1	0	1	0	0
Pyrrhosoma nymphula	0	1	0	0	1	10	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Rhantus suturalis	0	1	0	0	1	12	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Colymbetes fuscus	0	1	0	0	1	10	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Hydroglyphus pusillus	0	0	0	0	1	10	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hesperocorixa sahlbergi	0	1	2	1	2	11	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0
Sigara semistriata	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
Callicorixa praeusta	0	1	1	0	1	11	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Enochrus affinis	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0
Microvelia reticulata	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	2	0	0	1	0	0
Helochares punctatus	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	1	1	0	0	0	0
Chaoborus crystallinus	0	0	1	1	1	12	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0
Chaoborus obscuripes	0	0	1	1	1	10	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Dixella aestivalis	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notonecta obliqua	0	0	1	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notonecta viridis	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dixella amphibica	0	1	10	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Hydrobius fuscipes	0	0	2	2	2	12	0	0	0	0	0	0	2	1	0	0	1	0	1	0	0
Agabus sturmii	0	0	10	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus angustatus	0	0	1	10	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Agabus undulatus	0	1	1	7	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Haliplus heydeni	0	1	1	0	1	10	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Agrypnia obsoleta	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0
Ceriagrion tenellum	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acilius canaliculatus	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Xenopelopia nigricans	0	1	9	5	5	12	1	0	0	0	0	0	1	1	1	1	1	0	1	0	0
Hebrus pusillus	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Limnephilus marmoratus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Arrenurus batillifer	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Gerris lacustris	0	1	1	0	1	1	1	0	0	0	0	1	1	1	1	1	0	1	1	0	0
Psectrotanypus varius	0	1	1	1	3	9	0	0	0	0	1	0	1	2	1	1	1	0	1	0	0
Agabus bipustulatus	0	1	0	0	1	4	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Anacaena globulus	0	0	1	0	1	0	0	0	0	0	2	0	1	1	0	0	0	1	1	0	0
Hydroporus nigrita	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus planus	0	0	0	0	1	11	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Helophorus brevipalpis	0	1	1	1	2	1	0	0	0	0	1	0	1	1	1	1	1	1	1	0	0
Acricotopus lucens	0	1	1	1	1	1	0	0	0	0	0	1	1	5	1	1	0	0	1	0	0
Helophorus minutus	0	1	11	1	1	4	0	0	0	0	1	1	1	1	1	1	1	0	1	0	0
Anisus leucostoma/spirorbis	0	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Helophorus aquaticus/grandis	1	1	1	1	2	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0
Helophorus flavipes/obscurus	0	1	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Agabus chalconatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agabus didymus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Site group Taxon/	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Agabus paludosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aplexa hypnorum	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Gyrinus marinus	0	1	0	0	0	0	7	0	0	0	0	0	1	1	1	1	1	0	1	0	0
Hydroporus discretus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laccobius biguttatus	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Limnebius crinifer	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Nepa cinerea	0	1	1	1	2	2	1	0	0	0	0	2	1	1	0	2	1	1	1	0	0
Velia caprai	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Haliplus lineatocollis	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0
Dina lineata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haemopis sanguisuga	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hydryphantes sp	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydryphantes dispar/ruber	0	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Paratendipes gr albimanus	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Smittia sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paratendipes gr nudisquama	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Dicrotendipes gr notatus	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	0	0	1	1	0	0
Limnodrilus udekemianus	1	4	0	0	1	0	0	0	1	1	0	0	1	0	1	1	1	0	1	0	12
Phaenopsectra sp	0	1	0	2	1	1	1	2	1	1	5	1	1	1	1	1	1	1	1	0	0
Tubifex tubifex	1	3	1	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0	1
Cladotanytarsus sp	1	1	0	0	1	0	1	1	1	12	8	5	1	1	1	1	5	2	5	0	0
Conchapelopia sp	0	3	0	0	1	0	0	0	1	0	3	0	0	0	0	1	1	1	1	0	0
Dicrotendipes gr lobiger	0	1	0	4	1	1	1	2	0	0	1	1	1	7	1	0	0	0	1	0	0
Forelia variegator	0	1	0	0	0	0	0	0	0	12	0	0	0	0	0	0	1	0	1	0	0
Limnesia koenikei	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Mideopsis crassipes	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus lunatus	0	2	0	0	1	1	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0
Paracladopelma nigritula	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Athripsodes aterrimus	0	1	1	0	2	1	1	0	0	0	1	2	1	2	1	1	1	0	2	0	0
Aulodrilus pluriseta	0	2	0	0	2	1	1	0	0	1	1	0	1	1	1	0	1	2	1	0	0
Hydropsyche angustipennis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Haliplus flavicollis	0	1	10	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Limnephilus decipiens	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0
Potamothrix moldaviensis	11	1	0	0	0	0	0	12	12	12	11	1	1	0	1	1	1	12	1	0	0
Limnephilus rhombicus	0	10	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1	0	0	0
Haliplus ruficollis	0	1	12	2	6	2	1	0	0	1	1	0	1	5	1	2	1	1	2	0	0
Odontomyia sp	1	1	10	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0
Arrenurus fimbriatus	0	1	10	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0
Segmentina nitida	0	0	12	12	1	1	1	0	0	1	0	0	1	1	1	0	1	1	1	0	0
Enochrus melanocephalus	0	0	10	1	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Enochrus coarctatus	0	1	10	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Arrenurus globator	0	1	2	12	9	3	1	0	0	0	0	2	2	1	0	8	1	1	6	0	0
Bathyomphalus contortus	0	1	9	12	12	1	1	0	0	1	0	0	3	3	1	1	1	1	1	0	0
Cyphon sp/Hydrocyphon sp/Scirtes sp	0	1	6	12	1	2	0	0	0	0	1	1	5	1	1	1	1	0	1	0	0
Gyraulus riparius	0	0	0	10	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0
Hesperocorixa sp	0	1	0	11	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Hippeutis complanatus	0	1	3	11	3	1	1	0	0	1	0	1	3	6	1	1	1	0	1	0	0
Holocentropus picicornis	0	1	0	12	1	1	2	0	0	1	1	0	1	12	1	1	1	0	1	0	0
Notonecta glauca	0	1	2	12	2	12	1	0	0	1	0	0	2	5	1	2	1	1	1	0	0
Paroecetis struckii	0	1	0	10	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Piona nodata	0	1	1	10	1	1	0	2	0	0	0	0	1	1	0	1	1	1	1	0	0
Sciomyzidae	0	0	2	11	1	1	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0
Guttipelopia guttipennis	0	1	0	10	1	0	1	0	0	0	1	0	1	1	1	0	1	0	1	0	0
Hygrotus decoratus	0	0	1	11	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Anisus vorticulus	0	0	0	10	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Arrenurus integrator	0	0	1	11	1	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0
Enochrus testaceus	0	0	4	12	1	1	1	0	0	0	0	0	2	1	1	1	1	0	1	0	0
Limnesia connata	0	1	2	11	1	0	0	0	0	1	0	0	7	1	1	1	1	0	1	0	0
Helochares obscurus	0	1	1	10	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hidea orbiculata	0	0	1	10	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Tiphys ornatus	0	0	1	12	1	1	1	0	0	0	0	0	4	1	1	0	1	0	1	0	0
Arrenurus bifidicodulus	0	0	1	11	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0
Glyptotendipes caulicola	0	0	0	10	0	1	1	0	0	0	0	0	1	1	1	0	1	4	0	0	0
Arrenurus cuspidator	0	0	1	10	1	10	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Eylais tantilla	0	0	1	11	1	0	1	0	0	0	0	0	12	0	0	0	1	0	1	0	0
Hydrochara caraboides	0	0	1	10	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Porhydrus lineatus	0	0	1	10	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Succineidae	0	1	1	11	1	0	0	0	1	1	0	0	1	1	1	1	1	0	1	0	0
Limnesia fulgida	0	1	1	0	10	1	1	0	0	0	0	1	1	1	0	0	1	0	1	0	0
Lymnaea stagnalis	0	1	1	3	12	1	1	0	0	0	1	1	1	2	1	1	1	1	2	0	0
Planorbarius corneus	0	1	9	5	12	1	1	0	0	1	0	0	1	3	1	1	1	0	1	0	0
Viviparus contectus	0	1	1	1	10	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0

