6 AQUATIC ECOLOGY OF LOWLAND STREAMS

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6.1 Introduction

A stream is a dynamic but balanced environment (Huston 1979, Minshall 1988). Macro-invertebrates are seen as indicator species, and therefore they are used for making predictions for the impacts of climate change. Since the beginning of this century, lotic ecologists have assumed that the shapes of benthic macro-invertebrates in running waters resulted from natural selection to minimize the forces of flow that act on them. For a long time it was commonly accepted that the benthos lives in the boundary layer at the substratum surface, and is rather protected from the flow. More recently it has been shown that streamlined or dorsoventrally flattened animals experience rather complicated flows and consequently endure the forces of flow (Statzner et al. 1988).

Flow also stirs a species environment, it delivers nutrients and food particles and removes wastes and allelochemicals. It also removes macro-invertebrates. Flow characteristics are probably the most important actors in a stream ecosystem development. Every stream endures flow. But flow can be constant or varying. Most effects on the stream community are a consequence of low or high flow events. The intensity, frequency, and severity of such flow events determine the stability of the stream bed and thus of the macro-invertebrate habitat (Resh et al. 1988). Furthermore, Resh et al. assume that predictability of hydrologic regime is important with respect to ecological phenomena. The more predictable a flow regime will be, the more the biotic community will be adapted to it (Horwitz 1978). In this study predictability of flow was not included; we assume that our lowland-streams flow-regime is always unpredictable. The response of the macro-invertebrates to extreme flow events and their ability to recover are expected to be related to the discharge regime.

Meeting the general approach for predicting effects of climate change as outlined in Section 1, a distinction is made between the direct and indirect effects of climate change. Direct effects apply to the effects of temperature and indirect effects to the changes of the hydrology and of the stream bed acting as a substrate for the macro-invertebrates. This chapter describes how hydrology and substrates act as determinants of macro-invertebrate distribution in lowland streams. The effects of temperature are discussed in Chapter 10, along with the effects of temperature on terrestrial ecosystems.

6.2 Hydrology and substrates

In making predictions for indirect effects through hydrology and substrates we face the problem that the impact of climate change and of most human activities are at the scale of the drainage basin, whereas the effects on the in-stream habitats of macro-invertebrates are at the scale of square centimeters on the stream bed. The complexity of flow, substrates and communities is such that an accurate prediction is a step too far, especially if attempted at the scale of the habitat. But the distribution of macro-invertebrates in a stream is surely not coincidental. An ecologist standing at the bank of a stream is able to name several species present without have seen them.

Already more then ten years ago Statzner *et al.* (1988) pointed out that discharge and substrate are not enough to characterize the physical habitat of a stream. The question rises which parameters are necessary to tell the ecologist which species will be present. The discharge of a stream shapes the substrates (Verdonschot *et al.* 1998) and both together compose the habitat of the macro-invertebrates. In this study a number of relatively simple parameters acting at different scales are included and related to the macro-invertebrate distribution patterns in streams and in-stream habitats. The main question posed is: "How does discharge interact with stream substrates and how do the macro-invertebrates fit in?" For answering that question research has been conducted at ten field sites, each in a different stream with a different discharge regime.

6.3 Study sites

The ten studied streams all are soft-bottomed, lowland streams with a slope of about 0.5 - 5 m/km. They are located in the eastern and southern parts of the Netherlands. The streams are representative for upper and middle courses of natural lowland streams. All streams are near-natural and represent different hydrological regimes. The ten soft-bottomed lowland streams were selected based on the following criteria:

- the streams are not disturbed by human activities (near-natural)
- they have a near-natural morphology and water chemistry
- they represent different hydrological regimes

Based on these criteria the ten streams are categorized into so-called stream types (Verdonschot 1994), as indicated in Table 6.1.

The Netherlands has a temperate climate with a precipitation surplus of about 300 mm per year. Stream temperatures range between 0 and 18 ^oC. The streams are either fed by rainwater or by helocrene springs. In both types direct runoff is important too. The streams range between 0.5 and 4.0 m in width. The stream velocities range from 0 to more than 60 cm/s,

Table 6.1 Categorization of the ten studied streams into types (see also Verdonschot, 1994).

Code	Stream name	Stream type
BB	Forest stream	natural organic small upper course
FB	Frederik-Bernhard stream	natural spring-fed sandy upper course
KB	Cold stream	natural spring-fed sandy upper course
OB	Old stream	natural spring-fed sandy upper course
RB	Red stream	natural sandy middle course
RE	Reusel	semi-natural sandy middle course
RO	Rosep	semi-natural sandy middle course
SN	Springendael stream North	natural spring-fed sandy small upper course
SZ	Springendael stream South	semi-natural spring-fed sandy small upper course
TB	Tongerense stream	semi-natural spring-fed sandy upper course

Table 6.2 General physico-chemical characteristics of the ten streams studied (stream; codes are explained in Table 6.1, av. = average value, n = number of samples).

