

Exchange will be appreciated! Ouephner

Arch. Hydrobiol.

76

4

499-520

Stuttgart, Dezember 1975

Michael Hubbard

Diversity and some other parameters of Ephemeroptera and Plecoptera communities in subarctic running waters

By STAFFAN ULFSTRAND

Department of Animal Ecology, University of Lund

With 6 figures and 2 tables in the text and 2 tables in an appendix

Abstract

Samples of Ephemeroptera and Plecoptera were taken from nine localities in River Vindelälven and its tributaries in central Swedish Lapland in spring, summer and autumn. The samples were analyzed in terms of species richness, species diversity (richness and equitability being separated), abundance, dominance, biomass, biometric variation within populations and within whole communities, and seasonal as well as between-locality differences of community composition. Localities were chosen in streams varying from a very large river to a small creek. In communities of Ephemeroptera, the species diversity index was correlated with differences of relative species abundances (equitability), but in communities of Plecoptera, the species richness component governed the diversity index. Differences between Ephemeroptera and Plecoptera with respect to mean trophic levels, reproductive strategies and the relative influence of competitive forces are discussed and found to be probably important for the species diversity differences. It is concluded that Ephemeroptera and Plecoptera are to be placed rather far apart on the continuum of r- to K-selected strategies, although, as in the present study, they frequently inhabit closely similar environments, and that this greatly influences diversity in their respective communities.

Introduction

Diversity is widely regarded as one of the most informative parameters of animal communities. Several indices of diversity have been proposed, but comparative methodological studies have generally failed to single out any one as distinctly more useful than the rest (DE JONG, 1975; cf. HURLBERT, 1971). Species are the units most often used in diversity calculations, but other units may sometimes be more operational (LLOYD, 1964; DICKMAN, 1968; WILHM, 1968). SHANNON'S index (e.g. MACARTHUR, 1972), however, has the important property of being applicable to any kind of mathematical distribution of the frequencies of the components

in the sample. It may be used as a tool to quantify the diversity of environments as well as communities.

The diversity concept was developed on the basis of ornithological research (MACARTHUR & MACARTHUR 1961; see also for example MACARTHUR, 1965, 1972; RECHER, 1971; KARR, 1971). Important papers dealing with vertebrates other than birds include PIANKA (1967, 1973) and BROWN (1973). The diversity approach has also been adopted for the study of invertebrate communities, for example, by SANDERS (1968), MATHIS (1968), MACKAY & KALFF (1969), COPELAND & BECHTEL (1971), BOESCH (1972, 1973), HARMAN (1972), PIMENTEL & WHEELER (1973), CROSSLEY et al. (1973), ULFSTRAND et al. (1974), HEIP & DECRAEMER (1974), and ABELE (1974). Particularly valuable overviews of diversity as an ecological concept have been provided by MARGALEF (1968), MACARTHUR (1972) and WATT (1973).

However, further comparative studies of the diversity of animal communities at different levels of richness and in habitats at different levels of complexity seem necessary, before the significance of diversity can be more fully evaluated. Community is here loosely used for any set of coexisting species belonging to one or more higher-order taxa. It would conform with the concept of "nomocénose" according to DAGET et al. (1972).

The present study deals with taxonomic groups, viz. mayflies Ephemeroptera and stoneflies Plecoptera, and environments, viz. extremely oligotrophic subarctic rivers and streams, that have so far been neglected by students of animal community diversity. As a special bonus, my data allow the comparison of two different taxa sampled simultaneously and thus deriving from similar environments, as far as this can be achieved. My point of departure is a number of alpha diversity indices (WHITTAKER, 1960, 1972) computed for mayfly and stonefly communities at three different seasons and from nine localities. Several community and population parameters are then examined and related to the differences in diversity components between the two taxa.

Study area

The data derive from a field study carried out in River Vindelälven and some of its tributaries in Swedish Lapland (Figure 1). A full description has been published previously (ULFSTRAND 1968 A), so that only a few essential features of the study area need to be repeated here.

The field work was concentrated to the surroundings of the village Ammarnäs (65°58' N, 16°12' E). The bottom of the river valley is at about 400 m above sea level and is covered by coniferous forests. Some of the sampling localities were situated in the subarctic birch zone. There is

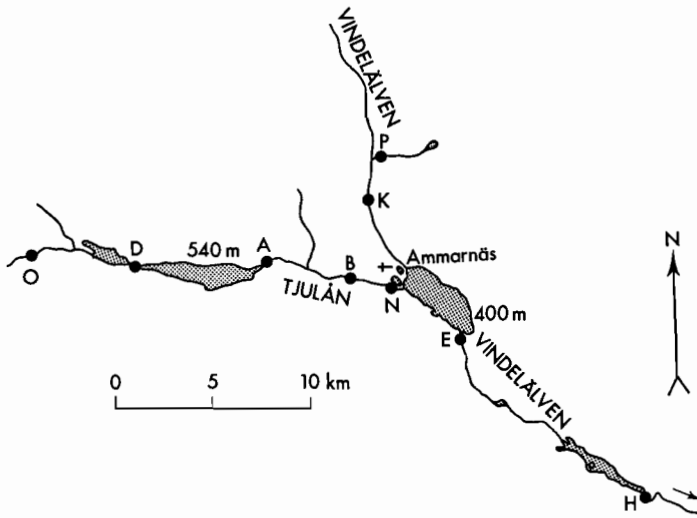


Fig. 1. Diagrammatic map of study area indicating the position of the nine sampling sites.

snow on the ground for more than half the year, and lakes and streams are frozen from about late November to May or June. The mean water temperature in July (the warmest month) is around 12°C . Seasonal fluctuations of flow volume are more than a hundredfold in many streams and rivers.

Extensive data are available from nine localities which were, therefore, selected for the present purpose. The localities are labelled so as to be recognizable in my previous publication (1968 A), where they were described in some detail. Three localities are situated in the main River Vindelälven (H, E and K). Locality E is at the outflow from a large lake, and H at the downstream end of a lake-like slow-flowing part of the river, while K is upstream of all lakes. At these three sites the river has a width of 15 to 30 m. Localities N, B and A are in River Tjulån, a major tributary with a width of less than 10 m. Like E, locality A is situated at the outlet of a lake, where a rich food supply is available for filter feeders, in this area chiefly blackfly larvae (Diptera Simuliidae). Localities D and O are in streams with a width of about 5 m and situated above the coniferous forest line. Finally, locality P is in a much smaller stream (width 1 to 2 m). Extremely different stream sizes from a large river to a quite small creek were thus encompassed in the selection. At all localities the bottom consists of boulders and rocks with rather little detritus, there are no macrophytes, and the current is fast.

Material and methods

Although all macroscopic animals were sampled, we are in this paper dealing only with the mayflies and stoneflies which made up sizeable fractions of the entire benthic communities (cf. ULFSTRAND, 1968 A). Samples were taken at water depths between 15 and 60 cm according to a very simple procedure. Stones were lifted from the bottom into a bucket and carried ashore. Downstream of the stones to be removed a nylon net was held which captured most of the debris and animals that started to drift away when the substrate was stirred. In fact, many more mayflies and stoneflies were taken in the net than on the stones. The method has been discussed elsewhere (ULFSTRAND et al., 1971). Obviously, if there were any animals deep in the bottom substrate, they were missed. So were also specimens smaller than 2 or 3 mm. Broadly speaking, however, mayflies and stoneflies were probably sampled with roughly similar efficiencies, since they are in the same size range and equally mobile. The undeniable weaknesses in the sampling procedure would be serious in, for example, production studies, but since they affect both mayflies and stoneflies in the same way, they do not seem to detract from the value of the data for the present purpose. Similarly, differences in bottom area sampled may be ignored since mayflies and stoneflies were obtained in the same samples and thus are directly comparable.