Site group Taxon/	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Anopheles sp	0	1	0	0	1	10	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0
Armiger crista	0	1	1	0	1	12	1	0	0	1	0	0	1	1	0	1	1	1	1	0	0
Arrenurus buccinator	0	1	1	4	1	10	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Cataclysta lemnata	0	1	2	1	2	12	1	0	0	0	0	0	1	1	1	1	1	0	1	0	0
Dero digitata	0	1	1	0	1	12	1	0	1	1	0	1	1	2	5	1	1	1	1	0	0
Noterus clavicornis	0	1	0	0	1	12	2	0	0	5	1	1	1	1	1	1	1	2	2	0	0
Sigara lateralis	0	1	0	0	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acilius sulcatus	0	1	0	0	0	10	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Laccobius minutus	0	1	1	0	1	11	0	1	0	0	0	1	1	1	1	1	1	1	1	0	0
Metriocnemus sp	0	1	2	0	1	12	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0
Helochares lividus	0	0	0	0	1	10	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0
Arrenurus mulleri	0	0	0	0	1	10	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Oligotricha striata	0	0	0	0	0	10	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Piona carnea	0	0	1	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodonta anatina	0	0	0	0	0	0	10	0	1	1	10	0	1	0	0	1	0	1	1	0	0
Cyrnus flavidus	0	2	0	0	0	1	12	1	1	1	2	9	1	2	1	8	1	12	1	0	0
Erythromma najas	0	1	0	0	1	0	12	1	0	0	1	12	1	8	2	1	1	1	1	0	0
Cryptocladopelma gr lateralis	1	1	0	0	1	0	11	0	0	0	0	1	1	2	1	1	1	1	1	0	0
Helius sp	0	1	2	4	1	1	12	0	0	0	0	0	1	4	1	1	1	0	0	0	0
Ripistes parasita	0	0	0	0	0	0	10	4	0	0	0	0	0	1	0	0	0	0	1	0	0
Sisyra sp	0	0	0	0	0	0	10	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Tricholeiochiton fagesi	0	0	1	1	1	0	10	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Cyrnus insolutus	0	1	0	0	0	0	12	0	0	0	1	1	1	1	0	0	0	10	1	0	0
Gyrinus sp	0	1	0	0	1	0	10	0	0	0	0	0	1	1	1	1	1	1	0	0	0
Arrenurus sp	0	1	1	1	1	0	1	12	0	0	0	0	1	1	1	1	1	1	1	0	0
Branchiura sowerbyi	1	1	0	0	0	0	1	12	2	0	1	0	1	1	1	0	1	10	1	0	0
Forelia liliacea	1	1	0	0	0	0	1	12	0	1	0	1	1	1	1	1	1	2	1	0	0
Mideopsis orbicularis	1	1	0	0	1	1	1	12	2	12	5	5	1	1	1	1	2	2	12	0	0
Nais variabilis	0	1	0	5	1	1	1	12	1	0	1	0	1	2	1	2	1	1	1	0	0
Piona pusilla	0	1	0	2	1	0	0	12	1	1	1	1	2	1	1	2	8	1	8	0	0
Piscicola geometra	0	1	0	0	1	0	1	11	5	1	1	1	2	1	5	12	5	2	12	0	0
Nais pardalis	0	0	0	0	0	0	1	12	1	0	11	0	1	1	1	1	4	0	1	0	0
Tinodes waeneri	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	1	0	0	0	0
Glyptotendipes gr signatus	0	0	0	0	1	0	0	12	1	0	1	0	1	0	1	1	1	0	1	0	0
Nais barbata	0	1	0	0	1	0	1	12	1	0	7	0	1	1	1	1	10	0	1	0	0
Eylais sp	0	1	0	0	1	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0
Forelia brevipes	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	1	0	0
Unionicola aculeata	0	0	0	0	0	0	0	10	0	1	0	0	0	1	1	10	1	0	1	0	0
Dicrotendipes gr nervosus	0	2	0	0	0	1	1	1	12	3	9	1	1	1	3	5	9	5	3	0	0
Dreissena polymorpha	1	0	0	0	1	0	1	5	12	1	1	0	1	0	1	0	1	10	1	0	0
Psammoryctides barbatus	1	1	0	0	1	0	1	0	12	12	1	0	1	1	1	2	8	5	2	0	0
Uncinais uncinata	0	0	0	0	0	0	0	0	10	0	1	0	1	0	0	0	1	0	1	0	0
Unio pictorum	0	1	0	0	0	0	1	0	11	11	11	1	1	0	1	1	0	1	1	0	0
Parachironomus sp Kampen	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0
Hydropsyche contubernalis	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0
Cryptochironomus sp	1	5	0	0	1	1	1	0	1	12	5	6	1	1	1	6	1	3	5	0	0
Limnodrilus claparedeianus	8	6	1	1	1	1	1	5	3	12	1	1	1	1	1	1	1	5	2	0	0
Limnodrilus profundicola	1	1	1	1	1	0	1	0	3	12	0	0	2	1	1	0	1	2	1	0	0
Lithoglyphus naticoides	0	0	0	0	0	0	0	2	0	11	0	0	0	0	0	0	1	1	1	0	0
Gammarus tigrinus	0	1	0	0	1	0	3	1	2	12	0	0	1	1	11	2	1	12	1	0	0
Microchironomus tener	0	0	0	0	0	0	0	0	1	10	0	0	0	1	1	0	1	1	1	0	0
Einfeldia gr insolita	1	0	1	0	0	1	1	0	0	12	0	1	1	1	1	0	1	0	1	0	0
Potamopyrgus jenkinsi	0	0	0	0	0	0	0	0	0	12	0	0	0	0	1	0	1	1	0	0	0
Gyraulus laevis	0	0	1	0	1	0	1	0	0	10	0	0	1	1	0	0	1	0	0	0	0
Assiminea grayana	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0
Fleuria lacustris	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0
Lipiniella arenicola	0	0	0	0	0	0	0	0	0	11	1	0	0	0	0	0	0	0	1	0	0
Anabolia nervosa	0	2	0	0	1	0	0	0	0	1	12	1	1	0	1	1	2	1	1	0	0
Calopteryx splendens	0	1	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	1	0	0	0
Cyrnus trimaculatus	0	1	0	0	0	0	1	0	0	1	12	1	0	0	0	1	1	7	1	0	0
Laccophilus hyalinus	0	1	0	0	1	0	0	2	1	0	12	1	1	1	1	1	1	2	12	0	0
Micronecta sp	0	1	0	0	0	0	1	0	1	1	12	5	1	1	2	1	1	0	1	0	0
Thienemanniella sp	0	1	0	0	1	0	1	0	0	1	10	1	0	0	0	0	0	0	1	0	0
Nanocladius sp	0	1	0	0	0	0	1	0	1	1	11	0	1	0	1	10	1	0	1	0	0
Arrenurus albator	0	1	0	0	0	1	1	0	0	0	0	12	0	1	0	1	0	0	1	0	0
Arrenurus biscissus	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	1	0	0
Arrenurus knauthei	0	1	0	1	0	0	0	0	0	0	0	10	0	1	0	1	0	0	1	0	0
Caenis luctuosa	0	1	0	0	0	0	1	0	0	0	5	12	0	1	0	0	1	1	1	0	0
Centroptilum luteolum	0	1	0	0	0	0	0	0	0	0	1	11	0	0	0	0	0	0	1	0	0
Chaoborus flavicans	0	1	0	1	1	9	8	0	0	1	0	12	1	5	3	2	5	1	1	0	0
Cloeon simile	0	1	0	0	1	0	0	0	0	0	1	11	0	0	0	0	1	1	10	0	0
Demicryptochironomus vulneratus	0	0	0	0	0	0	1	0	1	0	1	11	0	0	0	1	0	0	1	0	0

Site group Taxon/	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Gerris argentatus	0	0	0	0	0	0	1	0	0	0	0	10	1	1	1	1	1	0	1	0	0
Hydrodroma despiciens	1	1	0	1	0	1	2	1	1	0	1	12	1	1	1	12	1	1	2	0	0
Hygrobates trigonicus	0	1	0	0	0	0	0	0	0	1	1	11	0	0	0	1	1	0	1	0	0
Mesovelia furcata	0	0	0	0	0	0	1	0	0	0	0	10	1	1	0	10	0	0	1	0	0
Molanna angustata	0	1	0	0	0	0	1	0	0	0	0	11	1	1	0	1	1	1	11	0	0
Mystacides sp	0	1	0	0	1	0	1	0	0	1	1	12	1	1	1	6	9	5	12	0	0
Stictochironomus sp	0	1	0	0	0	0	1	0	1	1	1	11	0	0	1	1	1	0	1	0	0
Dicrotendipes gr tritomus	0	0	0	0	0	0	1	0	1	1	1	10	0	1	1	1	1	0	0	0	0
Ranatra linearis	0	0	0	0	0	1	1	0	0	0	0	10	0	1	1	10	0	0	1	0	0
Tribelos intextus	0	0	0	0	0	1	1	0	0	0	0	11	1	1	0	1	1	0	1	0	0
Pseudochironomus sp	0	0	0	0	0	0	1	0	0	0	0	12	0	1	0	1	0	0	0	0	0
Piona variabilis	0	1	1	1	1	0	0	0	0	0	0	0	11	1	0	3	5	1	8	0	0
Notonecta sp	0	1	1	0	1	1	1	1	0	0	0	1	12	1	1	2	1	0	2	0	0
Tanypus kraatzi	0	1	1	2	1	1	3	0	0	1	0	0	12	9	5	1	3	1	1	0	0
Spercheus emarginatus	0	0	1	1	1	1	1	0	0	0	0	0	12	1	2	1	0	0	1	0	0
Anatopynia plumipes	0	0	0	1	1	1	3	0	0	0	0	0	12	8	2	1	0	0	0	0	0
Dendrocoelum lacteum	0	1	1	4	1	0	1	0	0	1	1	0	1	11	1	1	1	0	1	0	0
Dero dorsalis	0	1	0	1	1	1	1	0	0	0	0	0	1	10	7	0	1	1	1	0	0
Theromyzon tessulatum	0	1	2	1	2	2	5	1	1	1	1	1	1	12	8	2	2	1	2	0	0
Hesperocorixa linnei	0	0	1	2	1	2	1	0	0	1	0	0	1	11	1	1	1	0	1	0	0
Agrypnia pagetana	0	0	1	1	1	0	7	0	0	0	0	2	1	10	1	0	0	0	0	0	0
Haemonais waldvogeli	0	0	0	0	0	0	1	0	0	0	0	0	1	10	1	1	1	0	0	0	0
Hemiclepsis marginata	0	1	1	0	1	0	1	0	0	1	1	1	1	9	12	1	1	8	2	0	0
Sigara distincta/falleni/longipalis	0	1	0	0	1	1	1	0	0	0	0	1	2	2	12	12	1	1	12	0	0
Hydrachna globosa	0	1	1	0	1	0	0	0	0	0	0	0	1	1	0	11	1	0	10	0	0
Ilyocoris cimicoides	0	1	2	1	2	1	1	0	0	0	1	5	1	2	1	12	1	0	5	0	0
Laccophilus sp	0	1	0	1	1	1	1	0	1	0	1	2	1	1	1	12	1	1	4	0	0
Limnesia sp	0	1	1	1	1	0	1	5	0	0	1	1	1	1	2	12	0	1	4	0	0
Oecetis lacustris	0	0	0	0	1	0	0	0	1	7	4	0	1	1	1	10	1	0	1	0	0
Piona conglobata	0	1	0	1	1	1	2	1	0	1	0	1	1	1	2	12	1	1	2	0	0
Polypedilum gr sordens	0	1	0	1	1	1	6	1	1	1	3	1	1	1	5	12	12	3	3	0	0
Enochrus sp	0	0	2	5	2	1	2	0	0	0	0	0	8	2	1	11	1	0	1	0	0
Cryptocladopelma gr laccophila	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	10	0	1	0	0
Oecetis furva	0	1	0	1	1	0	1	1	0	0	0	1	4	2	1	2	11	1	1	0	0
Parachironomus gr arcuatis	0	1	1	2	1	1	5	1	1	1	6	1	3	3	5	5	12	1	3	0	0
Eylais hamata	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	10	1	1	0	0
Ecnomus tenellus	0	1	0	0	1	0	4	0	2	0	4	8	1	0	1	2	4	11	1	0	0
Haliplus fluviatilis	0	2	0	0	1	1	0	0	1	1	8	1	1	1	1	1	1	12	2	0	0
Phryganea bipunctata	0	1	0	0	1	1	2	0	0	0	0	0	0	1	7	1	0	11	1	0	0
Eylais extendens	0	0	0	1	1	0	0	0	0	0	0	0	8	1	1	8	1	0	11	0	0
Limnesia maculata	1	1	0	0	1	0	1	9	1	9	1	1	2	1	1	3	1	1	12	0	0
Limnesia undulata	0	1	1	0	2	0	2	1	1	1	1	0	2	2	1	2	1	1	12	0	0
Oulimnius tuberculatus	0	1	0	0	1	0	0	2	1	0	1	0	0	0	1	0	1	1	10	0	0
Pionopsis lutescens	0	0	1	0	1	1	1	0	0	0	0	0	1	0	1	1	1	0	10	0	0
Parachironomus gr vitiosus	0	0	0	0	1	1	0	0	1	0	1	0	1	0	1	1	1	1	10	0	0
Acercinae	0	1	2	1	1	1	1	5	1	3	1	1	1	2	2	9	2	1	12	0	0
Gammarus pulex	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0
Agabus/Ilybius sp	0	1	1	3	1	6	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0
Endochironomus tendens	0	1	0	1	1	3	6	1	1	0	1	2	1	1	1	9	1	3	3	0	0
Corynoneura sp	0	1	1	1	1	1	1	1	1	0	5	1	1	1	1	1	9	1	3	0	0
Proasellus meridianus	1	1	1	3	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	0	0
Anacaena limbata	0	1	5	5	2	5	1	0	1	1	1	1	5	1	0	1	0	1	5	0	0
Hydroporus palustris	0	1	9	1	5	3	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0
Dugesia lugubris/polychroa	0	1	1	6	5	1	1	0	2	1	1	1	1	3	1	1	1	1	3	0	0
Polycelis sp	0	1	1	3	5	1	1	0	1	1	1	1	1	1	1	1	1	1	3	0	0
Caenis horaria	1	3	0	0	1	1	1	1	1	1	5	6	1	1	1	3	6	1	6	0	0
Hygrobates longipalpis	0	8	0	0	1	0	1	2	0	0	9	1	1	1	1	2	2	8	5	0	0
Sialis lutaria	0	1	0	0	2	1	2	1	0	0	1	1	1	5	1	6	1	1	2	0	0
Sigara distincta	0	0	0	0	1	1	1	0	1	0	0	0	1	1	0	1	0	0	1	0	0
Potamothrix hammoniensis	1	9	0	1	1	0	1	1	1	3	1	0	1	2	3	1	1	1	1	0	0
Helochares sp	0	1	7	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0
Anisus vortex	0	1	3	9	9	1	1	0	1	1	1	1	3	3	1	1	1	1	5	0	0
Endochironomus gr dispar	0	1	3	9	1	2	1	0	1	1	1	1	3	6	1	1	2	1	1	0	0
Noterus crassicornis	0	1	5	8	5	1	1	0	0	1	1	0	5	2	1	2	1	1	1	0	0
Stagnicola palustris	1	1	6	8	9	1	0	0	1	1	1	1	2	1	1	5	1	1	2	0	0
Valvata cristata	1	1	2	8	6	1	1	0	1	3	1	0	3	2	1	1	3	1	1	0	0
Planorbis carinatus	0	1	2	8	8	0	1	0	0	1	0	0	2	5	1	1	1	1	1	0	0
Aeshna sp	0	1	1	8	1	2	1	0	0	0	0	1	1	2	1	1	0	1	1	0	0
Bithynia leachi	1	1	1	3	9	0	1	1	1	3	1	1	3	3	1	1	3	1	6	0	0
Physa fontinalis	0	1	3	6	9	0	1	1	0	1	1	0	3	3	1	1	1	1	3	0	0
Planorbis planorbis	0	1	6	1	9	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	0
Sphaerium sp	0	1	1	1	9	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	0