stream	SN		SZ		RO		RE		RB		BB		TB		OB		KB		FB	
	av.	n	av.	n	av.	n	av.	n	av.	n	av.	n	av.	n	av.	n	av.	n	av.	n
Ca [mg/l]	16.2	32	18.2	29	42.7	4	49.7	6	32.4	9	13.3	8	17.0	9	18.8	9				
Cl [mg/l]	25.3	57	20.4	54	23.3	73	34.8	88	27.5	10	11.1	8	10.1	9	15.9	9	20.9	12	22.3	59
CO_3 [mg/l]	1.1	32	1.0	29	2.0	1	3.0	2					2.0	9	2.0	9				
Fe^{2+} [mg/l]	0.02	19	0.04	17	2.20	5	2.08	5					0.01	9	0.01	9				
Total hardness	0.61	17	0.64	14	0.86	1		0					0.51	9	0.59	9				
HCO_3 [mg/l]	12.5	32	16.0	29	98.5	4	38.0	5	56.5	9	9.00	8	43.2	9	25.6	9				
EC	221	56	216	54	315	3	510	6	323	9	126	8	131	9	174	9	244	12	286	57
K [mg/l]	4.6	56	6.6	53	8.0	16	16.9	19	5.4	9	1.5	8	1.7	9	2.6	9			9.9	4
Mg [mg/l]	8.3	32	6.3	29	4.7	1	12.5	7	5.2	9	1.6	8	2.0	9	3.0	9			4.6	4
Kj-N [mg/l]	0.53	57	0.84	54	1.30	38	1.77	41	2.16	9	1.00	8	0.91	9	0.85	9	0.99	12	1.56	59
Na [mg/l]	14.9	32	11.4	29	16.3	4	22.6	7	18.0	9	5.85	8	6.80	9	9.94	9			11.0	4
NH_4-N [mg/l]	0.10	57	0.11	54	0.24	107	0.50	123	2.10	10	0.34	8	0.04	9	0.04	9	0.08	12	0.25	46
NO_2-N [mg/l]	0.01	57	0.01	54	0.04	95	0.06	95	0.14	10	0.15	8	0.00	9	0.01	9	0.01	12	0.05	50
NO_3-N [mg/l]	10.3	57	9.11	54	3.27	95	8.78	95	1.34	10	0.43	8	0.62	9	5.85	9	5.68	12	5.20	59
o-P [mg/l]	0.03	56	0.04	54	0.20	1	0.09	4	0.07	10	0.05	8	0.02	9	0.02	9	0.02	12	0.09	45
total-P [mg/l]	0.07	57	0.12	54	0.83	1	0.09	117	0.24	10	0.10	8	0.08	9	0.07	9	0.07	12	0.19	55
SO_4 [mg/l]	27.0	57	33.8	54	32.7	107	101	123	49.1	10	33.1	8	14.8	9	17.0	9	29.3	12	29.7	59
pH [--]	6.4	55	6.6	53	7.3	107	6.6	119	7.6	10	7.0	8	7.3	9	6.9	9	7.3	12		

with an average of 20-30 cm/s. The depths range from 0-50 cm, and are on average about 10 cm. The streambeds are very diverse, each with their own mosaic of substrate types. The most important physico-chemical parameters are given in Table 6.2.

6.3 Material and methods

Hydrology

The streams were studied from July 1997 until October 1998, over a 15-month period. Discharge was recorded continuously, through registrations of the water level at 15-minute intervals. One stream appeared to have too few reliable data for being included in the analysis. Discharge data of the one available hydrological year were summarized into various groups of hydrological parameters to test the relevance for the macro-invertebrate community. The respective groups concern stream and temporal discharge characteristics, stream and temporal discharge dynamics, normal and extreme discharge events and cumulative discharge. In one method the discharge series of the studied streams were characterised by frequency curves for discharge. Of special interest for the predictions made in this study are also the specific low- and high-end discharge-extremity intervals defined in Section 5.5. These intervals are defined in relation to the 50% percentile, the median flow Q_{50}. The median flow is also used as estimation for the base flow. Base flow was also calculated separately for the summer and winter half-year. The ratio between the two indicates the importance of groundwater seepage: the lower the summer value compared to the winter one, the lesser the role of groundwater seepage.

Substratum

In each fifth week the cover percentages of major substrates were estimated over a stretch of 30 meters in each stream during the study period. This field estimation was done per stretch of two meters. So, for each site fifteen stretches were estimated. From the major substrate types also samples for measurement of grain size and organic matter content were taken.

Macro-invertebrates

Macro-invertebrates were sampled 3 times in all ten streams in autumn (1997), spring (1998) and autumn (1998). The samples were taken by means of a micro-macrofauna-shovel of 10 by

15 cm (so the sampled surface area is 150 cm^2). At each site the five major substrate types were sampled, sorted and preserved in alcohol (70% dilution), except for oligochaetes and watermites which were preserved in formalin (4% dilution) and Koenike fluid, respectively. All macro-invertebrates were identified down to species level, if possible.

Data processing

All data were analyzed by means of statistical techniques. The macro-invertebrate data were analyzed by multivariate analysis on habitat and stream level. The analyses of the relation between macro-invertebrates and environmental parameters was done by ordination analysis using the program CANOCO, option DCCA (Detrended Canonical Correspondence Analysis, Ter Braak 1989). DCCA is an ordination technique based on reciprocal averaging which results in an ordination diagram.

Environmental variables were selected on the basis of the inter-set correlation with the axes (correlation coefficient > 0.4: the correlation between a variable and an ordination axis). All variables selected by this procedure indicate important environmental gradients. For each ordination, the sites or habitat samples and the selected environmental variables were represented in the DCCA ordination diagrams. An environmental variable (indicated as an arrow in the diagram) points approximately in the direction of the steepest increase of that variable across the diagram; the length of the arrow is equal to the rate of change in that direction. This means that the value of an important environmental variable to a macro-invertebrate taxon is visualised by its perpendicular projection on the environmental arrow or its imaginary extension (in both directions).

Some other parameters of an ordination are of interest. The eigenvalue ranges between zero and unity and can be considered as a measure of between-site variability or beta-diversity. The eigenvalues of the individual axes are regarded as a measure of their relative importance within one analysis. The species-environment correlation coefficient measures the strength of the relation between species and the environment for a particular axis. The percentage of variance of the species-abundance data accounted for by the species-site biplot indicates the goodness of fit of the diagram with respect to the distribution of species abundance. The percentage of variance of the species-environment data in the species-environment biplot indicates the goodness of fit of the environmental variables. These parameters never reach 100% because of noise in the data and are always relatively low in large data sets. The total inertia is the total variance in the species data as measured by the chi-square of the sample-by-species table divided by the tables-total.