Data from three sampling series in June, July and September, 1964, will be used. They will be referred to as spring, summer and autumn samples, respectively. Although they are separated by only 4 to 7 weeks, they do reflect rather different phenological situations. The first series was taken only about a fortnight after the ice had broken up from most sampling sites, and the third after night frosts had become regular and most mayflies and stoneflies had terminated their flight periods (ULFSTRAND, 1969).

The nomenclature follows ILLIES (1967). Probability levels are based on the tables in BAILEY (1968) and SIEGEL (1956) for parametric and nonparametric tests, respectively.

Table 1. Mean values \pm 95 per cent confidence limits for number of species (S), species diversity (H'_S), equitability (J'_S) and biomass in g wet weight per m² (B).

| | Ephemeroptera | | | | |
|--------|-----------------|-----------------|-----------------|-----------------|---|
| | S | H'_S | J'_S | B | n |
| Spring | 5.22 \pm 0.51 | 1.39 \pm 0.34 | 0.59 \pm 0.14 | 1.78 \pm 1.01 | 9 |
| Summer | 7.22 \pm 1.32 | 1.48 \pm 0.42 | 0.52 \pm 0.13 | 2.73 \pm 1.11 | 9 |
| Autumn | 5.78 \pm 0.92 | 1.58 \pm 0.31 | 0.63 \pm 0.10 | 1.81 \pm 0.69 | 9 |
| | Plecoptera | | | | |
| | S | H'_S | J'_S | B | n |
| Spring | 8.33 \pm 1.84 | 1.84 \pm 0.42 | 0.60 \pm 0.10 | 1.34 \pm 0.54 | 9 |
| Summer | 4.89 \pm 0.90 | 1.52 \pm 0.44 | 0.66 \pm 0.14 | 0.41 \pm 0.48 | 9 |
| Autumn | 5.78 \pm 1.62 | 1.22 \pm 0.48 | 0.48 \pm 0.15 | 1.23 \pm 0.45 | 9 |

Results

1. Diversity and its components

The sampling data are condensed in Appendix A and B. Relevant mean values for each taxon and each season are presented in Table 1. Diversity indices (H'_S) were, generally speaking, low and did not differ significantly between mayflies and stoneflies, nor between seasons. Equitability (J'_S) values were around 0.5. These two parameters were calculated according to the standard formulae (MACARTHUR, 1972)

$$H'_S = - \sum_{i=1}^S p_i {}^2\log p_i, \text{ and } J'_S = \frac{H'_S}{{}^2\log S}.$$

The dependency of H'_S on the species richness component (${}^2\log S$) and the equitability component (J'_S), respectively, is examined in Figures 2 and 3. There was a clear difference between the mayflies and stoneflies: in all three seasons the diversity of stonefly communities showed, and that of mayfly communities lacked, a close dependency on the species richness component. Diversity differences among mayfly communities thus were due primarily to differences with respect to distribution of relative species abundances (the equitability component).

2. Species richness

The benthic samples from 9 localities at 3 seasons yielded 16 mayfly and 22 stonefly species. On average, 6.07 mayfly and 6.33 stonefly species were obtained per locality and sampling occasion, the difference being

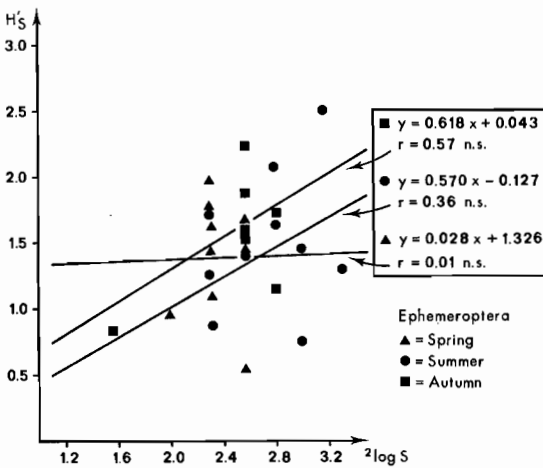


Fig. 2 Species diversity (H'_S) plotted against species richness (${}^2\log S$) in mayfly communities.

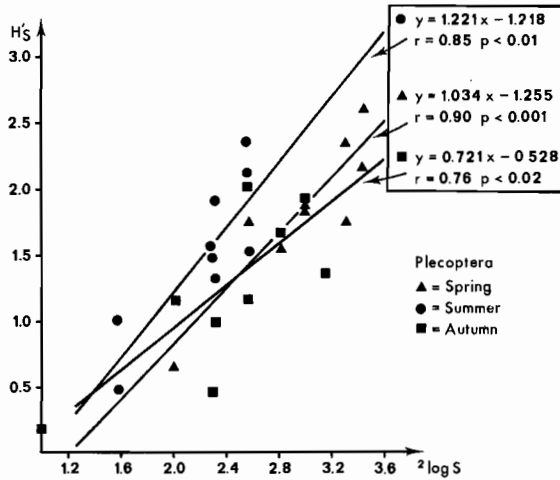


Fig. 3. Same as Fig. 2 for stonefly communities.

insignificant. The species richness per locality was higher in the mayflies in summer than in either spring (t-test, $p < 0.01$) or autumn ($p < 0.05$). By contrast, the species richness of the stoneflies was higher in spring than in either summer ($p < 0.01$) or autumn ($p < 0.05$). Mayfly communities were species-richer than stonefly communities in summer ($p < 0.01$), while the converse held in spring ($p < 0.01$), there being no difference in autumn.

The species richness values of one group was uncorrelated with that of the other in all seasons (Kendall rank correlation, $p > 0.3$ in all cases).

3. Abundance and dominance

As shown in the Appendices, the samples yielded about 4 times as many mayfly as stonefly nymphs, indicating considerably higher population densities in the former group. The most abundant mayfly species was *Baetis rhodani*, which made up more than 50 per cent of all mayfly nymphs and was present in 26 of the 27 samples. The second most abundant species, *Ephemerella aurivillii*, only made up 17 per cent of all mayfly nymphs but was as frequent as *B. rhodani*. *Heptagenia dalecarlica* was also a very frequent species. As discussed elsewhere (ULFSTRAND, 1968 A), it is doubtful whether *H. dalecarlica* and *H. sulphurea* are true species. The last-mentioned form was absent from all the upper localities in the study area, where *H. dalecarlica* was often abundant (see Appendix A).

Among the stoneflies, *Diura nanseni* was the most abundant species, making up approx. 40 percent of the total number. This is a large predaceous stonefly with an extremely northerly distribution (BRINCK, 1949). Next in abundance was *Isoperla grammatica*, a widespread species, mainly predaceous but perhaps best described as omnivorous (BRINCK, op. cit.).

Some species were taken in very small numbers, apparently having straggled into lotic habitats from nearby lenitic ones, where they may be numerous. However, some inhabitants of still waters were relatively often taken in the stream bottom samples, sometimes in considerable numbers, such as *Baetis macani*, *Ecdyonurus joernensis* and *Diura bicaudata*.

4. Biomass

Since stonefly communities in summer consisted in part of extremely small nymphs, in part of a few very large nymphs of long-living species (*Diura nanseni*, *Dinocras cephalotes*), biomass values were low and extremely variable at this season. In summer, the biomass of mayflies was significantly larger than that of stoneflies. In spring and autumn, however, biomass values were not significantly different. Evidently, for most of the year, mayfly nymphs were much smaller on average than stonefly nymphs (recall the higher density of mayfly nymphs).

Biomass values were plotted against the number of mayfly and stonefly species, respectively. In one case, viz. the mayflies in summer, a significant inverse correlation was found, using linear regression analysis ($r = -0.86$, $p < 0.01$), but the other five comparisons yielded low positive or negative correlation coefficients. Similarly, biomass was plotted against H'_s but again no significant correlations emerged.