Site group Taxon/	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Acroloxus lacustris	0	1	1	1	1	9	1	0	1	1	1	1	1	3	1	1	1	1	1	0	0
Coenagrion sp	0	1	1	1	1	9	3	1	1	1	1	3	1	6	1	1	1	1	1	0	0
Erpobdella testacea	0	1	3	3	3	9	1	0	0	1	1	1	1	9	1	1	1	2	1	0	0
Unionicola crassipes	0	1	0	0	1	0	8	2	0	0	0	0	2	2	2	5	5	2	5	0	0
Piona alpicola/coccinea	0	1	1	1	1	1	1	8	1	5	1	1	6	1	1	9	3	1	9	0	0
Psammoryctides albicola	1	1	1	0	0	1	1	0	1	8	1	0	1	1	1	1	2	1	1	0	0
Proasellus coxalis	0	1	0	0	0	0	0	0	1	0	8	1	1	1	1	5	1	2	1	0	0
Laccobius sp	0	1	0	0	1	0	0	2	0	0	1	7	1	1	1	1	0	0	1	0	0
Tanytarsus sp	1	3	1	1	1	1	1	1	1	1	3	9	1	1	1	1	1	1	3	0	0
Caenis robusta	0	1	1	5	2	0	1	1	1	0	1	1	8	9	1	1	1	0	3	0	0
Stylaria lacustris	0	3	1	1	1	1	1	1	1	1	3	1	9	1	3	1	6	1	6	0	0
Paramerina cingulata	0	0	1	4	1	1	1	0	0	0	0	2	1	7	1	2	1	0	1	0	0
Tanypus vilipennis	0	0	0	0	1	0	0	0	0	0	0	0	0	7	1	1	0	0	1	0	0
Sigara falleni	1	3	1	0	1	1	1	1	1	5	1	1	2	1	9	3	1	6	6	0	0
Sigara striata	1	3	1	1	1	1	1	0	1	3	1	1	3	6	9	3	1	3	6	0	0
Arrenurus crassicaudatus	0	2	1	2	1	1	3	3	0	1	1	3	1	1	1	9	1	1	9	0	0
Endochironomus albipennis	0	1	0	1	1	1	1	1	1	1	1	1	5	1	6	9	9	6	3	0	0
Graptodytes pictus	0	2	1	1	2	1	0	0	0	0	0	2	1	1	1	1	1	0	8	0	0
Ophidonais serpentina	0	2	0	1	1	2	1	1	1	1	1	0	2	1	1	2	5	1	9	0	0
Polypedilum gr bicrenatum	0	4	0	0	1	1	0	0	1	5	1	1	1	0	0	1	1	0	7	0	0
Microtendipes sp	0	1	0	1	1	1	3	1	0	0	1	1	1	3	1	1	1	3	5	0	0
Pisidium sp	1	1	1	1	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
Eukiefferiella sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Erpobdella octoculata	1	1	1	1	6	1	3	0	1	1	1	1	1	3	1	1	1	3	1	0	0
Limnodrilus hoffmeisteri	1	3	1	0	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	0	0
Lumbriculus variegatus	1	1	1	1	1	6	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Hydroporinae	0	1	2	1	2	1	1	1	0	0	1	1	2	2	1	3	1	1	2	0	0
Ceratopogonidae	1	1	1	1	1	6	1	1	1	1	1	1	1	3	1	1	1	1	1	0	1
Chironomus sp	1	6	1	1	1	3	1	1	1	1	1	1	1	3	3	1	1	1	1	0	0
Cloeon dipterum	1	3	1	1	1	6	1	0	1	1	1	3	1	3	1	1	1	1	3	0	0
Glyptotendipes sp	1	1	1	1	1	3	3	1	3	1	3	1	3	1	6	6	6	6	3	0	0
Polypedilum gr nubeculosum	1	6	1	1	1	1	1	0	1	3	1	1	1	1	3	1	1	3	1	0	0
Procladius sp	1	3	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	0	0
Radix peregra	1	1	3	3	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
Tubificidae juv. without hair setae	1	6	1	0	3	3	1	1	1	6	1	1	1	1	1	1	1	3	3	0	0
Tubificidae juv. with hair setae	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Paratanytarsus sp	0	5	2	1	1	1	1	0	0	1	6	1	1	3	1	1	1	2	1	0	0
Glossiphonia complanata	1	1	1	1	6	1	1	1	3	1	1	0	1	1	1	1	1	3	1	0	0
Valvata piscinalis	1	6	1	1	6	0	1	1	1	3	1	1	1	1	1	1	1	3	5	0	0
Glossiphonia heteroclita	0	1	1	6	6	1	1	0	1	1	1	1	3	5	3	1	3	1	3	0	0
Hyphydrus ovatus	1	1	3	5	5	6	1	0	0	0	0	1	3	6	1	2	1	1	2	0	0
Asellus aquaticus	1	3	1	1	6	1	1	1	1	1	1	1	1	3	1	1	1	1	3	0	0
Bithynia tentaculata	1	1	1	1	6	1	1	1	1	1	1	1	1	3	1	1	1	1	3	0	0
Clinotanypus nervosus	0	1	0	0	6	2	1	0	0	1	1	1	1	2	1	1	1	1	6	0	0
Haliplus sp	0	2	3	1	6	6	0	0	1	1	3	1	1	1	1	1	1	1	3	0	0
Laccophilus minutus	0	1	2	0	4	1	1	0	0	0	1	0	1	1	1	2	1	0	1	0	0
Gyraulus albus	1	1	1	1	1	6	1	0	1	1	1	1	1	3	1	3	1	1	3	0	0
Helobdella stagnalis	0	1	1	1	1	6	1	1	1	1	1	1	3	3	3	3	3	3	3	0	0
Plea minutissima	0	1	0	0	1	4	0	1	0	0	0	1	1	1	0	1	1	0	2	0	0
Ablabesmyia longistyla	0	1	0	0	1	0	6	1	1	1	3	6	1	1	1	6	6	1	3	0	0
Ischnura sp	0	2	0	1	1	2	5	3	1	0	1	2	1	1	1	6	3	3	6	0	0
Oulimnius sp	0	1	0	0	0	0	0	5	0	0	1	0	0	0	1	1	1	1	1	0	0
Cricotopus sp	1	1	1	1	1	1	1	3	6	1	6	1	3	1	3	3	6	3	3	0	0
Peloscolex ferox	1	1	1	0	2	0	1	1	1	5	1	0	1	2	1	1	2	1	1	0	0
Valvata macrostoma	0	0	0	0	1	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Neumania limosa	0	1	0	1	1	1	2	2	0	0	0	5	1	1	1	2	1	1	2	0	0
Arrenurus sinuator	0	1	0	1	1	1	1	1	0	1	0	1	2	5	1	2	1	1	5	0	0
Triaenodes bicolor	0	1	1	2	2	1	3	0	0	0	1	0	2	6	1	2	1	1	5	0	0
Radix auricularia	0	1	0	0	0	0	1	0	0	0	1	1	1	1	4	1	1	0	1	0	0
Haliplus immaculatus	0	1	0	0	1	1	1	0	0	1	0	0	1	1	0	5	0	1	4	0	0
Hygrotus versicolor	0	1	1	1	2	1	1	0	1	1	1	1	1	1	2	1	2	2	5	0	0
Proasellus sp	0	1	0	0	1	1	0	0	1	1	2	0	1	2	2	1	1	0	2	0	0
Odagmia ornata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notidobia ciliaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dugesia gonocephala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Halesus radiatus/digitatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lebertia glabra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neoascia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Silo sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simulium morsitans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sperchon setiger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adicella sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Site group	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Taxon/																					
Rheocricotopus fuscipes	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Simulium sp	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Stagnicola glabra	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Beraea pullata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galba truncatula	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0
Hydroporus gyllenhalii	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Apatania muliebris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hydroporus longulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lebertia duricoria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paraphaenocladius pseudirritus agg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rheocricotopus atripes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sperchon sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterotanytarsus apicalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudorthocladius sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beris sp	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0
Dolichopodidae	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12
Elmis aenae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eusimulium aureum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus extricatus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paraponyx sp	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	0	1	1	0	0
Rheotanytarsus sp	0	1	0	0	1	0	1	0	1	0	1	0	0	0	1	1	1	1	1	0	0
Coelostoma orbiculare	0	0	1	0	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0
Limnebius truncatellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Velia sp	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0
Apsectrotanypus trifascipennis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crunoecia irrorata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dixa nebulosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enoicyla pusilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eusimulium angustipes	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eusimulium latipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydraena sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydraena riparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ironoquia dubia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lebertia sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lype reducta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmylus fulvicephalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Physa acuta	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Planaria torva	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Prionocera sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhagionidae	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0
Thyas pachystoma	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Dryopidae	0	1	1	0	1	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0
Ephemera vulgata	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Nephrotoma sp	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eisena foetida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sargus sp	0	1	0	1	1	0	0	0	0	1	1	0	1	0	0	0	1	0	1	0	0
Orectochilus villosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platambus maculatus	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0
Anacaena sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigara nigrolineata	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Einfeldia gr pagana	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Eusimulium cryophilum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gerris najas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heleniella sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Helophorus sp	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Heterotrissocladius marcidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus incognitus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus melanarius	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptophlebia marginata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oulimnius troglodytes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachygaster sp	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Paracladopelma laminata agg	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rheocricotopus chalybeatus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Zonitidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Camptocladius stercorarius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copelatus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tachytrechus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyas barbigera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parakiefferiela sp	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Agabus labiatus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ochthebius minimus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0