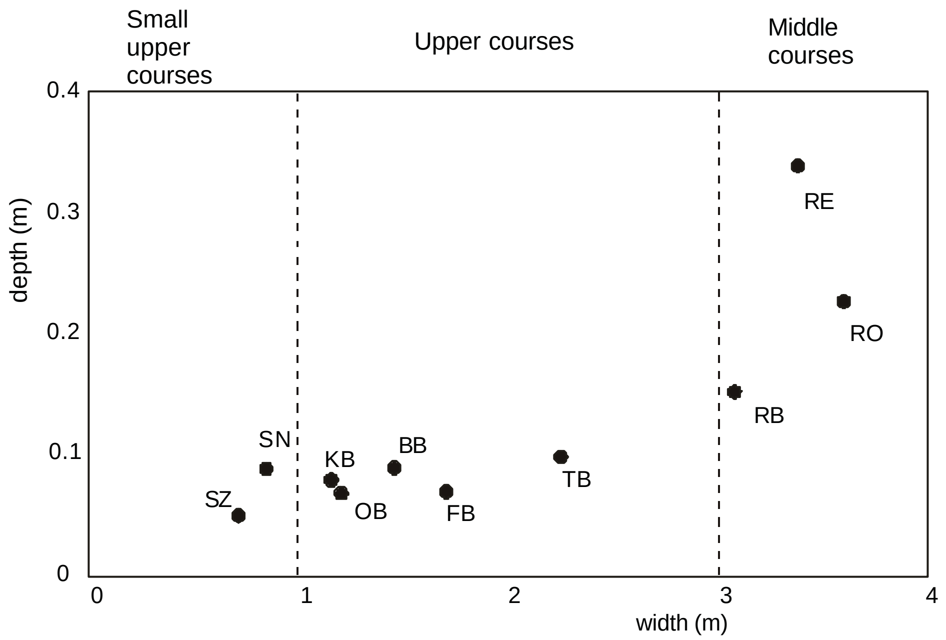
The distribution of the macro-invertebrate taxa over the different substrate types was calculated by using the index of representation IR (Hildrew & Townsend 1978) and the statistical significance of this index was tested by using a chi-square test (e.g. Lindgren & McElrath 1970). The index of representation supposes under the null hypothesis that a taxon occurs in all substrate types in equal densities. The null hypothesis is accepted when the difference between observed and expected densities is too small to reach chi-square values higher then the 5% significance level. Only in cases where the null hypothesis is rejected and the index shows an over-representation (positive IR with a value > 4) a taxon shows a preference for a substrate type.

6.4 Results

Stream type

Classification of streams into so-called stream types (Verdonschot 1994) is very useful for obtaining a better understanding of stream ecology. The type summarizes the key ecosystem characteristics into groups in this study, for small upper courses, upper courses and middle courses. Each group has a certain internal homogeneity of ecological key features and the

Figure 6.1 The studied streams typified by the width-depth relationship.



systems within a group function in a comparable way. A very simple technique to define stream types is to plot the width against the depth. There is an increase in wet cross-profile area (Figure 6.1) whereby two small upper courses (SN, SZ), five upper courses (KB, OB, BB, FB, TB) and three middle courses (RB, RE, RO) of lowland streams are distinguished.

Hydrology

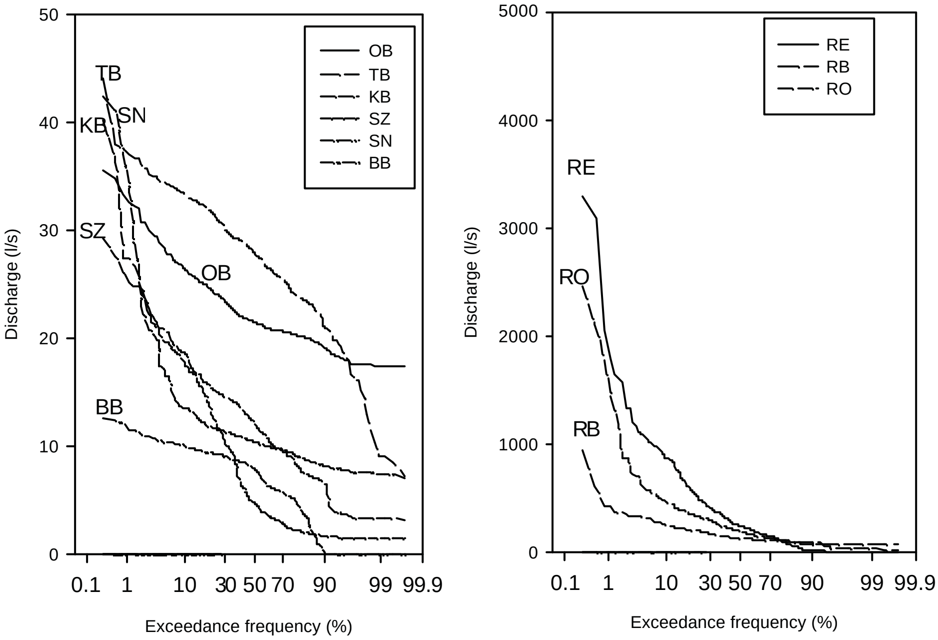
To compare the hydrology of all nine streams (the data of the tenth were not reliable), exceedance frequency curves (expressed in %) for discharges were plotted (Figure 6.2). A line that intersects (or nearly intersects) the horizontal axis indicates a stream with no (or low) discharge in summer, a so-called intermittent stream. The Forest stream (BB) is such an example. If a line is steep at the left, thus shows high discharges at low exceedance frequencies, then such stream has a flashy regime at moments of high discharge. An example of such a regime is shown by the Reusel (RE). Based on the exceedance frequency curves there are three (OB, BB, SN), three intermediate (RB, KB, TB) and three flashy streams (RE, RO, SZ) in the studied set.