5. Stream size

As mentioned before, the sampling sites were located in streams of extremely different size. However, no correlation was found at any season between stream size and the species richness, nor between stream size and diversity, of the mayfly or stonefly communities (Kendall's rank correlation, $p > 0.05$ in all cases). There was a tendency of an inverse correlation between stream size and biomass for both mayfly and stonefly communities; the correlation was significant in one of six possible comparisons ($p < 0.02$), and all the other agreed in their direction, though without reaching significant levels ($p > 0.09$ in all cases).

6. Biometric variation within populations

The total body-length, minus antennae and cerci, was measured to the nearest 0.1 mm for most of the animals. The biometric variation of the populations was expressed in terms of coefficients of variation (CV); only population samples comprising at least 20 animals were used.

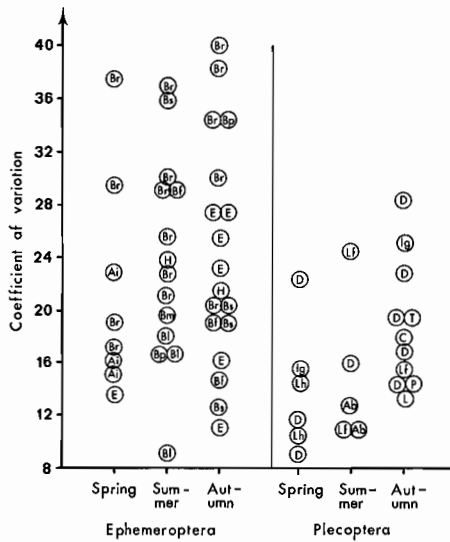


Fig. 4. Biometric (body length) variation of mayfly and stonefly populations. Each sample includes at least 20 animals. Abbreviations: Ai = *Ameletus inopinatus*, Bf = *Baetis fuscatus*, Bl = *B. lapponicus*, Bm = *B. macani*, Bp = *pumilus*, Br = *B. rhodani*, Bs = *B. subalpinus*, E = *Ephemerella aurivillii*, H = *Heptagenia dalecarlica*, Ab = *Amphinemura borealis*, C = *Capnia atra*, D = *Diura nanseni*, Ig = *Isoperla grammatica*, Lf = *Leuctra fusca*, Lh = *L. hippopus*, P = *Protonemura meyeri*, T = *Taeniopteryx nebulosa*.

On this criterion, 40 mayfly and 22 stonefly samples were available for analysis. The result is presented in Figure 4. The median CV value of the mayfly populations was significantly higher than that of the stonefly populations (median test, $p < 0.04$). No seasonal differences were detected either for the mayflies or for the stoneflies (extended median tests, $p > 0.05$ in both cases). The significant difference between mayflies and stoneflies was mainly due to conditions in spring and summer (Mann-Whitney U-tests, spring $p = 0.02$, summer $p < 0.02$, while the difference in autumn, though agreeing in direction, did not quite reach a significant level ($0.10 > p > 0.05$).

7. Biometric diversity within communities

The variation of body-length was examined after pooling all the populations making up a community; in these calculations populations comprising less than 20 individuals were also included. As a measurement of the biometric variation of whole communities, the diversity H'_R of size classes, all populations combined, was computed. The results are shown in Figure 5. No significant difference was found between the median H'_R

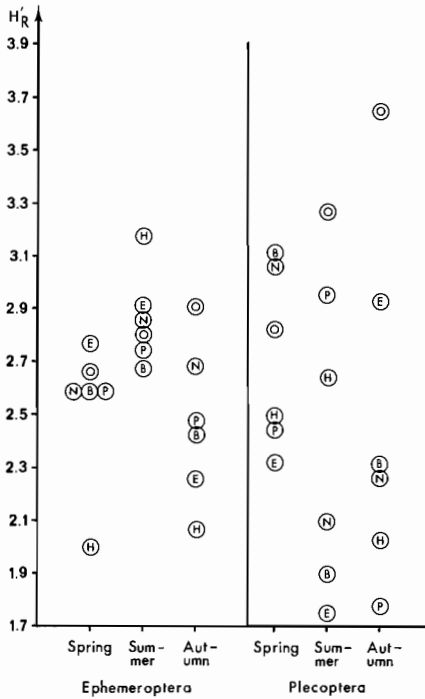


Fig. 5. Biometric (body length) diversity of mayfly and stonefly communities. Letters indicate localities.

values of the mayfly and stonefly communities, respectively, according to a median test ($p > 0.3$). The spread of index values evidently was much greater among the stonefly communities, and especially so in summer and autumn, because stonefly communities often were composed of extremely small newly-hatched nymphs and very large specimens belonging to a few longlived species. *Dinocras cephalotes*, with its three or four year life cycle, appreciably contributed to the high biometric diversity of the stonefly communities at locality O.

When the H'_S and H'_R values of mayfly and stonefly communities, respectively, were plotted against each other, linear regression analyses yielded correlation coefficients that were insignificant, both for the mayflies ($r = 0.19$) and for the stoneflies ($r = 0.35$). Nor was any correlation found between number of species and number of size classes (KENDALL's rank correlation).

8. Seasonal differences in community composition

The relative species richness of a given locality was not consistent through the seasons; observations in spring, for example, did not allow

any predictions of the relative species richness of the same site at other seasons. This was tested using KENDALL's coefficient of concordance.

The change in community composition between two contiguous sampling occasions was measured using the formula

$$Q_c^* = \frac{Q_c}{Q_c(\max)} = \frac{\sum_{i=1}^n [(p_i)_{t'} - (p_i)_{t'']]}{2}$$

where p_i is the proportion of the i :th species in the set of n species on sampling occasions t' and t'' . By dividing the Q_c value by $Q_c(\max) = 2$, an index (Q_c^*) varying from 0 (no change) to 1 (all species interchanged) is obtained.

Seasonal changes in community composition are illustrated in Figure 6. They were found to be greater in the stoneflies than in the mayflies (median test, $p < 0.05$). Closer inspection showed that this was basically due to conditions in the smallest streams (localities D, O and P); however, the tendency went in the same direction in the other triads of localities

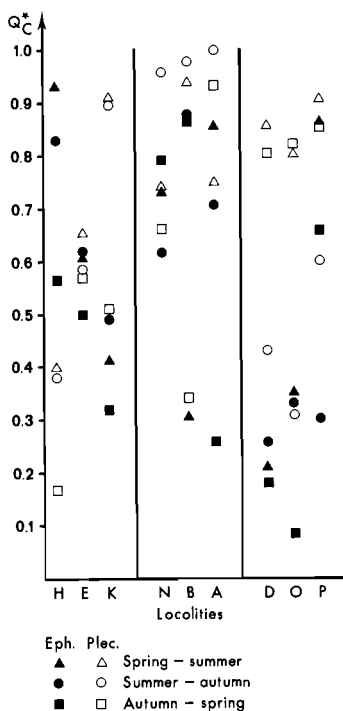


Fig. 6. Seasonal changes of community composition (Q_c^* , calculated as explained in the text).

(H, E, K = large river; N, B, A = medium-size river). No significant differences between different pairs of adjacent seasons (sampling occasions) were found.

9. Between-locality differences in community composition

Table 2 shows the mean Q_c^* for each locality, season and taxon. In summer, the mean between-locality difference in community composition was significantly higher in the stoneflies than in the mayflies (t-test, $p < 0.001$). In spring, the same tendency prevailed, though not reaching significance ($0.20 > p > 0.10$), while no difference was found in autumn.