Site group Taxon/	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Agabus uliginosus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus flavicornis	0	1	1	1	0	1	1	0	0	0	0	1	1	1	0	0	1	1	1	0	0
Coelambus impressopunctatus	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Laccobius bipunctatus	0	1	1	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0
Lestes sponsa	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0
Lestes viridis	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0
Monopelopia tenuicalcar	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Sympetrum flaveolum	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Hydroporus tristis	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Graphoderus zonatus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhantus suturellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pogonocladius consobrinus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Copelatus haemorrhoidalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichostegia minor	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Dolichopeza sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lestes dryas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus bicuspidator	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	1	0	0
Rhantus exsoletus	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0
Oecetis ochracea	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	0	0
Rhantus latitans	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corixa dentipes	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Graphoderus cinereus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Cymatia sp	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Notonecta lutea	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Arrenurus neumani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperocorixa castanea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigara scotti	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sympetrum danae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus stecki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus vietsi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus subcentralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paralimnophyes sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus confinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Orthetrum cancellatum	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Culex sp	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Dytiscus marginalis	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Somatochlora metallica	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0
Ilybius quadriguttatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hygrobia hermanni	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphula nymphaeata	0	0	0	1	0	1	1	0	0	0	0	0	1	1	1	0	1	0	1	0	0
Tiphys scaurus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Acilius sp	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Arrenurus maculator	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Acentria nivea	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0
Anax imperator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cybister lateralimarginalis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Chaoborus pallidus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilybius aenescens	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus compactus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Berosus sp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dytiscus circumflexus	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Hydrochus angustatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notonecta maculata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Sigara limitata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigara semistriata/nigrolineata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Normandia nitens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Panisopsis vigilans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pionacercus norvegicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trissocladius brevipalpis	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydroporus scalesianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxyethira sp	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Gerris gibbifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilybius fuliginosus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydryphantes planus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus dorsalis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Arrenurus latus	0	0	1	2	1	0	1	0	0	0	0	0	1	2	1	0	0	1	1	0	0
Hydaticus sp	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Hydrochus elongatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrochoreutes krameri	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Polycentropus irroratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eristalis sp	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	12	0

Site group	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Taxon/																					
Hydrometra sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Colymbetes sp	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ilybius ater	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dryops auriculatus	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Hydroporus rufifrons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus striola	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Gyrinus substriatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ochthebius pusillus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agabus nebulosus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus lineolatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Helophorus granularis	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnebius truncatulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilyodrilus templetoni	0	1	0	0	1	1	1	3	1	1	1	0	1	1	1	1	1	1	1	0	0
Limnochares aquatica	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	1	1	0	1	0	0
Lumbriculidae	1	1	1	2	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Peltodytes caesus	0	1	1	0	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1	0	0
Slavina appendiculata	0	1	0	1	0	1	0	0	0	1	1	1	0	1	0	1	1	0	1	0	0
Limnephilus affinis	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	1	0	0
Zavrelia pentatoma	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0
Oplodontha viridula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Gerris thoracicus	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Haliplus laminatus	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Helophorus avernicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parathyas thoracata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus fulvus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dixella autumnalis	0	0	1	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Coquillettidia sp	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Agabus affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydraena britteni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nais pseudoptusa	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Laccobius striatulus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontomesa fulva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Athripsodes cinereus	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hygrobates fluviatilis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neumania deltoides	0	1	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	0	1	0	0
Potthastia longimanis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hydrobaenus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinodes maculicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiphys torris	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrochus carinatus	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubifex ignotus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0
Agabus conspersus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agraylea multipunctata	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0
Chaetogaster diaphanus	0	1	0	0	0	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	0
Dugesia tigrina	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0
Haliplus wehnkei	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hygrobates sp	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Lebertia insignis	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Potamonectes depressus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Stempellina sp	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Unionicola minor	0	1	0	0	0	0	1	1	0	0	0	1	0	1	1	1	1	0	1	0	0
Kiefferulus tendipediformis	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Limnebius papposus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neumania vernalis	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0
Limnebius sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haementeria costata	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0
Lebertia bracteata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gomphus vulgatissimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heptagenia flava	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Tinodes assimilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Wettina podagrica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydropsyche exocellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxycera sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphlonurus armatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orchestia cavimana	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ancylus fluviatilis	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus cylindratus	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus securiformis	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Baetis buceratus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baetis fuscatus	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Caenis pseudorivulorum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrnus crenaticornis	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0

Site group Taxon/	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Dero nivea	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Dero obtusa	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
Gammarus roeselii	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Limnesia pseudundulata	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Neureclepsis bimaculata	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0
Neumania sp	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0
Phryganea grandis	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0
Piona longipalpis	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	1	1	0	0
Piona rotundoides	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0
Pseudanodonta complanata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Roederiodes juncta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stictotarsus duodecimpustulatus	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0
Sympecma sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Syrocax sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionicola gracilipalpis	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Hydrobius sp	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Trissopelopia longimanus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potamothrix heuscheri	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	1	0	0
Arrenurus inexploratus	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0
Myxas glutinosa	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0
Harnischia sp	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Tanypus punctipennis	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	0
Potamothrix bavaricus	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Eylais koenikei	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0
Hebrus sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hydrometra stagnorum	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
Peloscolex speciosus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Plectrocnemia geniculata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Protzia eximia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boophtora erythrocephala	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hygrobates longiporus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Arrenurus octagonus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Gomphidae	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Brachypoda versicolor	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0
Zavreliella marmorata	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	1	0	0
Arrenurus mediorotundatus	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0
Microvelia umbricola	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Rhantus grapii	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydaticus seminiger	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachna leegei	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
Brachytron pratense	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Enochrus bicolor	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lauterborniella agrayloides	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnebius atomus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxygastra curtisii	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stratiomys sp	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus truncatellus	0	0	0	1	1	0	1	0	0	1	0	0	1	1	1	1	0	1	1	0	0
Viviparus viviparus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Limnephilus politus	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0
Hydrovatus cuspidatus	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Piona obturbans	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Hydrometra gracilenta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
Arrenurus virens	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Arrenurus schreuderi	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hydrophilus piceus	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Limnephilus stigma	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Neumania spinipes	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Orthotrichia sp	0	0	0	0	1	0	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0
Tiphys sp	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ilybius fenestratus	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	1	0	1	1	0	0
Piona neumani	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	1	1	1	0	0
Sympetrum sanguineum	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Oxus ovalis	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0
Hydrachna goldfeldi	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0
Corixa sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Cordulia aenea	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Allolophora sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erythromma viridulum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
Haliplus obliquus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Tetanocera sp	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0
Pseudosmittia sp	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piona clavicornis	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Site group / Taxon/	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Chaetarthria seminulum	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Erpobdella nigricollis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camptochironomus tentans	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Limnephilus binotatus	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tiphys pistillifer	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Arrenurus leuckarti	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Neumania imitata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Sympetrum striolatum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus cuspidifer	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulodrilus limnobius	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Agraylea sexmaculata	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Arrenurus pugionifer	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelambus nigrolineatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colymbetes paykulli	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochrus quadripunctatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hydrachna skorikowi	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus elongatulus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pristina menoni	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhantus frontalis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigara fossarum/scotti nymphe	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiphys bullatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus tubulator	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dryops luridus	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	1	1	0	0
Micronecta minutissima	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	1	0	0
Nais simplex	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Demeijerea rufipes	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Stenochironomus sp	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Piona paucipora	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Arrenurus claviger	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrenurus forpicatus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eylais discreta	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxus oblongus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unionicola intermedia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptotendipes sp	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cordulegaster sp	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atyaephyra desmarestii	0	0	0	0	0	0	0	2	1	0	1	0	0	0	0	0	0	1	1	0	0
Potamothrix bedoti	0	0	0	0	0	0	0	10	1	0	0	0	0	0	0	0	0	0	0	0	0
Nais bretscheri	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Anodonta cygnea	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0
Ceraclea sp	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Chaetogaster diastrophus	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0
Trocheta bykowskii	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Parachironomus gr longiforceps	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rheocricotopus effusus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Synorthocladius semivirens	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Xenochironomus xenolabis	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Unionicola sp	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	0
Hydrachna processifera	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Eclipidrilus lacustris	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Microchironomus deribae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Paracorixa concinna	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Paranais frici	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Paranais litoralis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Tubifex newaensis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Procloeon bifidum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0
Micronecta meriodionalis	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	2	1	1	1	0	0
Anacaena bipustulata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Heptagenia sp	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Limnebius nitidus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pionacercus vatrax	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Vejdovskyella intermedia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Arrenurus perforatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Orconectus sp	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Forelia longipalpis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Epitheca bimaculata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pagastiella orophila	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Arrenurus tricuspidator	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Hydrochoreutes sp	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Leptocerus tineiformis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Forelia curvipalpis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Hydrachna cruenta	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0
Noterus sp	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0

Site group / Taxon	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Marstoniopsis scholtzi	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Hydrachna conjecta	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Haliplus variegatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Arrenurus falciger	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Forelia koenikei	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Limnephilus fuscicornis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cybister sp	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Plea sp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0
Sigara fossarum	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Atractides ovalis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0
Microvelia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Atractides sp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Endochironomus sp Ubbergen	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Unionicola figuralis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Criorhina berberina	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	12
Oxus nodigerus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Notonecta reuteri	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Dictenidia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Thyas palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Limnephilus nigriceps	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Arrenurus bruzelii	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Arrenurus tetracyphus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Eylais infundibulifera	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Frontipoda musculus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Oecetis testacea	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Peltodytes sp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Myathropa florea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Psammoryctides moravicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Unionicola inusitata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Atractides nodipalpis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Paracymus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Haliplus varius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Thyopsis cancellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Forelia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Chaetogaster cristallinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Gomphus pulchellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Unio tumidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Hydropsyche pellucidula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Arrenurus nodosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hydraena testacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Mideopsis sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Oligostomis reticulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Setodes sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Coelostoma sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Platycnemis pennipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Paracladius conversus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Piona dispersa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Stempellinella sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Laccobius atrocephalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pristina amphibiotica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Sympetrum vulgatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Brachycercus harrisella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Limnoporus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Lepidostomatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Theodoxus fluviatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Paraleptophlebia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hydrachna globosa/uniscutula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Appendix 2 Number of sites, means, and standard deviations of the quantitative environmental variables and percentages of the nominal environmental variables per site group for all data. Abbreviations are explained in Table 10.5.