The analysis of the base-flow ratio (Q_{50} of summer divided by Q_{50} of winter) yielded the values given in Table 6.3. Four hydrological stream types are distinguished. A group of stream types that are constantly fed by groundwater within a drainage basin having a high retention capacity consists of RB, OB, SN and TB. Springendal stream south (SZ) is intermediate. The summer flow regimes of KB, BB and RO are partly dependent on precipitation events in summer, while the flow regime of RE is almost completely determined by the precipitation in summer.

Table 6.3 Baseflow ratios ($Q_{50,summer}$/ $Q_{50,winter}$) of the studied streams.

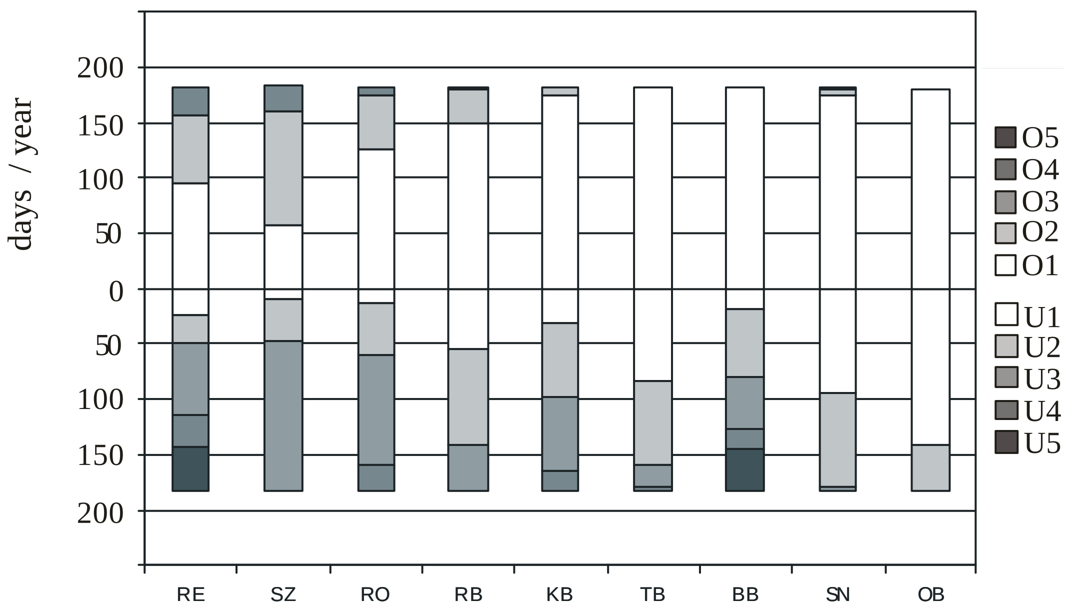
Stream	RB	OB	SN	TB	SZ	KB	BB	RO	RE
Baseflow ratio(-)	0.968	0.942	0.919	0.913	0.818	0.605	0.588	0.545	0.379

Figure 6.2 Exceedance frequency curves for discharges of the nine studied streams.



Of the different groups of hydrological parameters the discharge dynamics seem to be important and not mutually correlated. The results of group comparisons are not included in this report. Discharge dynamics are characterized by means of discharge extremity classes O_1 through O_5 for the high discharges, and U_1 through U_5 for the low discharges (see Section 5.5). Both are plotted in a histogram (Figure 6.3). The streams on the left-hand side of the plot are strongly dynamic (RE, SZ); towards the right-hand side the streams become more constant (SN, OB).

Figure 6.3 Duration of discharges (days/year) in discharge extremity classes (see for their definition Section 5.5) , for the nine studied streams.



Substratum

The average percentages of substrate cover for the five main substrate types were determined for each stream. The streams are ordered according to stream type (Figure 6.4). The proportion of each substrate type differs between all streams and no relation to stream type is seen. Important to macro-invertebrates are the dynamics in their habitat, and thus the movement of the substrate. Therefore, the standard deviations of each substrate type per stream was cumulatively plotted (Figure 6.5). The higher the bar, the more change occurred in substrates. Two streams are quite constant (RB, SN), two are intermediate (TB, OB), five are dynamic (BB, SZ, KB, RE, FB) and one stream is very dynamic (RO) in its substrate pattern in time.

Figure 6.4 Average percentages of substrate cover for the five main substrate types.