Using Kendall's coefficient of concordance, some localities were examined to determine if any were characterized by consistently higher Q_c^* values. There was a tendency for some localities, such as N and K, to score low mean Q_c^* values, but not strong enough for the concordance to reach a significant level ($0.20 > p > 1.10$).

10. Summary of results

A) Mean diversity and equitability values were not significantly different between mayfly and stonefly communities.

B) The diversity index of the stonefly communities was closely correlated with the species richness component; this was not so in the mayfly communities, where diversity differences were dependent on the equitability component.

C) The two groups were represented by approximately similar numbers of species per locality. Species richness peaked in spring for the stoneflies, in summer for the mayflies.

Table 2. Mean Q_c^* values for each locality computed against the other eight localities. The localities are arranged from top to bottom in order of diminishing stream size.

| Locality | Ephemeroptera | | | Plecoptera | | |
|----------|---------------|--------|--------|------------|--------|--------|
| | Spring | Summer | Autumn | Spring | Summer | Autumn |
| H | 0.607 | 0.653 | 0.546 | 0.760 | 0.665 | 0.328 |
| E | 0.442 | 0.591 | 0.391 | 0.749 | 0.648 | 0.772 |
| K | 0.437 | 0.346 | 0.352 | 0.525 | 0.574 | 0.309 |
| N | 0.663 | 0.349 | 0.445 | 0.541 | 0.602 | 0.364 |
| B | 0.437 | 0.354 | 0.611 | 0.593 | 0.671 | 0.362 |
| A | 0.765 | 0.470 | 0.508 | 0.581 | 0.654 | 0.373 |
| D | 0.479 | 0.368 | 0.496 | 0.717 | 0.660 | 0.305 |
| O | 0.579 | 0.407 | 0.517 | 0.658 | 0.804 | 0.662 |
| P | 0.625 | 0.336 | 0.419 | 0.626 | 0.734 | 0.427 |
| Mean | 0.559 | 0.430 | 0.476 | 0.639 | 0.668 | 0.434 |
| S.D. | 0.245 | 0.204 | 0.191 | 0.197 | 0.305 | 0.253 |

Appendix A. Survey of sampling results of Ephemeroptera.

| | Sampled bottom area (m ²) | <i>Siphonurus</i> sp. | <i>Ameletus inopinatus</i> | <i>Baetis fuscatus</i> | <i>B. lapponicus</i> | <i>B. macani</i> | <i>B. pumilus</i> | <i>B. rhodani</i> | <i>B. subalpinus</i> | <i>Centroptilum luteolum</i> |
|----------|--|-----------------------|----------------------------|------------------------|----------------------|------------------|-------------------|-------------------|----------------------|----------------------------------|
| H spring | 1.8 | | 19 | | | | 1 | 1 | | |
| summer | 1.2 | | | 49 | 25 | 14 | | 48 | 52 | |
| autumn | 1.4 | | | | | | | 24 | | |
| E spring | 2.0 | | 24 | | | | 1 | 50 | | |
| summer | 2.1 | | | 4 | 2 | 343 | 1 | 212 | | 1 |
| autumn | 2.1 | | | | 12 | | | 195 | 42 | |
| K spring | 3.2 | | 102 | | | | | 179 | | |
| summer | 1.8 | | 2 | 7 | 61 | | 8 | 250 | | |
| autumn | 1.1 | | 1 | | | | | 75 | 9 | |
| N spring | 2.2 | | 256 | | | | | 49 | | |
| summer | 0.8 | 1 | 9 | | 4 | | 18 | 98 | | |
| autumn | 1.4 | | | 44 | | | 2 | 52 | 14 | |
| B spring | 2.3 | | 23 | | | | | 71 | | |
| summer | 1.0 | | 1 | | | | 19 | 248 | | |
| autumn | 2.1 | | | 170 | | | 12 | | 55 | |
| A spring | 2.9 | | 1 | | | | 4 | 6 | | |
| summer | 1.6 | | | 2 | 16 | 83 | 7 | 113 | | |
| autumn | 1.5 | | | | | | | 26 | 5 | |
| D spring | 3.3 | | 41 | | | | 8 | 317 | | |
| summer | 2.3 | 1 | | 1 | 9 | | 34 | 602 | | |
| autumn | 2.5 | | | | | | 21 | 310 | 14 | |
| O spring | 1.4 | | 2 | | | | 6 | 110 | | |
| summer | 2.4 | | | 12 | 354 | | 29 | 601 | | |
| autumn | 1.9 | | | 12 | 11 | | 20 | 704 | | 1 |
| P spring | 1.3 | | 7 | | | | 4 | 6 | | |
| summer | 1.1 | | | | 55 | | 80 | 411 | | |
| autumn | 1.1 | | | 11 | | | 41 | 524 | 70 | |
| Σ spring | 20.4 | — | 475 | — | — | — | 24 | 789 | — | 1 |
| summer | 14.3 | 2 | 12 | 68 | 526 | 440 | 196 | 2,583 | 52 | — |
| autumn | 15.1 | — | 1 | 244 | 23 | — | 96 | 1,910 | 209 | 1 |
| Σ | 49.8 | 2 | 488 | 312 | 549 | 440 | 316 | 5,282 | 261 | 2 |
| % | | 0.02 | 4.84 | 3.10 | 5.45 | 4.37 | 3.14 | 52.41 | 2.59 | 0.02 |

D) Species richness values of one taxon were not correlated with those of the other at the same locality.

E) Four times as many mayfly as stonefly nymphs were obtained in the samples. In each taxon, the most abundant species made up 40 to 50 per cent of the total number of individuals.

| <i>Metretopus</i> sp. | <i>Ecdyonurus joernensis</i> | <i>Heptagenia sulphurea</i> | <i>H. dalecarlica</i> | <i>Paraleptophlebia</i> sp. | <i>Ephemerella aurivillii</i> | <i>E. mucronata</i> | No. of species (S) | No. of inds. (N) | Biomass (B) (g/m ²) | H' | J' |
|-----------------------|------------------------------|-----------------------------|-----------------------|-----------------------------|-------------------------------|---------------------|--------------------|------------------|---------------------------------|------|------|
| | | | | | 15 | 1 | 5 | 37 | 0.3 | 1.44 | 0.62 |
| | 2 | | 3 | 1 | 8 | | 9 | 202 | 1.0 | 2.51 | 0.79 |
| | | | 13 | | 184 | | 3 | 221 | 1.8 | 0.81 | 0.51 |
| | | 3 | 1 | | 12 | | 6 | 91 | 0.4 | 1.67 | 0.65 |
| 1 | 6 | 11 | | | 1 | 1 | 10 | 582 | 1.0 | 1.30 | 0.39 |
| | 8 | 6 | 16 | | 280 | | 7 | 559 | 1.4 | 1.73 | 0.62 |
| | | | 43 | | 76 | 14 | 5 | 414 | 2.6 | 1.97 | 0.85 |
| | | | 25 | | 20 | 12 | 7 | 378 | 2.6 | 1.64 | 0.58 |
| | | | 28 | | 77 | | 6 | 197 | 1.3 | 1.87 | 0.72 |
| | | | 4 | | 15 | | 4 | 324 | 2.2 | 0.96 | 0.48 |
| | | | 1 | | 5 | 1 | 8 | 137 | 2.6 | 1.47 | 0.49 |
| | | | 16 | | 33 | | 6 | 161 | 0.7 | 2.22 | 0.86 |
| | | | 9 | | 14 | | 5 | 118 | 0.6 | 1.61 | 0.69 |
| | | | 4 | | 23 | | 5 | 295 | 5.7 | 0.86 | 0.37 |
| | | | 8 | | 127 | | 5 | 372 | 1.6 | 1.73 | 0.75 |
| | | 11 | 2 | | 268 | | 6 | 292 | 4.4 | 0.57 | 0.22 |
| | | 26 | | | 18 | | 7 | 265 | 2.0 | 2.08 | 0.74 |
| | 5 | 18 | 10 | | 135 | | 6 | 199 | 0.9 | 1.56 | 0.60 |
| | | | 34 | | 41 | 5 | 6 | 446 | 2.2 | 1.44 | 0.56 |
| 1 | | | 41 | | | 1 | 8 | 690 | 2.7 | 0.76 | 0.25 |
| | | | 98 | | 43 | 1 | 6 | 487 | 3.5 | 1.55 | 0.60 |
| | | | 22 | | 3 | | 5 | 143 | 1.2 | 1.10 | 0.47 |
| | | | 46 | | 2 | | 6 | 1,044 | 3.5 | 1.42 | 0.55 |
| | | | 64 | | 88 | | 7 | 900 | 2.6 | 1.17 | 0.42 |
| | | | 21 | | 46 | | 5 | 84 | 2.1 | 1.77 | 0.76 |
| | | | 14 | | 5 | | 5 | 565 | 3.5 | 1.25 | 0.54 |
| | | | 17 | | 178 | | 6 | 841 | 2.5 | 1.61 | 0.62 |
| — | — | 14 | 136 | — | 490 | 20 | 8 | 1,957 | | | |
| 2 | 8 | 37 | 134 | 1 | 82 | 15 | 15 | 4,173 | | | |
| — | 13 | 24 | 270 | — | 1,145 | 1 | 12 | 3,948 | | | |
| 2 | 21 | 75 | 540 | 1 | 1,717 | 36 | 16 | 10,078 | | | |
| 0.02 | 0.21 | 0.74 | 5.36 | 0.01 | 17.04 | 0.36 | 0.16 | | | | |