Quantitative environmental variables

Site group		H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Number of sites		14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
T		5.	4.	4.	7.	11.	8.	3.	7.	3.	6.	14.	13.	15.	7.	19.	19.	7.	16.	9.	8.	9.
	sd	2.	1.	1.	3.	3.	3.	3.	3.	0.	2.	5.	7.	6.	1.	6.	1.	3.	5.	3.	3.	4.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
PH		7.1	6.3	4.9	7.2	7.9	7.6	6.1	7.4	4.1	5.9	4.2	4.3	5.1	5.8	6.9	6.9	7.2	7.6	7.4	7.5	7.4
	sd	0.2	0.4	0.3	0.4	0.4	0.4	0.7	0.5	0.2	0.5	0.3	0.5	0.7	1.0	1.1	0.4	0.7	0.5	0.3	0.8	0.3
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
EC		242.	240.	175.	302.	396.	368.	207.	292.	125.	274.	122.	91.	72.	199.	533.	462.	452.	416.	400.	426.	442.
	sd	80.	58.	5.	89.	111.	48.	45.	54.	10.	94.	52.	32.	27.	33.	232.	77.	168.	118.	195.	200.	108.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
O2		9.	7.	9.	11.	11.	10.	7.	9.	17.	12.	8.	9.	8.	11.	7.	4.	10.	6.	9.	11.	10.
	sd	4.	2.	3.	1.	1.	2.	3.	2.	3.	3.	1.	1.	1.	2.	2.	1.	4.	6.	1.	2.	2.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
O2%		70.	56.	65.	86.	98.	86.	51.	73.	128.	92.	80.	82.	82.	87.	80.	40.	85.	59.	70.	91.	88.
	sd	26.	19.	27.	10.	15.	18.	26.	19.	25.	22.	0.	5.	13.	15.	30.	16.	31.	42.	10.	18.	21.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
NH4		0.2	0.1	0.2	0.2	0.4	0.5	0.2	1.5	0.2	1.7	5.9	3.7	2.1	5.4	2.5	2.4	2.1	4.1	6.7	1.9	2.2
	sd	0.2	0.1	0.0	0.1	0.2	0.4	0.1	1.6	0.1	0.9	6.2	3.2	1.6	2.3	3.1	2.3	2.0	9.3	5.1	2.9	3.7
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
O-P		.20	.11	.05	.42	.14	.26	.11	.36	.04	.42	.01	.03	.05	.27	.53	.34	.27	.39	2.51	.83	.43
	sd	.10	.07	.01	.89	.08	.27	.11	.14	.02	.94	.01	.03	.05	.40	1.56	.09	.41	.10	1.88	1.45	.62
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	7	11	12	18
T-P		.21	.14	.06	.38	.28	.42	.13	.51	.08	.51	.06	.13	.11	.51	1.00	1.20	.41	1.92	2.53	1.27	.88
	sd	.10	.06	.02	.36	.14	.46	.09	.29	.04	.89	.03	.11	.08	.49	2.79	.39	.44	1.45	1.90	2.10	1.15
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
FE		.04	.04	.30	.08	.16	.14	.75	.08	.00	.43	.38	.41	.35	1.45	.57	.50	.61	.00	.44	.67	.25
	sd	.09	.07	.30	.09	.20	.17	.83	.07	.00	.49	.11	.35	.24	.99	1.33	.55	.87	.00	.42	.70	.44
	n	12	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	7	6	11	13
CL		31.	28.	25.	37.	34.	43.	26.	36.	13.	33.	9.	8.	10.	53.	42.	47.	57.	35.	112.	45.	67.
	sd	14.	9.	1.	16.	12.	13.	7.	12.	3.	18.	4.	3.	4.	40.	11.	4.	95.	10.	89.	15.	115.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
SO4		29.	39.	36.	42.	60.	49.	45.	44.	30.	77.	17.	12.	14.	107.	91.	54.	78.	55.	77.	65.	71.
	sd	12.	7.	11.	14.	26.	16.	4.	13.	5.	28.	8.	5.	8.	35.	45.	16.	21.	13.	28.	18.	18.
	n	6	10	4	17	5	21	4	5	5	7	9	15	11	4	10	11	25	7	11	12	19
NA		27.	22.	11.	20.	15.	23.	14.	22.	5.	27.	4.	5.	8.	38.	35.	17.	39.	14.	60.	36.	36.
	sd	16.	19.	1.	12.	9.	8.	5.	4.	1.	28.	2.	2.	4.	35.	18.	2.	59.	6.	46.	33.	60.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	7	11	12	19
K		12.	14.	10.	11.	12.	14.	12.	12.	5.	12.	2.	2.	3.	38.	11.	42.	10.	21.	13.	10.	10.
	sd	6.	8.	2.	4.	2.	5.	8.	5.	0.	2.	1.	1.	2.	51.	8.	16.	4.	6.	4.	3.	3.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	7	11	12	19
MG		7.	9.	7.	10.	8.	9.	9.	11.	3.	6.	1.	1.	3.	21.	8.	8.	8.	10.	8.	8.	8.
	sd	1.	3.	2.	4.	2.	3.	4.	3.	1.	1.	1.	1.	2.	22.	3.	1.	2.	4.	2.	2.	2.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	7	11	12	19
CA		40.	51.	41.	29.	41.	38.	42.	25.	13.	38.	1.	3.	5.	64.	54.	27.	67.	34.	51.	40.	59.
	sd	19.	17.	6.	8.	18.	9.	19.	12.	2.	16.	1.	2.	3.	67.	29.	4.	28.	5.	21.	13.	20.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	7	11	12	19
NO3		9.1	14.3	10.8	12.8	8.0	9.3	9.0	8.4	6.3	12.4	0.1	0.1	0.2	3.0	3.2	8.8	5.5	3.3	5.3	4.9	5.5
	sd	7.0	8.4	4.6	7.4	1.7	5.6	7.6	3.6	2.4	10.3	0.0	0.1	0.1	1.7	3.9	4.9	4.7	3.0	2.3	2.8	3.1
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
HCO3		34.	-	-	38.	47.	79.	-	50.	-	14.	0.	2.	8.	175.	114.	65.	84.	119.	115.	62.	88.
	sd	29.	-	-	17.	10.	33.	-	42.	-	9.	0.	5.	9.	293.	59.	14.	60.	60.	54.	36.	63.
	n	2	0	0	17	5	21	0	5	0	7	9	15	11	4	10	11	25	7	11	12	19
JR		66.	74.	75.	59.	66.	61.	70.	55.	65.	66.	24.	33.	42.	63.	65.	50.	73.	63.	50.	61.	69.
	sd	13.	12.	3.	7.	12.	9.	14.	6.	8.	14.	13.	16.	19.	9.	14.	6.	14.	6.	14.	9.	15.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	7	11	12	19
HN		7.	9.	7.	6.	8.	7.	8.	6.	3.	7.	0.	1.	1.	14.	9.	6.	11.	7.	9.	7.	10.
	sd	3.	3.	1.	2.	2.	2.	3.	2.	0.	3.	0.	1.	1.	14.	5.	1.	4.	2.	3.	2.	3.
	n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	7	11	12	19
SA		-	-	-	-	-	-	-	-	-	-	.12	.43	.33	-	-	-	-	-	-	-	-
	sd	-	-	-	-	-	-	-	-	-	-	.13	.57	.48	-	-	-	-	-	-	-	-
	n	-	-	-	-	-	-	-	-	-	-	9	15	9	-	-	-	-	-	-	-	-
W		0.6	0.7	0.2	0.8	1.9	2.2	0.4	1.0	0.4	1.6	-	-	2.6	3.6	1.9	1.0	1.9	1.5	3.1	3.1	4.5
	sd	0.5	1.0	0.2	0.5	0.6	1.2	0.6	0.4	0.2	0.6	-	-	0.4	3.0	2.1	0.8	0.6	0.6	1.7	1.4	4.5
	n	14	14	4	18	5	21	6	5	5	7	-	-	2	4	10	11	25	8	11	12	19

Site group	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
D	8	14	6	11	44	26	6	19	11	37	56	81	116	36	21	16	28	28	33	38	54
sd	7	18	6	10	30	23	7	10	7	14	10	36	65	37	22	10	13	13	21	26	53
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
S	18	11	10	23	28	33	2	17	6	1	0	0	0	0	2	0	24	2	26	25	22
sd	17	10	9	11	12	17	1	10	5	1	0	0	0	0	6	0	97	4	27	12	15
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
FALL	62	74	63	16	3.0	2.8	70	4.4	70	.68	0	0	0	0	0	3.1	.97	2.4	2.1	1.3	1.1
sd	35	36	22	22	3.1	1.5	42	1.3	40	.79	0	0	0	0	0	0.5	1.3	.80	1.7	1.1	1.4
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
SOURDIST	0.2	0	0	1	4	4	0	1	0	0	-	-	-	-	2	4	1	3	4	7	12
sd	0.4	0	0	1	2	1	0	1	0	0	-	-	-	-	0	1	1	1	3	5	17
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
S-T	9	19	25	1	0	0	18	4	9	1	6	4	18	3	9	0	8	6	11	1	8
sd	16	20	26	5	0	1	13	8	11	1	6	6	28	4	14	0	10	16	16	1	16
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%-A	0	0	0	0	0	0	0	0	0	22	0	0	12	30	2	0	19	0	5	8	6
sd	0	0	0	0	0	1	0	0	0	28	0	0	21	35	4	0	32	0	14	25	14
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%-F	0	0	0	0	0	0	0	0	0	2	0	0	3	13	2	0	10	0	1	3	5
sd	0	0	0	0	0	0	0	0	0	2	0	0	8	21	6	0	25	0	3	8	9
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%-S	0	3	0	0	0	3	0	18	0	11	40	29	20	0	6	0	12	0	11	11	8
sd	0	10	0	1	0	9	0	31	0	21	39	29	35	0	12	0	23	0	19	25	18
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%-E	0	0	0	5	1	2	0	2	0	0	23	13	23	8	12	0	4	1	1	1	4
sd	0	0	0	11	0	5	0	4	0	0	19	13	22	13	13	0	9	4	2	1	8
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%-B	12	24	34	16	3	2	41	2	36	1	33	28	17	3	1	0	0	0	2	1	5
sd	24	29	31	27	4	2	34	2	31	0	30	22	26	4	2	0	1	0	2	1	9
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%-T	12	27	34	21	3	7	41	22	36	28	97	66	65	40	20	0	41	2	14	15	19
sd	24	32	31	29	4	12	34	31	31	36	5	25	26	37	23	0	42	4	20	26	25
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MM-B	6	10	8	5	6	6	23	6	30	23	2	6	2	30	23	0	15	3	16	1	20
sd	9	19	13	6	8	9	19	5	40	17	6	13	5	30	16	0	14	7	17	3	18
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MM-E	1	4	0	7	11	8	0	4	0	20	34	40	37	18	20	0	17	0	0	5	7
sd	5	11	0	15	16	13	0	8	0	15	20	27	17	18	24	0	24	0	0	8	13
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MM-F	0	0	0	0	0	0	0	0	0	16	0	0	11	15	12	0	5	0	0	0	1
sd	0	0	0	0	0	0	0	0	0	25	0	0	13	26	18	0	12	0	0	0	4
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MM-S	0	1	0	3	4	6	0	8	0	6	36	28	28	23	12	0	25	0	2	7	11
sd	0	5	0	11	8	10	0	16	0	9	22	25	14	25	16	0	19	0	6	17	20
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MMSILT	6	15	0	8	14	11	23	12	0	20	0	1	8	5	25	50	28	60	44	35	28
sd	12	21	0	15	13	12	21	10	0	18	0	2	11	9	16	0	24	18	30	20	25
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MMSAND	25	21	15	30	18	30	17	24	4	6	1	5	0	5	7	50	6	38	20	36	19
sd	15	23	17	15	18	15	22	13	8	9	4	9	0	9	13	0	10	22	22	19	19
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MMPEAT	0	0	0	0	0	0	0	0	0	0	9	17	7	5	0	0	0	0	0	0	0
sd	0	0	0	0	0	0	0	0	0	0	13	12	11	9	0	0	0	0	0	0	0
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MMCLAY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sd	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MMDETR	49	44	78	31	36	29	37	29	66	10	18	2	7	0	0	0	4	0	13	14	12
sd	21	22	15	21	15	13	33	11	38	16	13	4	10	0	0	0	9	0	17	11	15
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MMSTONE	1	0	0	5	1	2	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0
sd	5	0	0	7	2	5	0	0	0	0	0	0	0	0	0	0	2	0	7	3	0
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
%MMGRAVE	11	4	0	11	11	10	0	16	0	0	0	0	0	0	0	0	1	0	2	3	1
sd	13	11	0	9	16	9	0	10	0	0	0	0	0	0	0	0	3	0	6	4	4
n	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19