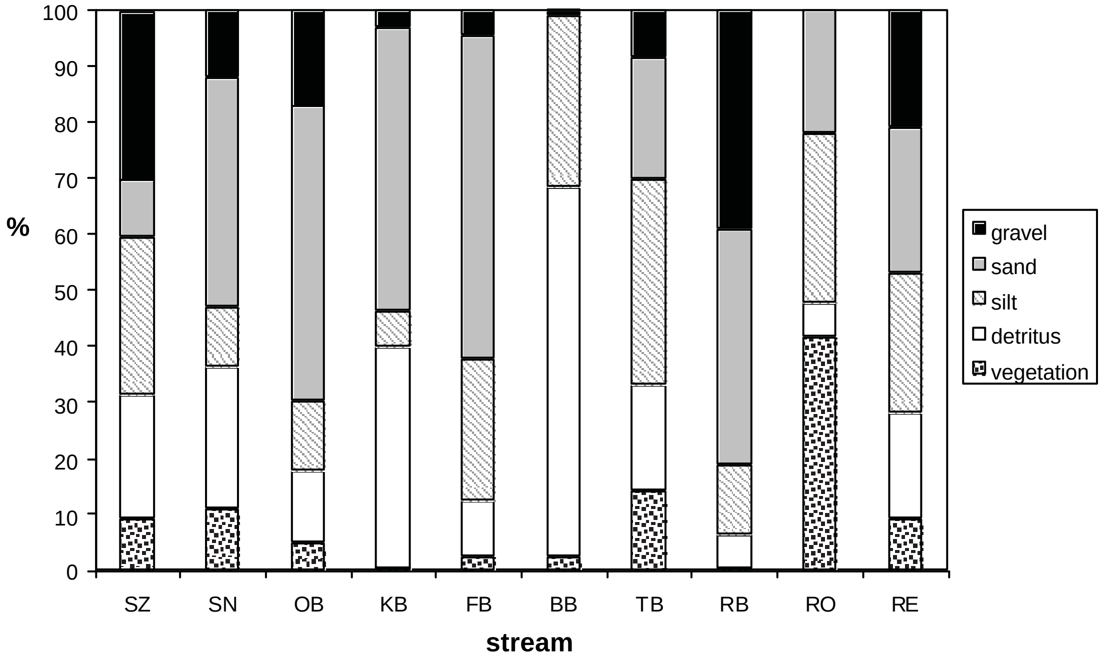
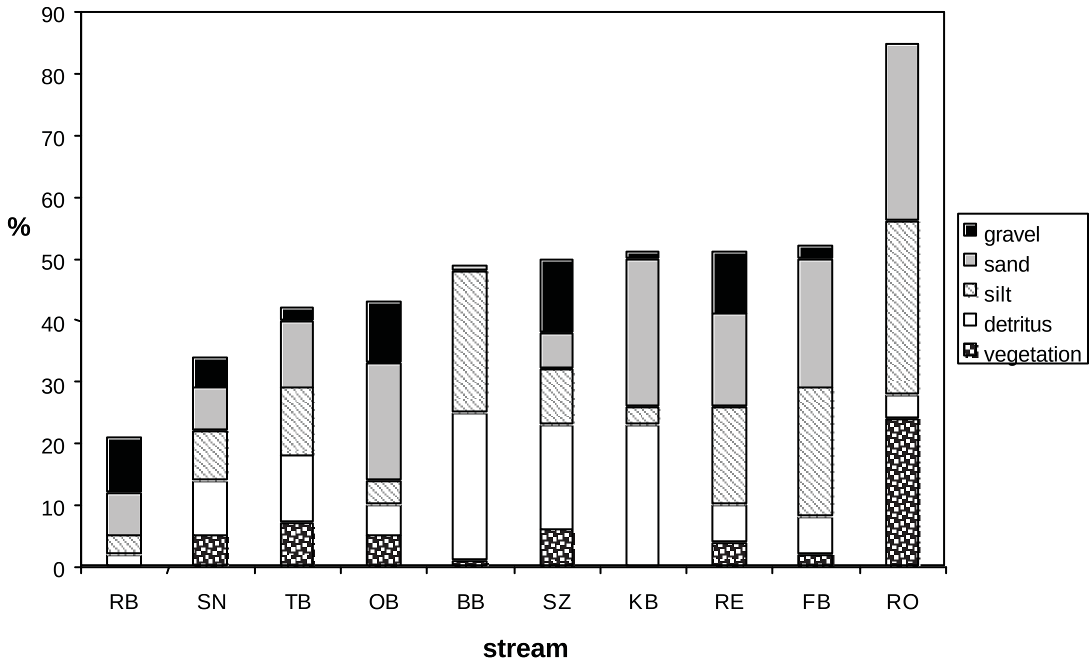


Figure 6.5 Percentage of variation in substrate cover in time.



Hydrology – substratum relationships

To relate hydrology to substratum a procedure was set up to select the best possible regression model in which the hydrological parameters are the predictors and the individual substrates the response parameters. Therefore, the hydrological parameters were grouped taking into account the discharge characteristics, the extreme and normal ranges, and of both the temporal patterns.

The procedure RSELECT (program GENSTAT) was used to select the best test group with the best subset of predictor parameters in the best generalized linear model. Best is defined as having:

- a minimum number of predictors
- the highest goodness of fit checked by its variance ($R^2 > 50\%$), and
- predictors that are significant to a 95 % level ($P > 0.05$)

To test the major hydrological parameters the predictors were divided into two test groups. Test group I refers to stream discharge characteristics and their temporal parameters. Test group II refers to extreme and normal ranges and their temporal parameters.

Table 6.4 Relative chance of prediction for test group I.

Test group I											
discharge parameter	$Q_{av.}$	Q_{10}-Q_{50}	Q_{50}- Q_{70}	< Q_{10}	> Q_{70}						total
	0.18	0.12	0.12	0.14	0.07						0.13
substrate type	sand	sand-silt	gravel	leaves	fine detritus	coarse detritus	vege-tation	bran-ches	clay	Nuphar	
	0.28	0.33	0.17	0.23	0.40	0.25	0.30	0.60	1.00	0.80	0.32
stream	RE	SN	SZ	TB	OB	KB	RB	BB	RO		
	0.51	0.09	0.30	0.20	0.34	0.20	0.00	0.95	0.33		0.32
discharge period (days)	1	7	14	21	28						
	0.24	0.33	0.29	0.35	0.35						0.31

Table 6.5 Relative chance of prediction for test group II.