F) Mayfly nymphs on average weighed less than stonefly nymphs. No correlation between species richness and biomass could be demonstrated.

G) There was a clear tendency of higher biomass values per unit area being associated with smaller stream sizes; this held for both mayflies and stoneflies. By contrast, there was no apparent relationship be-

Appendix B. Survey of sampling results of Plecoptera.

| | Sampled bottom area (m ²) | <i>Brachyptera risi</i> | <i>Taeniopteryx nebulosa</i> | <i>Amphinemura borealis</i> | <i>A. standfussi</i> | <i>A. sulcicollis</i> | <i>Nemoura avicularis</i> | <i>N. cinerea</i> | <i>Nemurella picteti</i> | <i>Protonemura meyeri</i> | <i>Leuctra digitata</i> | <i>L. fusca</i> | <i>L. hippopus</i> |
|----------|--|-----------------------------|----------------------------------|---------------------------------|----------------------|-----------------------|-------------------------------|-------------------|------------------------------|-------------------------------|-----------------------------|-----------------|--------------------|
| H spring | 1.8 | | | | | | | | | 1 | | | |
| summer | 1.2 | | | | 4 | 1 | | | | | | 14 | |
| autumn | 1.4 | | 8 | | | | | | | | | | |
| E spring | 2.0 | | | | | | | | | | | | 1 |
| summer | 2.1 | | | | 3 | | | | | | | 1 | |
| autumn | 2.1 | | 112 | | | | | | | | | 48 | |
| K spring | 3.2 | 1 | | | | 1 | 2 | 2 | | 1 | | | 27 |
| summer | 1.8 | | | 20 | 2 | | | | | | | 1 | |
| autumn | 1.1 | | 4 | | | | | | | 9 | | | |
| N spring | 2.2 | | | 4 | | 1 | | 1 | 2 | 1 | | | 16 |
| summer | 0.8 | | | 20 | | | | | | | | 1 | |
| autumn | 1.4 | | 3 | | | | | | | | | | |
| B spring | 2.3 | 1 | | | | 1 | | 1 | | | | | 6 |
| summer | 1.0 | | | 54 | | | | | | | | 1 | |
| autumn | 2.1 | | 3 | | | | | | | | | 8 | |
| A spring | 2.9 | | | 8 | | | | | | | | | 88 |
| summer | 1.6 | | | 12 | | 1 | | | | | | | |
| autumn | 1.5 | | 8 | | | | | | | | | 2 | |
| D spring | 3.3 | 22 | | | | | | | | | | | 5 |
| summer | 2.3 | | | | 10 | | | | | | 3 | 37 | |
| autumn | 2.5 | 1 | 4 | | | | | | | 5 | | 2 | |
| O spring | 1.4 | 9 | | | 8 | | | 4 | | | 1 | | 43 |
| summer | 2.4 | | | | 1 | | | | | 17 | | 27 | |
| autumn | 1.9 | | | | | | | | | 19 | 9 | 3 | |
| P spring | 1.3 | 6 | | | | 20 | | 21 | | 6 | | | 196 |
| summer | 1.1 | | | | 10 | | | | | 8 | 5 | 3 | |
| autumn | 1.1 | | | 4 | | | | 10 | | | 28 | 2 | 1 |
| Σ spring | 20.4 | 39 | — | 12 | 8 | 23 | 2 | 29 | 2 | 9 | 1 | — | 382 |
| summer | 14.3 | — | — | 106 | 30 | 2 | — | — | — | 25 | 17 | 85 | — |
| autumn | 15.1 | 1 | 146 | — | — | — | — | 10 | — | 61 | 2 | 64 | — |
| Σ | 49.8 | 40 | 146 | 118 | 38 | 25 | 2 | 39 | 2 | 95 | 20 | 149 | 382 |
| % | | 1.55 | 5.66 | 4.58 | 1.47 | 0.97 | 0.08 | 1.51 | 0.08 | 3.69 | 0.78 | 5.78 | 14.82 |

tween stream size and species richness, nor between stream size and species diversity.

H) The biometric variation (in terms of body length) was greater in mayfly than in stonefly populations.