Site group		R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Number of sites		5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
T		15.	10.	17.	21.	13.	14.	18.	18.	12.	12.	11.	16.	20.	15.	19.	19.	16.	16.	15.	12.	6.
	sd	6.	3.	9.	5.	7.	3.	3.	1.	4.	1.	3.	3.	3.	6.	3.	2.	4.	4.	4.	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
PH		7.8	7.6	6.8	7.1	7.5	7.3	7.5	8.7	7.8	8.4	7.8	7.5	7.6	7.5	7.8	8.3	7.9	7.5	7.9	-	7.6
	sd	0.6	0.6	0.6	1.0	0.6	0.7	0.5	0.3	0.3	0.2	0.5	1.1	0.4	0.5	0.5	0.4	0.4	0.3	0.5	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	0	1
EC		475.	564.	329.	276.	454.	194.	369.	418.	695.	569.	489.	257.	466.	430.	418.	390.	459.	433.	501.	-	650.
	sd	109.	283.	151.	122.	157.	81.	122.	93.	255.	181.	82.	131.	137.	165.	127.	125.	210.	107.	137.	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	0	1
O2		7.	9.	7.	10.	7.	6.	15.	11.	11.	10.	12.	10.	11.	10.	13.	10.	12.	13.	10.	-	-
	sd	4.	2.	6.	6.	3.	3.	4.	5.	3.	2.	2.	1.	4.	5.	5.	2.	4.	4.	3.	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	0	1
O2%		76.	79.	79.	110.	69.	59.	158.	116.	86.	91.	99.	99.	120.	95.	141.	109.	123.	83.	92.	0.	32.
	sd	40.	22.	75.	59.	32.	31.	37.	49.	16.	18.	13.	12.	53.	57.	57.	18.	43.	8.	31.	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	0	1
NH4		1.6	1.8	1.4	0.7	1.2	1.8	0.3	0.1	0.7	0.2	1.4	0.3	0.7	0.7	1.3	0.3	0.4	0.7	0.6	65.	28.
	sd	1.4	1.9	1.1	0.4	2.1	2.7	0.2	0.0	0.6	0.1	1.2	0.3	1.0	0.7	1.9	0.3	0.4	0.4	0.7	-	-
	n	5	45	9	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
O-P		.15	.66	.08	.08	.17	.36	.03	.01	.16	.04	.16	.01	.14	.14	.05	.04	.03	.23	.13	-	2.51
	sd	.12	1.01	.07	.05	.37	.84	.04	.00	.12	.06	.12	.01	.41	.27	.04	.03	.03	.28	.57	-	-
	n	4	43	9	9	53	21	28	4	10	9	10	7	52	28	23	11	21	13	49	0	1
T-P		.50	1.02	.37	.34	.38	.55	.10	.17	.39	.34	.49	.10	.29	.30	.26	.14	.15	.34	.38	22.0	10.6
	sd	.26	1.16	.39	.12	.43	.90	.07	.03	.17	.14	.43	.08	.49	.44	.28	.12	.08	.37	.81	-	-
	n	5	45	9	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
FE		.82	.82	.33	.23	.48	.40	.57	1.09	.16	.98	.21	.30	.92	.68	.80	1.07	.28	1.05	.67	-	.60
	sd	.38	1.27	.29	.23	.72	.46	1.07	.51	.21	.39	.44	.39	1.67	.86	1.09	1.50	.28	.55	1.30	-	-
	n	2	27	9	9	51	21	28	4	9	9	9	7	49	28	24	12	21	2	45	0	1
CL		80.	70.	81.	30.	63.	21.	54.	54.	94.	99.	32.	26.	57.	67.	66.	54.	57.	74.	58.	82.	51.
	sd	20.	89.	76.	16.	38.	17.	21.	14.	69.	46.	11.	12.	27.	39.	33.	34.	59.	37.	31.	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
SO4		73.	72.	42.	7.	56.	7.	40.	55.	67.	75.	69.	27.	24.	31.	32.	38.	53.	78.	60.	-	39.
	sd	8.	28.	33.	0.	30.	8.	26.	20.	18.	39.	15.	19.	7.	23.	17.	24.	25.	13.	19.	-	-
	n	5	45	8	1	49	21	12	4	10	9	10	7	8	22	16	12	16	16	47	0	1
NA		49.	55.	41.	28.	47.	12.	22.	32.	75.	57.	33.	16.	59.	35.	32.	29.	44.	46.	43.	-	61.
	sd	11.	58.	40.	0.	36.	9.	14.	9.	51.	25.	18.	13.	27.	28.	19.	17.	39.	17.	30.	-	-
	n	5	45	10	1	48	21	28	4	10	9	10	7	8	24	24	12	16	16	47	0	1
K		10.	11.	4.	2.	8.	15.	4.	10.	7.	8.	7.	6.	4.	7.	7.	6.	4.	8.	8.	-	66.
	sd	2.	4.	3.	0.	5.	12.	2.	3.	3.	2.	2.	5.	6.	6.	6.	4.	2.	2.	4.	-	-
	n	5	45	10	1	49	21	28	4	10	9	10	7	25	24	24	12	20	16	49	0	1
MG		8.	8.	9.	6.	10.	8.	7.	6.	9.	10.	5.	5.	6.	9.	7.	7.	8.	9.	8.	-	16.
	sd	0.	5.	3.	0.	7.	3.	2.	2.	4.	5.	2.	3.	3.	4.	2.	3.	4.	2.	3.	-	-
	n	5	45	10	1	49	21	28	4	10	9	10	7	31	24	24	12	20	16	49	0	1
CA		73.	71.	55.	44.	58.	23.	50.	42.	69.	54.	60.	33.	66.	62.	52.	52.	54.	81.	63.	-	75.
	sd	19.	20.	21.	22.	18.	12.	24.	9.	15.	12.	14.	18.	26.	22.	18.	20.	12.	22.	15.	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	35	28	24	12	20	16	49	0	1
NO3		3.2	10.3	2.0	0.2	0.7	0.1	1.6	3.3	2.9	2.5	3.3	1.1	0.2	0.5	0.6	0.6	1.4	2.4	1.7	0.1	0.0
	sd	1.7	23.1	3.5	0.1	1.1	0.1	3.2	1.8	1.6	1.8	1.5	2.0	0.1	0.8	1.3	0.8	2.6	1.5	1.6	-	-
	n	5	45	9	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
HCO3		86.	66.	197.	159.	165.	86.	181.	80.	50.	104.	2.	49.	165.	197.	163.	100.	58.	16.	98.	-	427.
	sd	14.	90.	149.	0.	86.	35.	74.	13.	70.	12.	0.	62.	34.	84.	39.	22.	76.	0.	76.	-	-
	n	2	35	10	1	48	21	27	4	9	9	9	5	7	13	13	4	13	1	39	0	1
IR		61.	70.	60.	72.	64.	66.	60.	59.	61.	52.	77.	66.	66.	63.	59.	65.	67.	66.	66.	-	72.
	sd	11.	15.	16.	7.	15.	19.	13.	5.	14.	7.	5.	10.	17.	12.	13.	16.	14.	10.	13.	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	18	28	23	12	16	16	47	0	1
HN		12.	12.	10.	12.	11.	5.	9.	7.	12.	10.	10.	6.	19.	12.	9.	9.	10.	13.	11.	-	14.
	sd	3.	3.	4.	6.	4.	2.	4.	2.	3.	3.	2.	3.	10.	5.	3.	3.	3.	3.	2.	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	18	28	24	12	16	16	47	0	1
SA		-	-	-	-	.57	.16	2.6	-	1200	0348.	-	2.8	.03	1.4	15.	4.1	30.	4.4	2.7	-	-
	sd	-	-	-	-	.43	.64	4.4	-		0399.	-	.7	.00	2.9	42.	6.1	41.	.0	2.8	-	-
	n	-	-	-	-	2	21	28	-	1	9	-	6	1	20	24	8	4	1	5	-	-
W		65.	12.	2.8	4.0	3.7	-	-	38.	96.	-	29.	10.	10.	5.9	-	20.	34.	33.	15.	0.8	1.9
	sd	17.	7.	1.6	1.0	3.2	-	-	10.	52.	-	12.	0.	7.	3.8	-	8.	32.	20.	10.	-	-
	n	5	45	8	9	53	-	-	4	9	-	10	1	51	8	-	4	18	15	44	1	1
D		460	124	24	49	39	126	143	338	412	487	247	419	68	81	196	358	248	280	176	20	35
	sd	49	72	17	12	22	66	160	41	75	397	99	339	29	44	230	220	283	100	163	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
S		0	15	0	0	3	0	0	0	30	2	14	1	0	0	0	0	1	1	2	2	0
	sd	0	18	0	0	14	0	0	0	46	2	30	2	0	0	0	0	4	1	3	-	-
	n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1