Test group II											
discharge parameter	U5	U4	U3	U2	U1	O1	O2	O3	O4	O5	
	0.02	0.01	0.03	0.03	0.01	0.02	0.02	0.01	0.01	0.00	0.02
substrate type	sand	sand-silt	gravel	leaves	fine detritus	coarse detritus	vege-tation	bran-ches	clay	Nuphar	
	0.30	0.35	0.27	0.40	0.45	0.18	0.30	0.70	1.00	0.80	0.32
stream	RE	SN	SZ	TB	OB	KB	RB	BB	RO		
	0.69	0.34	0.53	0.03	0.34	0.20	0.00	0.65	0.30		0.34
discharge period (days)	1	7	14	21	28						
	0.15	0.33	0.44	0.40	0.45						0.35

Taking the criterium that the probability should at least be greater than 0.5 for both test group I and II it is concluded that only the substrates which are always present in about the same cover percentages are well predicted (branches, clay and Nuphar). Furthermore, the Forest stream (BB) and the Reusel (RE) are predicted in both groups while in group II also Springendal stream South (SZ) joins. The prediction of the Forest stream is a consequence of its constant discharge with a seasonal character and its dominant organic substrate layer also seasonally established. The Reusel and Springendal stream South are predicted because of their more flashy regimes, which during low flows show strong increases in silt cover.

It can be concluded that substrate patterns are difficult to predict in near-natural streams. A careful conclusion could be that a more flashy stream would be better predicted by discharge dynamics (extreme and normal ranges) parameters. A combination of several arguments explain the absence of a relation:

- major substrate changes are due to seasonal events of litter fall (autumn) and leaf decomposition

- discharge extremes occur quite unpredictable and rarely (with a recurrence interval of one year or longer)
- unpredictable natural processes like dam formation, sand-bar movement and erosion-deposition change substrate patterns without clear and direct hydrological causes, and
- human interference like maintenance of streams disturb the substrates independently

These arguments do support the hypothesis that lowland streams compose an unpredictable environment for macro-invertebrates.

Macro-invertebrates

In total 249 macro-invertebrate taxa were collected in the 162 habitat samples. All taxa were identified, most of them down to species level. All data collected during 1997 and 1998 were ordinated to describe the variations in taxon distribution and abundances. The major ordination parameters are listed in Table 6.6. The DCCA-ordination (Figure 6.6) shows the relationships between macro-invertebrates and habitat variables. The variables significantly explain the macro-invertebrate distribution (P=0.05; unrestricted permutation test). The individual streams were used as an explaining environmental variable. Six out of ten streams occurred to be important explanatory variables in the analysis. Furthermore, several habitat variables are important. Both habitat variables and streams are not completely independent. Several habitats are more or less dominant in only one or a few streams.

A second DCCA-ordination (not shown) was done by leaving streams out as explaining variables. Then there was a slight drop of the eigenvalue, indicating the importance of streams as explanatory variable. The species-environment correlation drops from 92 to 75 %. Streams are thus important in the distribution of the macro-invertebrates. But the resulting diagram also shows that the macro-invertebrate distribution pattern remains the same over the habitat variables. This confirms a strong relationship between streams and certain habitats.

Table 6.6 Ordination (DCCA) characteristics of the habitat - macro-invertebrate analysis.

Ordination characteristics	**axis 1**	**axis 2**	**axis 3**	**axis 4**	**Over-all parameters**
Eigenvalue	0.40	0.25	0.17	0.14	
Taxa – environment correlation	0.98	0.96	0.96	0.91	
Cumulative % variance in taxa	7.8	12.6	15.9	18.6	sum ‘unconstrained’ 5.2
Cumulative % variance in taxon-environ.	12.0	19.5	24.5	28.7	sum ‘canonical’ 3.4
Significance axis 1: eigen value	0.40				
F-ratio	5.50				2.10
P value	0.01				0.01

Figure 6.6 DCCA ordination diagram for axes 1 and 2. Only environmental variables with an interset correlation > 0.4 are shown (arrows). Letters in grey refer to macro-invertebrate habitat types (OM = organic material); bold letters refer to streams