I) The biometric diversity of communities of mayflies and stoneflies,

| <i>Capnia atra</i> | <i>C. pygmaea</i> | <i>Capnopsis schilleri</i> | <i>Arcynopteryx compacta</i> | <i>Diura bicaudata</i> | <i>D. nanseni</i> | <i>Isoperla grammatica</i> | <i>I. obscura</i> | <i>Dimocras cephalotes</i> | <i>Chloroperla burmeisteri</i> | No. of species (S) | No. of inds. (N) | Biomass (B) (g/m ²) | H' | J' |
|--------------------|-------------------|----------------------------|------------------------------|------------------------|-------------------|----------------------------|-------------------|----------------------------|--------------------------------|--------------------|------------------|---------------------------------|------|------|
| | | | | 1 | 66 | | 7 | | | 4 | 75 | 1.9 | 0.65 | 0.32 |
| | | | | | 30 | 1 | | | | 5 | 50 | 0.1 | 1.47 | 0.63 |
| 1 | | | | 2 | 80 | 7 | | | | 5 | 98 | 1.3 | 0.99 | 0.43 |
| 5 | | | | 2 | 4 | 20 | 1 | | | 6 | 33 | 0.3 | 1.77 | 0.68 |
| | | | | | 8 | 3 | 1 | | | 5 | 16 | 0.04 | 1.91 | 0.82 |
| 1 | | | | 4 | 48 | 83 | | | | 6 | 296 | 0.9 | 2.01 | 0.78 |
| 4 | 1 | | | | 34 | 1 | | | 4 | 11 | 78 | 1.5 | 2.16 | 0.63 |
| | | | 1 | | 2 | 2 | | | | 6 | 28 | 0.1 | 1.51 | 0.58 |
| 3 | | 1 | 1 | | 62 | | | | | 6 | 80 | 0.6 | 1.19 | 0.46 |
| 3 | 1 | | | | 20 | 9 | | | 1 | 11 | 59 | 1.1 | 2.60 | 0.75 |
| | | | | | 1 | 5 | 1 | | | 5 | 28 | 0.6 | 1.31 | 0.56 |
| | | | | | 110 | | | | | 2 | 113 | 1.0 | 0.18 | 0.18 |
| 4 | | | 1 | | 33 | 3 | | | | 8 | 50 | 1.1 | 1.82 | 0.61 |
| | | | | | | 1 | | | | 3 | 56 | 0.5 | 0.48 | 0.30 |
| | | 1 | 1 | | 174 | | | | | 5 | 187 | 1.3 | 0.47 | 0.20 |
| 2 | | | | 2 | 7 | 32 | 1 | | | 7 | 140 | 1.0 | 1.59 | 0.56 |
| | | | | | | 3 | | | | 3 | 16 | 0.02 | 1.01 | 0.64 |
| | | | | 23 | 82 | | | | | 4 | 115 | 2.0 | 1.18 | 0.59 |
| 1 | | | 1 | 5 | 2 | 8 | | | 1 | 8 | 45 | 0.8 | 1.88 | 0.63 |
| | | | | | 61 | 1 | | | | 5 | 113 | 0.1 | 1.56 | 0.67 |
| 2 | | 1 | 2 | 1 | 64 | | | | | 9 | 82 | 0.6 | 1.36 | 0.43 |
| 2 | | | | | 2 | 1 | | 13 | 3 | 10 | 86 | 1.7 | 2.35 | 0.71 |
| | | | | | 15 | | | 52 | | 6 | 121 | 2.0 | 2.11 | 0.82 |
| 1 | | 1 | | | 41 | 1 | | 74 | | 7 | 140 | 2.3 | 1.67 | 0.59 |
| | | 1 | | | 14 | 7 | | 2 | 10 | 10 | 283 | 2.7 | 1.75 | 0.53 |
| | | | | | 7 | 1 | | | | 6 | 34 | 0.1 | 2.35 | 0.91 |
| 17 | | | | | 91 | | | 4 | | 8 | 157 | 1.1 | 1.90 | 0.63 |
| 21 | 1 | 2 | 2 | 10 | 182 | 81 | 9 | 15 | 19 | 20 | 849 | | | |
| — | — | — | 1 | — | 124 | 17 | 2 | 52 | — | 11 | 461 | | | |
| 25 | — | 4 | 4 | 30 | 752 | 91 | — | 78 | — | 13 | 1,268 | | | |
| 46 | 1 | 6 | 7 | 40 | 1,058 | 189 | 11 | 145 | 19 | 22 | 2,578 | | | |
| 1.78 | 0.04 | 0.23 | 0.27 | 1.55 | 41.04 | 7.33 | 0.43 | 5.62 | 0.74 | | | | | |

respectively, was not demonstrably different. Stonefly communities, however, covered a wider range of diversity values than did mayfly communities.

J) Species diversity and size diversity values were not correlated in either taxon.

K) Relative species richness of a given locality changed between seasons.

L) Seasonal changes of community composition were significantly greater among the stoneflies than among the mayflies.

M) Between-locality differences of community composition were greater in stoneflies than in mayflies in two out of three seasons; in the third season no difference could be demonstrated.

Discussion

Differences in the diversity of stonefly communities were strongly correlated with the species richness component, while those of mayfly communities — from the same habitats — were regulated by differences in relative species abundances. Several population and community parameters have been invoked to explain corresponding discrepancies between taxa, and the following discussion will be devoted to an examination of what factors may be relevant for the mayfly and stonefly assemblages described above (WILBUR et al., 1974).

In avian communities, which are more fully studied from these aspects than most others, TRAMER (1969) and KRICHER (1972) found that species richness exerted a dominant influence on community diversity. The stonefly communities showed the same relationship. Bird communities yielded distinctly higher diversity and equitability indices than those found in the present mayfly and stonefly communities. Equitability was found to have an impact on bird community diversity only in certain habitats, such as marshes, where large amounts of food attracted large aggregations of single species, or at most a few species of birds.

The present results emphasize that similar diversity index values may result from rather divergent communities. To be useful, diversity indices must be accompanied by an evaluation of the role of the components of species richness and equitability.

The mayflies and stoneflies were obtained in the same samples. Thus, they inhabited closely similar environments. Therefore, we may discount environmental factors such as, for example, habitat and climatic stability and predictability (CODY, 1974; SOUTHWOOD et al., 1974) or frequency of predation (PIANKA, 1966) when discussing differences in diversity between the mayfly and stonefly communities. Such external factors may be regarded as constant in the present study. Therefore, we have to examine what intrinsic properties of the animal populations and communities may shed light on the reasons for the differences in the composition of the diversity.

Although the sampling sites were designed to encompass streams of widely different size classes, the species richness of both mayflies and

stoneflies was approximately the same at all localities. Certainly, inspection of the data presented in the appendices will reveal that several species were restricted to one or a few localities. Especially the lake outlet localities and the smallest streams were inhabited by certain species that were wanting elsewhere. Evidently, however, species were exchanged for each other, since the total sum remained about the same. This suggests that the communities were saturated and that the available resources were being shared by a maximum number of species. One may question whether some habitat types quite generally possess fewer potential niches than others, and more specifically, whether lotic habitats whose animal populations are supported by a comparatively unstructured food source, viz. allochthonous detritus (MINSHALL, 1967; MADSEN, 1972; MANN et al., 1972), may constitute such an inherently niche-poor habitat type. This idea perhaps finds some support in the fact that running waters differ from most habitats (but see OWEN & OWEN, 1974) in showing no increase in terms of species richness from the pole to the equator (PATRICK, 1966; MACARTHUR, 1969; TRAMER, 1974).

Mayflies, on average, exploit a lower trophic level than do stoneflies. As far as is known, all mayflies subsist on detritus and/or living plant tissues, chiefly epilithic algae (BROWN, 1961; ALBRECHT, 1968; THORUP, 1970; MADSEN, 1972). Some stoneflies also consume a mixture of detritus and living algae, but a number of species are completely or mainly predaceous, such as *Diura*, *Dinocras*, and *Isoperla* (BRINCK, 1949; SHELDON, 1969). It is an astonishing fact that dense populations of such a large predator as *Diura nanseni* (SHELDON, 1972) can be supported by highly oligotrophic subarctic streams and rivers. Clearly, the stoneflies as a group occupy a more varied set of food niches and, as a group average, a higher trophic level than the mayflies.

That trophically lower-level animals, in this case the mayflies, produce large numbers of small progeny in comparison to higher-level ones, such as the stoneflies, is a finding that seems to accord with expectation (cf. also CROSSLEY et al., 1973).

Large cohorts of progeny may mean intense intraspecific competition for food or other resources. Such competition may be mitigated, if the progeny are present in variable sizes at the same time — assuming that large and small individuals draw on partly different resources (VAN VALEN, 1965; SHUGART & BLAYLOCK, 1973). As shown above the mayfly populations were distinguished by a comparatively great morphometric variability. This may be interpreted as a mechanism of reducing intraspecific competition and nymphal mortality. If different age classes have different abilities of surviving environmental stresses, such as droughts or spates, so much the better.

The most abundant mayfly species in the study area, *Baetis rhodani*, is an agile species seeking much of its food on top of illuminated stones, where algal growth is copious. This food niche is presumably rewarding, but hazardous, because of the foraging animal's exposure to predators and to the force of the water current (BISHOP & HYNES, 1969; THIBAUT et al., 1972). The period of maximum growth of most mayflies in Lapland, including *B. rhodani*, falls in the months around the summer solstice. This may be an adaptation to the maximum primary production rate in those months. I have argued elsewhere (ULFSTRAND, 1969) that food requirements of the nymphs of stoneflies and mayflies may influence life history patterns more than demands by the short-lived adults (cf. ILLIES, 1952).