Site group	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
FALL	.01	.31	.00	.00	.03	.00	.00	.00	.14	.00	.22	.16	.00	.00	.00	.00	.07	.07	.08	.01	.00
sd	.00	.35	.00	.00	.12	.00	.00	.00	.29	.00	.13	.38	.00	.00	.00	.00	.22	.17	.26	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
SOURDIST	18	26	-	-	1	-	-	-	212	-	90	3	-	-	-	-	4	26	14	-	-
sd	15	22	-	-	2	-	-	-	366	-	50	8	-	-	-	-	10	20	30	-	-
n	5	45	-	-	53	-	-	-	10	-	10	7	52	28	24	12	22	16	49	1	1
S-T	18	9	26	1	12	7	25	13	5	40	0	1	13	34	24	3	11	7	5	10	100
sd	22	16	36	2	22	11	28	22	15	0	0	1	24	33	28	4	24	19	12	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%-A	0	4	1	8	9	4	1	1	0	0	0	3	1	1	0	0	2	0	6	20	0
sd	0	15	3	16	23	17	4	1	0	0	0	7	6	2	1	0	6	1	16	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%-F	0	5	16	77	13	34	39	0	0	0	1	3	27	27	13	4	7	14	10	0	0
sd	0	13	32	24	24	40	29	0	0	0	2	4	23	33	19	4	14	24	13	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%-S	0	11	46	43	33	9	4	0	3	0	1	13	10	13	1	9	5	2	13	0	0
sd	0	22	43	23	38	23	8	0	9	0	1	31	16	23	2	28	13	5	23	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%-E	0	3	27	13	12	16	4	1	3	3	1	2	8	9	6	3	4	27	4	10	0
sd	0	8	32	14	21	19	5	1	6	3	0	3	11	11	17	3	5	24	5	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%-B	1	1	4	3	3	5	7	0	0	0	2	12	9	5	3	0	3	0	1	0	0
sd	0	3	6	2	4	15	5	0	0	0	3	18	11	10	5	0	4	0	2	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%-T	1	17	57	93	53	61	52	1	7	3	2	27	47	54	18	14	16	42	27	10	0
sd	0	29	43	13	40	35	29	0	15	3	3	33	26	37	21	27	22	32	27	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MM-B	20	30	9	13	20	1	19	40	0	6	42	10	31	22	18	28	29	37	26	0	0
sd	40	27	18	9	18	6	20	40	0	12	33	13	31	22	21	30	29	29	24	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MM-E	40	7	28	13	16	44	16	3	40	23	17	49	8	19	14	21	33	28	17	0	0
sd	49	16	27	9	20	24	17	4	29	13	24	35	17	19	17	22	25	28	19	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MM-F	0	8	7	27	10	24	39	5	8	0	5	5	37	18	36	17	10	13	19	0	0
sd	0	16	13	8	13	20	20	9	17	0	11	7	32	17	19	18	15	15	22	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MM-S	16	16	17	27	30	8	8	21	8	0	0	10	8	16	6	8	6	6	12	0	0
sd	32	27	20	8	22	14	14	25	24	0	0	16	15	19	15	18	12	12	18	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MMSILT	24	20	13	7	20	12	4	13	6	37	5	8	6	15	10	15	9	10	14	50	100
sd	39	18	10	9	12	9	8	8	9	10	9	8	9	13	12	12	8	13	14	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MMSAND	0	11	0	0	2	2	1	19	20	27	22	18	2	2	3	4	6	4	7	0	0
sd	0	14	0	0	5	4	4	27	27	15	25	11	7	5	8	9	9	8	11	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MMPEAT	0	0	7	13	1	3	7	0	0	0	0	0	5	4	1	2	2	0	1	0	0
sd	0	0	14	9	4	7	9	0	0	0	0	0	8	9	3	6	6	0	3	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MMCLAY	0	1	0	0	1	1	0	0	7	0	0	0	0	0	1	2	1	1	1	0	0
sd	0	4	0	0	5	4	0	0	13	0	0	0	2	0	6	8	2	4	6	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MMDETR	0	2	0	0	0	5	6	0	4	7	4	0	3	4	6	3	3	0	2	50	0
sd	0	8	0	0	3	8	6	0	6	8	12	0	6	9	8	7	7	0	7	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MMSTONE	0	2	0	0	0	0	0	0	8	1	3	0	0	0	0	0	2	0	0	0	0
sd	0	5	0	0	0	0	0	0	10	2	5	0	0	0	2	0	4	0	2	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1
%MMGRAVE	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0
sd	0	3	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	4	0	-	-
n	5	45	11	9	53	21	28	4	10	9	10	7	52	28	24	12	22	16	49	1	1

Nominal environmental variables

Site group	H1	H3	H5	S1	S2	S4	H2	S3	H6	S12	P1	P2	P3	D6	D8	S13	S10	S9	S5	S6	S7
Number of sites	14	14	4	18	5	21	6	5	5	7	9	15	11	4	10	11	25	8	11	12	19
SPRING	14	00	00	44	40	52	00	40	00	100	89	73	36	100	10	00	88	25	73	58	53
SUMMER	00	00	00	00	00	00	00	00	00	00	11	13	27	00	80	100	00	75	00	00	00
AUTUMN	00	00	00	50	60	48	00	60	00	00	00	13	36	00	10	00	08	00	27	42	47
WINTER	86	100	100	06	00	00	100	00	100	00	00	00	00	00	00	00	04	00	00	00	00
SHAPVIR	14	29	50	06	00	00	100	00	40	00	00	00	00	00	00	00	00	00	00	00	00
SHAPIRR	14	14	00	00	00	00	00	00	00	00	78	20	45	00	00	100	00	75	00	00	00
SHAPREG	00	07	00	00	00	00	00	00	00	00	22	80	36	00	00	00	00	00	00	00	00
SHAPLSRE	07	00	00	06	40	24	00	20	00	100	00	00	18	100	100	00	92	25	73	67	84
SHAPLSIR	64	50	50	89	60	81	00	80	60	00	00	00	00	00	00	00	08	00	27	33	16
TEMPOR	00	29	00	00	00	57	83	60	60	71	33	00	18	25	50	100	76	88	18	00	11
WATLF	57	50	50	00	40	05	17	00	100	43	67	33	36	00	30	00	20	00	27	33	53
SEE	86	100	100	17	00	05	100	00	100	14	00	00	00	25	50	00	36	00	27	42	26
COLORLES	86	64	100	39	00	10	67	00	100	00	44	27	18	00	30	00	24	13	09	17	11
YELLOW	14	36	00	50	100	81	33	60	00	71	44	53	09	75	60	100	64	75	27	67	58
BROWN	00	00	00	11	00	10	00	40	00	29	11	20	64	25	00	00	04	00	27	08	16
GREEN	00	00	00	00	00	00	00	00	00	00	00	00	09	00	00	00	04	13	00	00	00
BLACK	00	00	00	00	00	00	00	00	00	00	00	00	00	00	10	00	04	00	36	08	16
SMELL	00	00	00	00	00	10	00	20	00	00	22	27	18	00	10	00	04	13	36	08	21
CLEAR	100	100	100	89	60	76	100	80	100	86	89	93	82	50	80	00	76	13	45	58	37
SLTURB	00	00	00	11	40	19	00	20	00	14	11	00	18	50	10	100	20	75	18	33	26
TURBID	00	00	00	00	00	05	00	00	00	00	00	07	00	00	10	00	04	13	36	08	37
BACTNONE	100	100	100	100	100	100	100	80	100	100	78	100	100	100	80	100	92	88	64	100	89
BACTSL	00	00	00	00	00	00	00	00	00	00	11	00	00	00	00	00	08	00	00	00	11
BACTABUN	00	00	00	00	00	00	00	20	00	00	11	00	00	00	20	00	00	13	36	00	00
POLLUT	00	14	00	06	20	19	00	20	00	00	00	00	00	25	10	00	08	13	73	08	26
CLEANIN	36	14	00	00	20	14	50	40	00	57	00	00	00	75	50	00	12	13	45	08	58
SAND	100	93	100	100	80	100	100	100	100	86	56	67	73	50	90	100	96	88	100	100	89
SASILT	00	00	00	00	00	00	00	00	00	00	33	00	09	00	00	00	00	13	00	00	11
CLAY	00	07	00	00	00	00	00	20	00	00	33	13	09	25	00	00	08	00	09	00	05
FENLAND	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00
PEAT	00	00	00	00	00	00	00	00	00	14	33	53	45	25	10	00	00	00	00	00	00
STCDLE	71	57	50	39	80	62	33	100	20	14	00	00	00	00	00	00	00	00	18	08	11
STSILT	07	21	25	11	60	52	50	60	00	43	00	00	27	50	70	100	80	100	73	67	79
STCMSI	00	00	00	00	00	05	00	00	00	00	00	00	00	25	10	00	00	00	09	00	00
STSAND	14	00	00	89	40	95	00	100	00	00	33	20	00	25	20	100	20	75	55	83	58
STPEAT	00	00	00	00	00	00	00	00	00	00	00	40	09	00	00	00	00	00	00	00	00
STFDPESI	00	00	00	06	20	00	00	00	00	00	00	07	27	00	10	00	00	00	00	08	00
STCOMB	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00
STCLAY	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00
STFDEPE	14	07	00	44	40	29	00	20	60	14	67	33	36	25	10	00	04	00	00	00	00
STCDLESI	00	00	00	17	40	19	00	20	00	29	00	07	00	00	00	00	04	00	27	50	26
STSASI	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	11
STCMDLPE	36	36	50	22	00	10	33	00	40	00	00	00	00	00	00	00	00	00	00	00	00
STCM	14	00	00	67	40	43	00	80	00	00	00	00	00	00	00	00	04	00	18	42	05
STCMDELE	00	00	00	28	00	10	00	00	00	00	00	00	00	00	00	00	04	00	09	17	05
PS30	00	00	00	00	00	00	00	00	00	00	00	07	09	00	00	100	04	75	00	00	05
PS45	00	00	00	00	00	05	00	20	00	29	00	00	27	00	00	00	44	00	27	08	26
PS75	07	00	00	00	40	14	00	00	00	71	00	07	09	50	80	00	36	25	36	25	47
PS90	00	00	00	00	00	00	00	00	00	00	00	00	09	25	10	00	08	00	09	08	05
PSCON	00	00	00	00	00	00	00	00	00	00	00	00	00	00	10	00	00	00	00	00	00
PSIRR	100	100	100	94	60	81	100	80	100	00	100	87	45	25	00	00	08	00	27	58	16
SHADOW	86	86	100	83	60	76	67	100	40	29	33	40	55	25	50	64	16	88	73	75	53
ISOL	00	00	00	00	00	00	00	00	100	00	100	100	82	00	00	00	00	00	00	00	00
SURFOR	57	86	100	50	40	52	67	100	60	00	89	73	55	00	10	18	00	75	18	42	32
SURWOB	29	00	00	44	00	38	00	00	00	00	00	00	00	25	00	64	12	88	45	25	37
SURGRA	21	14	00	39	60	43	50	20	00	71	00	00	27	50	70	55	72	50	55	67	47
SURREE	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00	00
SURHEA	00	00	00	00	00	00	00	00	40	00	67	60	27	00	00	00	00	00	00	00	00
SURFIE	00	00	00	06	00	00	00	00	00	29	11	00	09	50	40	00	32	13	18	00	26
SURURB	07	00	00	00	20	14	00	00	00	00	00	00	00	00	00	00	12	13	18	08	11
REGULNT	93	100	100	94	60	71	100	80	100	00	100	100	82	00	00	100	04	75	18	42	21
REGULSL	00	00	00	06	00	05	00	00	00	00	00	00	00	00	00	00	08	00	09	17	05
REGUL	07	00	00	00	40	24	00	20	00	100	00	00	18	100	100	00	88	25	73	42	74
PROCON	00	00	00	06	40	10	00	20	00	14	00	00	00	00	10	00	08	00	64	42	37
MEANDNT	29	50	50	06	40	14	83	20	40	100	00	00	00	100	100	00	76	00	73	33	68
MEANDSL	07	00	00	22	00	38	00	20	00	00	00	00	00	00	00	00	20	00	18	42	16
MEAND	64	50	50	72	60	48	17	60	60	00	00	00	00	00	00	00	04	00	09	25	16