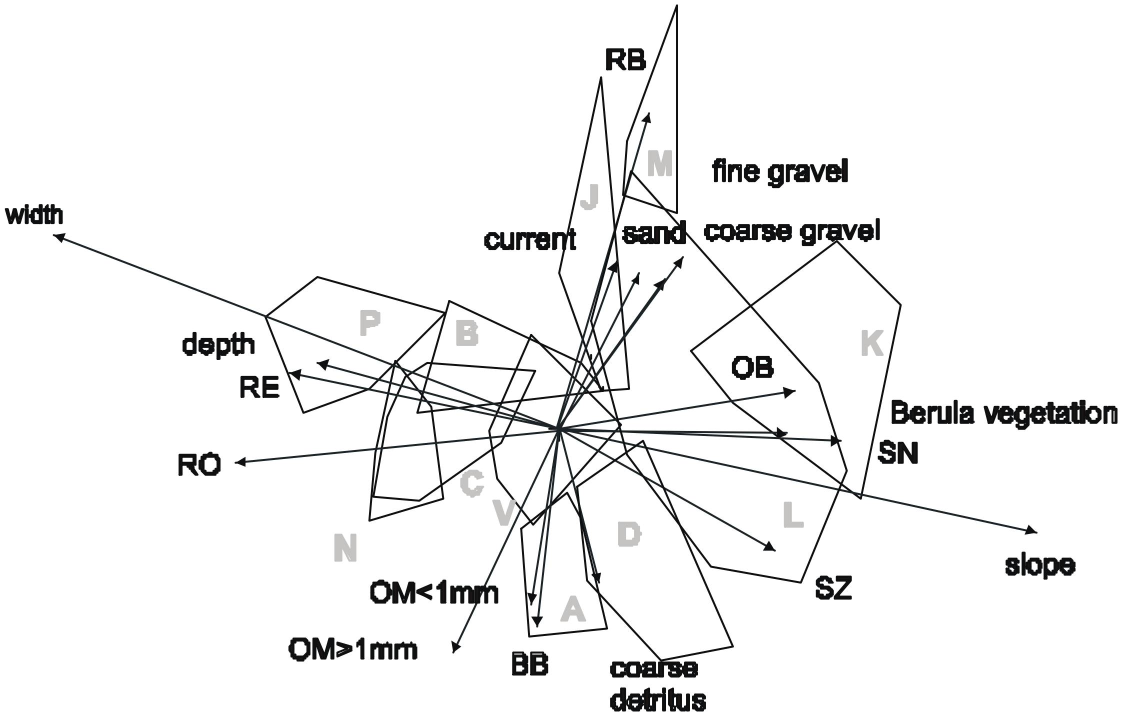
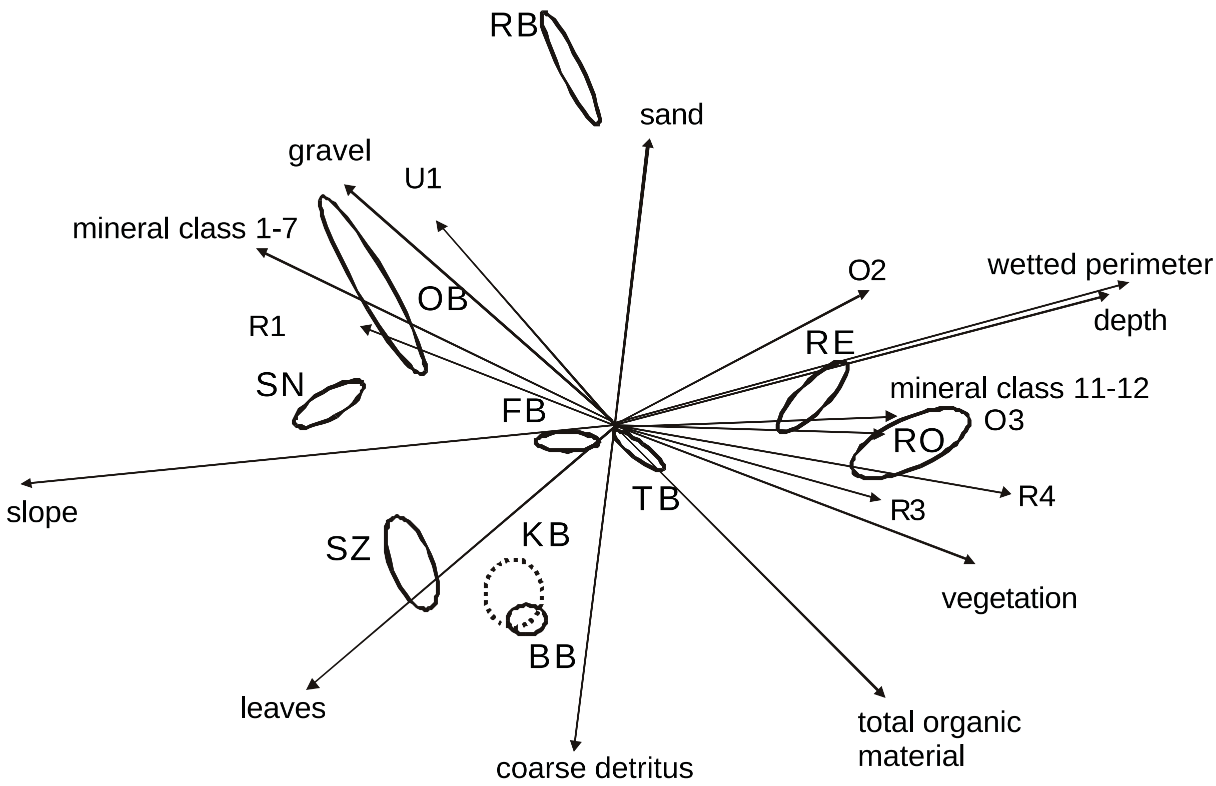


Table 6.7 Ordination (DCCA) characteristics of the stream – macro-invertebrate analysis.

Ordination characteristics	axis 1	axis 2	axis 3	axis 4	Over-all parameters
Eigenvalue	0.45	0.28	0.18	0.12	
Taxa – environment correlation	1.00	1.00	1.00	1.00	
Cumulative % variance in taxa	18.9	30.5	38.2	43.3	sum ‘unconstrained’ 2.39
Cumulative % variance in taxon-environ.	19.0	30.4	38.2	43.5	sum ‘canonical’ 2.39
Significance axis 1: eigen value	0.45				
F-ratio	5.50				2.10
P value	0.01				0.01

Figure 6.7 DCCA ordination diagram for axes 1 and 2. Only environmental variables with an interset correlation > 0.4 are shown (arrows). Letters refer to streams (ellipses).



Therefore, another ordination was performed (Figure 6.7) at the level of the whole stream by combining all habitat samples per stream into one sample per season. In this run hydrology parameters were included too. The ordination characteristics are given in Table 6.7. Besides substratum variables also hydrology explains the macro-invertebrate distribution. Macro-invertebrates respond to variables that together compose individual streams. The ordination diagram shows a strong gradient along the first axis that is explained by the high and low discharge extremity classes on the right (R_3, R_4) versus the normal range (R_1) on the left. Discharge dynamics do somehow relate to slope and dimensions of the streams. Along the second axes the substrates explain the remaining differences between streams.

From both the habitat and the stream analysis it becomes clear that both substrates and hydrology explain the macro-invertebrate composition in the studied streams. The sum of all constrained eigenvalues using all explanatory hydrological and substrate variables and no covariables was 2.391. The total amount of variance (inertia) in the species data was also 2.391, and thus all variance in species data (100%) is explained by the explanatory variables.

Table 6.8 Proportion of variance explained by environmental variables for groups of hydrological, substrates and stream variables.