Morphologically, *B. fuscatus* and *B. subalpinus* closely resemble *B. rhodani*. They seem to differ from each other with respect to their preference for different current speeds (ULFSTRAND, 1968 A), and both differ from *B. rhodani* in having a distinctly later flight period (ULFSTRAND, 1969). Also *B. macani* is similar to *B. rhodani* in external morphology, but lives in lakes and, to some extent, lake outlets, and so differs from the other *Baetis* species. The remaining two species, *B. lapponicus* and *B. pumilus*, have such deviating morphologies that they are evidently adapted to microhabitats markedly different from the other *Baetis* species; *B. lapponicus* being dorsoventrally flattened and tending in the direction of the heptageniids, and *B. pumilus* being cylindrical and, at least superficially, singularly ill-shaped to resist the force of the current.

Thus, the genus *Baetis* provides examples of ecological segregation of several types (cf. LACK, 1971; GRANT & MACKAY, 1969). However, the number of mayfly species obtained in the same samples and thus inhabiting the same patches within the same habitat was relatively higher than among the stoneflies. Note that many of the mayflies recorded in the study area (list in ULFSTRAND, 1969) were not eligible, because they exclusively inhabit lenitic habitats. Almost all the stoneflies, by contrast, primarily belong to running waters. Consequently, proportionately more mayflies coexist, if one takes into account that the number of mayfly species available was smaller than one might judge from a total species list.

The stonefly communities in many respects differ from the mayfly communities. Primarily, the distinctly larger seasonal and inter-locality differences in terms of community composition must be pointed out. Such differentiation suggests a high degree of latent competition, or its inverted value, specializations to avoid competition (cf. BROWN, 1973). The lesser morphometric variation of stonefly populations speaks in favour of the same interpretation; each species sits on a narrower adaptive peak. Almost all species grow most rapidly in autumn and early spring, that is, when primary production may be low, and hence largely subsist on a non-

replenishable supply of detritus, excepting *Leuctra fusca* which does grow in summer (BRINCK, 1949) and, of course, the predaceous species. Some stoneflies are relatively big and may take more than one year to complete their life cycles (*Dinocras cephalotes*; in some years also *Diura nanseni*, ULFSTRAND, 1968 B). Stoneflies are extreme specialists of lotic environments and may not easily evade competitive pressures through taking refuge into lacustrine environments. However, *Diura bicaudata*, which in Lapland exclusively inhabits large lakes with stony shores, dwells in streams in Britain (HYNES, 1952). This may be a case of competitive exclusion.

The parameters that are diagnostic between the mayfly and stonefly communities may be integrated in terms of differential selective pathways (MACARTHUR & WILSON, 1967; SOUTHWOOD et al., 1974). The strategy of the mayflies appears to be one of copious output of young that are relatively unspecialized but do achieve a certain amount of intraspecific resource division through a great variation in body size at any point in time. In the stonefly communities, on the other hand, one finds narrower feeding specializations, less violent numerical fluctuations, and strong interspecific interactions. In short, the two groups we have been comparing seem to be placed relatively far from each other on an r to K selection scale.

Zusammenfassung

Quantitative Proben der Ephemeropteren- und Plecopteren-Gesellschaften wurden von Steinoberflächen im Bereich starker Wasserströmung an neun Stationen des Flusses Vindelälven (Schwedisch-Lapland) sowie einiger seiner Nebenflüsse verschiedener Größe entnommen. Das Material wurde im Frühling, Sommer und Herbst gesammelt. Die Proben wurden sowohl auf Artenreichtum, Artendiversität (in Artenreichtum und Equitabilität gegliedert), Individuenreichtum, Dominanz der häufigsten Art, Biomasse, biometrische Variation innerhalb von Populationen und ganzen Artgesellschaften als auch auf zeitliche und räumliche Unterschiede hin untersucht. In den Plecopteren-Gesellschaften war der Index der Artendiversität (H') eng mit dem Faktor Artenreichtum korreliert, in den Ephemeropteren-Gesellschaften dagegen mit dem Faktor Equitabilität. Die Erklärung dieses Unterschiedes ist die Hauptaufgabe der Analyse. Zwischen den Ephemeropteren und den Plecopteren wurden beträchtliche Unterschiede in bezug auf die durchschnittliche trophische Ebene, die relative Bedeutung biotischer und abiotischer Umweltfaktoren (besonders Konkurrenz im weiteren Sinne) und Fortpflanzungsstrategien nachgewiesen, die wahrscheinlich von Bedeutung für die Diversitätsdifferenz zwischen den zu vergleichenden Artengruppen sind. Abschließend werden die Anpassungsmuster der Ephemeropteren und Plecopteren in den Begriffskreis „r- und K-selection“ eingefügt.

Acknowledgements

The field work was supported by the Swedish Natural Science Research Council (grants to Professor PER BRINCK), and later work by further grants to

the author (2196—12, —15). I am most grateful to Professor K. W. CUMMINS and Professor H. B. N. HYNES for encouragement and critical comments and to Dr. CHRISTINE DAHL for assistance in the preparation of the German summary.

References

- ABELE, L. G. (1974): Species diversity of decapod crustaceans. — *Ecology* **55**: 156—161.
- ALBRECHT, M.-L. (1968): Die Wirkung des Lichtes auf die quantitative Verteilung der Fauna im Fließgewässer. — *Limnologica* (Berlin) **6**: 71—82.
- BAILEY, N. T. J. (1968): Statistical methods in biology. — English Universities Press, London, 200 pp.
- BISHOP, J. E. & HYNES, H. B. N. (1969): Downstream drift of the invertebrate fauna in a stream ecosystem. — *Arch. Hydrobiol.* **66**: 56—90.
- BOESCH, D. F. (1972): Species diversity of marine macrobenthos in the Virginia area. — *Chesapeake Sci.* **13**: 206—211.
- (1973): Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. — *Marine Biology* **21**: 226—244.
- BRINCK, P. (1949): Studies on Swedish stoneflies (Plecoptera). — *Opuscula Entomol.*, Suppl. **11**: 1—250.
- BROWN, D. S. (1961): The food of the larvae of *Chloeon dipterum* L. and *Baetis rhodani* (PICTET) (Insecta, Ephemeroptera). — *J. Anim. Ecol.* **30**: 55—75.
- BROWN, J. H. (1973): Species diversity of seed-eating desert rodents in sand dune habitats. — *Ecology* **54**: 775—787.
- CODY, M. L. (1974): Competition and the structure of bird communities. — Princeton Univ. Press (Princeton, N. J.), 318 pp.
- COPELAND, B. J. & BECHTEL, T. J. (1971): Species diversity and water quality in Galveston Bay, Texas. — *Water Air Soil Poll.* **1**: 89—105.
- CROSSLEY, D. A., JR., COULSON, R. N. & GIST, C. S. (1973): Trophic level effects on species diversity in arthropod communities of forest canopies. — *Environm. Entomol.* **2**: 1097—1100.
- DAGET, J., LECORDIER, C. & LÉVÊQUE, C. (1972): Notion de nomocénose: ses applications en écologie. — *Bull. Soc. Ecol.* (Brunoy) **3**: 448—462.
- DEJONG, T. M. (1975): A comparison of three diversity indices based on their components of richness and evenness. — *Oikos* **26**: 222—227.
- DICKMAN, M. (1968): Some indices of diversity. — *Ecology* **49**: 1191—1193.
- GRANT, P. R. & MACKAY, R. J. (1969): Ecological segregation of systematically related stream insects. — *Can. J. Zool.* **47**: 691—694.
- HARMAN, W. N. (1972): Benthic substrates: their effect on freshwater Mollusca. — *Ecology* **53**: 271—277.
- HEIP, C. & DEGRAEMER, W. (1974): The diversity of nematode communities in the southern North Sea. — *J. mar. biol. Ass. U. K.* **54**: 251—255.
- HURLBERT, S. H. (1971): The nonconcept of species diversity: a critique and alternative parameters. — *Ecology* **52**: 577—586.
- HYNES, H. B. N. (1952): The Plecoptera of the Isle of Man. — *Proc. R. Ent. Soc. London, Ser. A*, **27**: 71—76.
- ILLIES, J. (1952): Die Plecopteren und das Monardsche Princip. — *Ber. Limnol. Flusst. Freudenthal* **3**: 53—69.