Site group	R5	R9	P5	D2A	D3	P4	P6	R7	R11	R8	R3	P7	R2	P8	P9	P11	R12	R1	R4	S14	D11
Number of sites	5	45	11	9	53	21	28	4	10	9	10	7s	52	28	24	12	22	16	49	1	1
SPRING	60	44	09	00	32	10	00	25	70	100	90	14	67	11	00	08	77	19	47	100	100
SUMMER	40	02	64	89	42	10	82	75	20	00	10	71	33	75	100	92	23	63	41	00	00
AUTUMN	00	53	09	11	23	81	18	00	10	00	00	14	00	14	00	00	00	19	10	00	00
WINTER	00	00	18	00	04	00	00	00	00	00	00	00	00	00	00	00	00	00	02	00	00
SHAPVIR	00	00	00	00	00	00	00	00	00	00	00	29	00	04	00	00	00	00	00	00	00
SHAPIRR	00	00	27	00	04	29	29	00	10	100	00	00	00	36	67	08	18	06	06	00	00
SHAPREG	00	00	00	00	00	71	71	00	00	00	00	57	02	25	33	58	14	00	06	00	00
SHAPLSRE	100	82	73	56	94	00	00	100	90	00	90	14	90	32	00	33	59	94	88	100	100
SHAPLSIR	00	18	00	44	02	00	00	00	00	00	10	00	08	04	00	00	09	00	00	00	00
TEMPOR	00	00	00	11	02	00	00	00	00	00	00	00	00	00	00	00	00	00	00	100	00
WATLF	00	60	36	00	17	14	14	75	30	00	30	57	02	04	17	08	14	19	29	100	00
SEE	00	07	18	00	13	10	04	00	00	00	00	00	10	11	00	08	00	00	10	00	00
COLORLES	00	04	18	00	23	14	14	00	10	00	00	43	06	14	00	08	00	00	10	00	00
YELLOW	40	73	73	89	68	43	54	50	70	33	100	57	65	64	42	83	86	63	78	00	00
BROWN	20	18	00	11	08	33	07	25	00	22	00	00	08	07	17	08	09	31	10	00	00
GREEN	20	00	09	00	02	10	25	25	10	44	00	00	19	07	42	00	05	06	02	00	00
BLACK	20	07	00	00	00	00	04	00	10	00	00	00	02	04	00	00	00	00	00	100	100
SMELL	20	16	00	00	04	00	00	00	30	00	20	00	04	04	04	00	05	06	08	100	100
CLEAR	00	20	18	56	66	57	82	00	20	22	30	86	35	57	42	50	32	06	57	00	00
SLTURB	60	42	45	44	23	38	07	50	80	67	60	14	40	36	42	42	55	75	31	00	00
TURBID	40	38	36	00	11	05	11	50	00	11	10	00	25	07	17	08	14	19	10	100	100
BACTNONE	100	100	91	100	98	100	100	100	100	100	100	100	96	100	100	100	100	100	94	00	100
BACTSL	00	00	00	00	02	00	00	00	00	00	00	00	00	00	00	00	00	00	06	100	00
BACTABUN	00	00	00	00	00	00	00	00	00	00	00	00	02	00	00	00	00	00	00	00	00
POLLUT	60	27	09	00	06	14	00	100	30	00	00	00	15	07	04	17	09	31	14	100	100
CLEANIN	60	42	00	00	36	05	57	00	20	100	40	00	63	18	33	17	45	56	31	100	00
SAND	100	87	00	11	47	67	07	75	70	100	100	100	19	32	42	50	59	69	78	00	100
SASILT	00	09	00	00	02	00	00	00	20	00	00	00	04	07	04	00	09	06	04	100	00
CLAY	00	13	45	00	28	33	32	00	40	00	00	00	27	14	38	42	27	38	10	00	00
FENLAND	00	02	36	89	25	00	89	25	00	00	00	00	60	39	38	08	23	13	10	00	00
PEAT	00	00	18	00	00	05	00	00	00	00	00	00	02	04	00	00	00	00	00	00	00
STCDLE	00	04	00	00	00	00	00	00	00	11	00	00	00	00	04	08	00	00	00	100	00
STSILT	100	69	36	00	72	52	11	50	40	89	30	43	38	61	38	67	73	75	67	100	100
STCMSI	00	02	09	00	00	00	21	00	00	44	00	00	00	00	13	08	00	00	00	00	00
STSAND	00	24	09	11	15	10	00	00	50	89	80	57	10	04	13	17	23	19	33	00	00
STPEAT	00	00	27	00	00	05	07	00	00	00	00	00	13	00	00	00	00	00	02	00	00
STFDPESI	00	02	18	00	13	19	36	50	00	11	00	00	15	25	08	00	05	00	08	00	00
STCOMB	00	00	00	00	00	00	21	00	00	00	00	00	08	04	21	00	05	00	00	00	00
STCLAY	00	00	00	00	00	05	00	00	30	00	00	00	04	00	08	00	09	00	02	00	00
STFDEPE	00	00	00	89	02	14	07	00	00	00	00	00	08	07	00	08	14	00	02	00	00
STCDLESI	00	00	00	00	00	10	00	00	00	11	00	00	00	00	00	08	00	00	00	00	00
STSASI	00	00	00	00	00	00	00	00	10	00	00	00	02	00	00	00	00	00	00	00	00
STCMDLPE	00	04	00	00	00	00	00	00	00	00	00	00	04	00	00	00	00	00	02	00	00
STCM	00	07	00	00	00	00	00	00	10	11	10	00	00	00	00	00	09	13	04	00	00
STCMDELE	00	02	00	00	00	00	00	00	10	00	00	00	00	00	00	00	00	00	00	00	00
PS30	20	04	00	00	00	19	00	00	20	89	20	00	00	00	00	00	05	31	06	00	00
PS45	00	16	09	11	09	33	00	00	20	11	10	14	00	00	00	00	09	06	22	00	00
PS75	00	58	18	11	53	24	00	00	20	00	60	00	08	11	00	08	23	25	41	00	100
PS90	60	04	18	22	25	00	93	100	30	00	00	00	83	36	50	17	45	13	14	100	00
PSCON	00	00	00	00	00	00	00	00	00	00	00	00	06	00	00	00	00	00	00	00	00
PSIRR	20	18	45	56	13	24	07	00	10	00	10	86	04	54	54	67	18	25	12	00	00
SHADOW	00	27	36	22	17	33	32	50	10	00	20	86	17	46	38	75	32	06	24	100	100
ISOL	00	00	27	00	04	95	39	00	00	00	00	86	06	46	46	67	32	00	08	00	00
SURFOR	00	13	00	00	08	10	21	00	10	00	20	43	10	21	21	00	05	00	02	00	00
SURWOB	00	16	09	00	00	00	07	25	00	00	00	43	04	11	08	42	18	00	08	00	00
SURGRA	40	67	64	89	94	81	07	50	80	44	100	29	52	64	50	67	68	94	96	100	00
SURREE	00	00	09	11	04	00	75	00	00	89	00	00	54	21	42	00	14	00	00	00	00
SURHEA	00	00	00	00	00	05	00	00	00	00	00	29	00	00	00	00	00	00	00	00	00
SURFIE	20	22	00	00	06	10	04	00	10	00	10	29	02	00	00	08	05	06	04	00	00
SURURB	40	09	09	00	04	10	00	50	20	11	20	00	04	07	00	00	09	25	12	00	100
REGULNT	00	13	27	11	06	00	00	00	00	00	30	86	02	71	100	67	23	19	10	00	00
REGULSL	00	04	00	00	00	00	00	00	00	00	20	00	00	00	00	00	00	19	00	00	00
REGUL	100	82	73	89	94	00	00	100	90	00	50	14	98	29	00	33	77	63	90	100	100
PROCON	100	38	00	00	04	00	00	100	100	11	40	00	02	04	00	17	18	56	16	00	00
MEANDNT	100	78	100	100	96	100	100	100	90	00	40	100	100	100	100	100	91	81	96	100	100
MEANDSL	00	09	00	00	04	00	00	00	00	00	40	00	00	00	00	00	05	19	04	00	00
MEAND	00	13	00	00	00	00	00	00	00	00	20	00	00	00	00	00	05	00	00	00	00

CURRICULUM VITAE

Petrus Franciscus Maria Verdonschot werd op 10 augustus 1955 geboren te Asten. Van 1967 tot 1973 volgde hij de middelbare school aan het Peelland College te Deurne (Atheneum-B). Van 1973 tot 1978 studeerde hij biologie aan de Landbouwhogeschool (nu Landbouwuniversiteit) te Wageningen. In de kandidaatsfase koos hij de richting 'populatie/ecosystemen'. Deze fase werd in 1976 afgesloten. Voor de ingenieursfase werden natuurbeheer en vegetatiekunde als hoofdvakken en entomologie als bijvak gekozen. Praktijkervaring werd opgedaan bij het waterschap de Dommel te Boxtel en het Staatsbosbeheer te Roermond. In 1978 werd de studie met lof afgesloten.

In de periode van 1978 tot september 1980 deed hij respectievelijk als vrijwilliger, op basis van een tijdelijke arbeidsplaats en als tijdelijk medewerker ervaring op bij het Delta Instituut voor Hydrobiologisch Onderzoek. Hier ontwikkelde hij zijn kennis betreffende de ecologie en taxonomie van oligochaeten.

In september 1980 trad hij in dienst van de Provinciale Waterstaat in Overijssel, afdeling Waterhuishouding waar hij in 1981 begon aan het project 'Ecologische Karakterisering van Oppervlaktewateren in Overijssel (EKOO)'. Daarnaast verleende hij medewerking aan het opstellen van een provinciaal waterkwaliteitsplan alsmede aan andere beleidsrelevante onderwerpen op het gebied van de aquatische ecologie en het waterbeheer.

In september 1984 trad hij in dienst van het Rijksinstituut voor Natuurbeheer. Hier zette hij, in samenwerking met de provincie Overijssel, het EKOO-project voort. De wetenschappelijke weerslag van het EKOO-project is in dit proefschrift vastgelegd.

Drukwerk en afwerking: Casparie Almere