Parameter groups (number)	Variance (%)	Discharge dynamics parameters per number of days	Variance (%)
short term discharge characteristics (15)	70	1	35
long term discharge characteristics (12)	82	3	44
discharge dynamics (16)	92	7	49
stream discharge characteristics (14)	84	14	74
substrates (17)	100	21	68
stream characteristics (9)	65	28	76
streams (10)	75	35	75
		70	92
		140	85

The different groups of hydrological, substrate and stream variables were explored (Table 6.8). The substrates explain the macro-invertebrate distribution best (variance 100%), though notice that this group also includes the highest number of parameters. The number of parameters can influence the percentage of variance explained, because each variable will add some explanation (even that based on coincidence) to the total. Still, it can be concluded that a second best explaining variable group is discharge dynamics. Looking over different time periods, it becomes clear that events in the period up to 70 days before sampling took place best explain the invertebrate distribution.

Substrates differed between streams and though we cannot yet explain fully their occurrence and variability in space and time, they strongly influence the macro-invertebrate distribution. Therefore, the relation between macro-invertebrates and substratum expressed in the mineral material parameter 'grain size fraction' and the organic material parameter 'organic matter content', is calculated. The mineral material was classified in the following manner, with the grain size between brackets:

- coarse sand (> 0.50 mm)
- intermediate sand (0.25 - 0.50 mm)
- fine sand (0.125 and 0.25 mm)
- very fine sand (0.063 - 0.125 mm)
- silt (< 0.063 mm)

The organic material was classified in the following manner, with the organic matter content indicated between brackets:

- very high organic matter content (> 10 %)
- high organic matter content (4 - 10 %)
- medium organic matter content (1 - 4 %)
- low organic matter content (< 1 %)
- leaves
- vegetation

All mineral and organic material classes and also the field observed substrates were tested by a chi-square test combined with an IR-score (Table 6.9). The same was done for stream velocity classes (Table 6.10).

Table 6.9 Number of indicative taxa per substratum class.

Field observed substrates	gravel	sand	fine detritus	coarse detritus	leaves	plants
Number of indicative taxa	14	7	22	50	38	71
Grain size fractions	gravel	coarse sand	intermediate sand	fine sand	very fine sand	silt and lutum
Number of indicative taxa	21	14	11	44	27	32
Organic matter content	low	mediair	high	very high	leaves	plants
Number of indicative taxa	13	37	27	51	32	38

Table 6.10 Number of indicative taxa per stream velocity class.

Stream velocity class (cm/s)	0-2.5	2.5-5	5-7.5	7.5-10	10-15	15-20	20-25	> 25
Number of indicative taxa	11	36	33	17	27	12	8	7

The number of taxa indicating a specific substrate, either a grain size fraction, the organic matter content or the field observed substrate type, is high to very high. This supports the ordination results. More in detail taxa are more indicative for certain grain sizes and/or organic matter classes than the observed mineral or organic matter types observed in the field. On the other hand the leaves and plants show more indicative taxa observed in the field. The number of indicative taxa for a stream velocity range are about equally distributed, only the highest classes have less.

6.5 Discussion

Hydro-morphology

Looking at the results of discharges and discharge regimes it can be concluded that all nine streams are classified by both parameters into the same classes. These three discharge classes are given in the columns of Table 6.11. Furthermore, substrate patterns differ between all streams and show more or less dynamic patterns. The streams are also classified according to substrate dynamics classes (rows in Table 6.11). By combining both, Table 6.11 shows the discharge–substratum relationships that are here called the hydro-morphological character.

Table 6.11 Hydro-morphological characterisation of nine studied streams.

Substrate classes	Discharge classes		
	constant	intermediate	flashy
constant	SN	RB	
intermediate	OB	TB	
dynamic		BB, KB	SZ, RE
very dynamic			RO

Discharge–substratum combinations appear not to show simple linear relationships. As expected, flashy streams with a constant substrate pattern do not occur, and neither are there any constantly discharging streams with a dynamic substrate pattern. Streams can have a more constant discharge in time and still show intermediate substrate dynamics, as is shown by the stream (RB) with an intermediate discharge and a constant substrate pattern. This is due to a number of stable gravel banks within the streambed. Also dominated by gravel and thus more stable is the streambed of the ‘Springendal stream South’ (SZ), despite the flashy discharge dynamics.

Macro-invertebrate distribution

Despite the fact that the macro-invertebrate-habitat ordination without stream parameters versus the one with stream parameters showed a slight decrease in eigenvalues, and their species-environment correlations, and the explanatory variables remained almost the same. The six out of ten stream explaining streams in the first ordination can thus be left out without a major change in the diagram. Only gravel was replaced by median grain size, though both parameters describe roughly the same habitat feature. The macro-invertebrate distribution is related to habitat and these habitats seem to be strongly represented in often only one or two of the studied streams.

The ordination on the scale of streams included also a number of hydrological variables. The major ordination pattern is comparable to the habitat ordination, with about the same explanatory habitat variables combined with some of the discharge dynamics ones. The stream level ordination showed a gradient from flashy streams (R_3 and R_4) towards constantly discharging streams (R_1) according to the series: RO, RE, TB, group of BB, FB, KB; RB, SZ, and group of OB, and SN. This gradient does not fully correspond to Table 6.10 because of the effect of substrate and other environmental conditions affecting the ordination diagram. Note the apparently the specific position of SZ in relation to OB and SN.

In general, most indicative macro-invertebrates prefer specific habitats. These habitats occur under specific conditions which, within these ten streams, occur in one or a few streams, which in their turn are related to individual discharge regimes. More data on different streams with different and comparable hydrological regimes are necessary to decide on a discharge-related preference for macro-invertebrates.