- (1967): (Ed.) *Limnofauna Europaeae*. — G. Fischer Verl. Stuttgart, 474 pp.
- KARR, J. R. (1971): Structure of avian communities in selected Panama and Illinois habitats. — *Ecol. Monogr.* **41**: 207—233.
- KRICHER, J. C. (1972): Bird species diversity: the effect of species richness and equitability on the diversity index. — *Ecology* **53**: 278—282.
- LACK, D. (1971): *Ecological isolation in birds*. — Blackwell, Oxford and Edinburgh, 404 pp.
- LLOYD, M. (1964): Weighting individuals by reproductive value in calculating species diversity. — *Amer. Nat.* **98**: 190—192.
- MACARTHUR, R. H. (1965): Patterns of species diversity. — *Biol. Rev.* **40**: 510—533.
- (1969): Patterns of communities in the tropics. — *Biol. J. Linn. Soc.* **1**: 19—30.
- (1972): *Geographical ecology*. — Harper & Row, New York, 269 pp.
- MACARTHUR, R. H. & MACARTHUR, J. (1961): On bird species diversity. — *Ecology* **42**: 594—598.
- MACARTHUR, R. H. & WILSON, E. O. (1967): *The theory of island biogeography*. — Princeton Univ. Press (Princeton, N. J.), 203 pp.
- MACKAY, R. J. & KALFF, J. (1969): Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream. — *Ecology* **50**: 101—109.
- MADSEN, B. L. (1972): Detritus on stones in small streams. — *Mem. Ist. Ital. Idrobiol.* **29** (Suppl.): 385—403.
- MANN, K. H., BRITTON, R. H., KOWALCZEWSKI, A., LACK, T. J., MATHEWS, C. P., & McDONALD, I. (1972): Productivity and energy flow at all trophic levels in the River Thames, England. — Productivity problems of freshwaters. ed. Z. KAJAK and A. HILLBRICHT-ILKOWSKA, PWN Polish Scientific Publishers (Warszawa and Krakow): 579—596.
- MARGALFF, R. (1968): *Perspectives in ecological theory*. — Chicago Univ. Press (Chicago, Ill.), 111 pp.
- MATHIS, B. J. (1968): Species diversity of benthic macroinvertebrates in three mountain streams. — *Illinois State Acad. Sci.* **61**: 171—176.
- MINSHALL, G. W. (1967): Role of allochthonous detritus in the trophic structure of a woodland springbrook. — *Ecology* **48**: 139—149.
- OWEN, D. F., & OWEN, J. (1974): Species diversity in temperate and tropical Ichneumonidae. — *Nature* (London) **249**: 583—584.
- PATRICK, R. (1966): *The Catherwood Peruvian* — Amazon Expedition. I. Limnological observations and discussion of results. — *Monogr. Acad. Nat. Sci. Philadelphia* **14**: 5—40.
- PIANKA, E. R. (1966): Latitudinal gradients in species diversity: a review of concepts. — *Amer. Nat.* **100**: 33—46.
- (1967): On lizard species diversity: North American flatland deserts. — *Ecology* **48**: 333—351.
- (1973): *Evolutionary ecology*. — Harper & Row (New York), 356 pp.
- PIMENTEL, D., & WHEELER, A. G., Jr. (1973): Species and diversity of arthropods in the alfalfa community. — *Environm. Entomol.* **2**: 659—668.
- RECHER, H. (1971): Bird species diversity: a review of the relation between species number and environment. — *Proc. Ecol. Soc. Australia* **6**: 135—152.
- SANDERS, H. L. (1968): Marine benthic diversity: a comparative study. — *Amer. Nat.* **102**: 243—282.

- SHELDON, A. L. (1969): Size relationships of *Acroneuria californica* and its prey. — *Hydrobiologia* **34**: 85—94.
- (1972): Comparative ecology of *Arcynopteryx* and *Diura* (Plecoptera) in a California stream. — *Arch. Hydrobiol.* **69**: 521—546.
- SHUGART, H. H., JR. & BLAYLOCK, B. G. (1973): The niche-variation hypothesis: an experimental study with *Drosophila* populations. — *Amer. Nat.* **107**: 5—378.
- SIEGEL, S. (1956): Nonparametric statistics for the behavioral sciences. — McGraw-Hill Book Co., New York, 312 pp.
- SOUTHWOOD, T. R. E., MAY, R. M., HASSELL, M. P. & CONWAY, G. R. (1974): Ecological strategies and population parameters. — *Amer. Nat.* **108**: 791—804.
- THIBAUT, M., CUINAT, R. & LESEL, R. (1972): Etude écologique d'un ruisseau à truites des Pyrénées, le Lissuraga. — Productivity problems of freshwaters, ed. by Z. KAJAK and A. HILLBRICHT-ILKOWSKA, PWN Polish Scientific Publishers (Warszawa and Krakow): 597—613.
- THORUP, J. (1970): Frequency analysis in running waters and its application on a springbrook community. — *Arch. Hydrobiol.* **68**: 126—142.
- TRAMER, E. J. (1969): Bird species diversity: components of Shannon's formula. — *Ecology* **50**: 927—929.
- (1974): On latitudinal gradients in avian diversity. — *Condor* **76**: 123—130.
- ULFSTRAND, S. (1968 A): Benthic animal communities in Lapland streams. — *Oikos Suppl.* **10**: 1—120.
- (1968 B): Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera Simuliidae). — *Oikos* **19**: 167—190.
- (1969): Ephemeroptera and Plecoptera from River Vindelälven in Swedish Lapland. — *Entomol. Tidskr.* **90**: 145—165.
- ULFSTRAND, S., NILSSON, L. M. & STERGAR, A. (1974): Composition and diversity of benthic species collectives colonizing implanted substrates in a South Swedish stream. — *Entomol. Scand.* **5**: 115—122.
- ULFSTRAND, S., SVENSSON, B., ENCKELL, P. H., HAGERMAN, L. & OTTO, C. (1971): Benthic insect communities of streams in Stora Sjöfallet National Park, Swedish Lapland. — *Entomol. Scand.* **2**: 309—336.
- VAN VALEN, L. (1965): Morphological variation and width of ecological niche. — *Amer. Nat.* **99**: 377—390.
- WATT, K. E. F. (1973): Principles of environmental science. — McGraw-Hill Book Co. (New York), 319 pp.
- WILBUR, H. M., TINKLE, D. W. & COLLINS, J. P. (1974): Environmental certainty, trophic level, and resource availability in life history evolution. — *Amer. Nat.* **108**: 805—817.
- WILHM, J. L. (1968): Use of biomass units in Shannon's formula. — *Ecology* **49**: 153—156.
- WHITTAKER, R. H. (1960): Vegetation of the Siskiyou mountains, Oregon and California. — *Ecol. Monogr.* **30**: 279—338.
- (1972): Evolution and measurement of species diversity. — *Taxon* **21**: 213—251.

Address of the Author:

STAFFAN ULFSTRAND, Department of Animal Ecology, University of Lund, S-22362 Lund (Sweden).