

Composition and Diversity of Benthic Species Collectives Colonizing Implanted Substrates in a South Swedish Stream

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Abstract

Trays with stones were implanted in a south Swedish stream. They rapidly became covered by large quantities of debris and detritus. The composition and diversity of the colonizing species collectives were examined after 2, 4, 8, 15 and 32 days. The changing substrate conditions were accompanied by a successive exchange of species

demonstrating their capability of active habitat selection. The species diversity first rose but apparently approached an asymptotic level at the end of the experiment. Species richness was the major factor affecting the diversity, while the evenness component played a minor role, at least in more comprehensive samples.

Introduction

The extraordinary motility of many lotic animal populations has been demonstrated in numerous investigations. Thus, for example, after the bottom animals had been dislodged during dredging operations, or when logs were thrown into a river, or dried-up stream beds were re-inundated, large quantities of benthic animals belonging to many species quickly invaded the empty bottom areas (Müller, 1953, 1954; Harrison, 1966; Chutter, 1968; Nilssen & Larimore, 1973). Even unicellular algae have been shown by Müller-Haeckel (1973) to drift along streams with a distinct diel periodicity. There are several comprehensive papers reviewing the upstream and downstream movements in various lotic populations (e.g. Bishop & Hynes, 1969A, 1969B).

However, the relatively detailed information about the drift process and some of the factors affecting its magnitude is not matched by a corresponding understanding of the ecological role of this phenomenon. Moon (1940) was probably the first to employ artificial substrates implanted in a stream as a tool for the study of drift and colonization processes. Later this technique has been adopted for various purposes, i.a., by Waters (1964), Ulfstrand (1968), Cairns & Ruthven (1970) and Glime & Clemons (1972). In a previous study one of us used artificial substrates to study, amongst other things, the habitat requirements of several

benthic insect species in Lapland rivers (Ulfstrand, op. cit.). In south Sweden conditions are quite different, and this prompted comparative studies. One of the chief differences is the extremely high rate of sedimentation in south Swedish streams in comparison with Lapland water-courses which, apart from brief periods during the snow-melting, carry almost pure "drinking water". Therefore, whilst colonization trays remain almost free from organic debris during an exposure time of up to several weeks in Lapland, they undergo a rapid transition within days in south Sweden.

The purpose of the study on which we now report was to examine the colonization process in a south Swedish stream and the composition and diversity of the colonizing species collective.

Study area and methods

The experiment was carried out in April to May 1973 at Rövarekulan, Bråån, in south Sweden (55°50'N, 13°30'E)—a moderately small stream running through farmland, pastures, and deciduous groves, locally along a fairly steep gradient. At the site for our work the stream is shadowed by a dense canopy mainly of beech *Fagus sylvatica*. The current is relatively rapid, the depth is less than 75 cm, and the bottom consists of large stones and coarse gravel with copious quan-

tities of organic debris in different stages of decomposition filling all crevices and inter-spaces.

The colonization trays were circular with a surface area of 0.25 m² and had an 8 cm high rim. They were placed inside a nylon net bag with 22 meshes/cm. During exposure in the stream the bag was rolled down around the rim, and when a tray was to be lifted from the stream, the bag was first rapidly unrolled, so that all animals, unable to escape through the meshes, were contained inside the bag. The substrate placed in the trays consisted of stones and gravel from a nearby quarry and hence initially was devoid of periphyton. The debris accumulating inside the trays was not quantified, but after about a fortnight it had covered the contents to the extent that only the largest stones and the metal rims protruded from the debris. Thus, the substrate in the trays changed from pure hard bottom to a mixture of hard and soft bottom.

Twenty trays were implanted in the stream and removed in sets of four after 2, 4, 8, 15 and 32 days, respectively. The animals were sorted out alive and preserved in alcohol. They were identified to species level except for the following taxa which had to be discounted, viz. Oligochaeta, Coleoptera, Mollusca (mainly *Pisidium* sp.), Diptera: Tipulidae and related families, and Diptera: Chironomidae, Chironominae. Apart from the last-mentioned these groups together made up <1% of the total material, whilst the Chironominae were obtained in a number of about 4000 individuals and thus represented a sizeable fraction of the total community.

Shannon's information index has been adopted for the diversity expressions according to the formula

$$H = - \sum_i p_i^2 \log p_i$$

where p_i is the proportion of the i :th species in the sample. A measurement of the evenness of the species abundances was calculated as

$$E = \frac{H}{\log S}$$

where S is the total number of species in the sample.

Results

Table 1 presents a survey of the successive colonization of the trays. A total of approx.

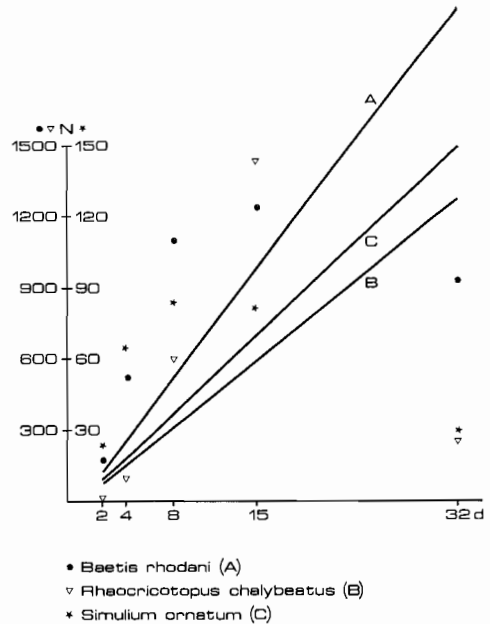


Fig. 1. Numbers of individuals of three species whose rate of colonization decreased towards the end of the period. If the average rate had prevailed throughout, the numbers would have risen as indicated by the lines.

23,000 specimens was obtained. Among the taxa that could be broken down to species level, Amphipoda, Ephemeroptera and Chironomidae Orthoclaadiinae strongly dominated. Five species attained totals of more than 1000 individuals, viz. *Gammarus pulex*, *Baetis rhodani*, *Rheocricotopus chalybeatus* and *Rheorthocladus* *eg.* *rubicundus/majus*. The last-mentioned taxon possibly consisted of more than one species, and this also applies to *Hydropsyche* sp. Apart from these two cases, however, the list contains only taxa consisting of one species only, although sometimes this could not be named.

A glance at the table reveals that the process of colonization was widely different in different species. Several examples are shown in figs. 1 to 3, where we also have entered lines showing the colonization process if the daily rate had been constant for a given species all the time (based on averages for the experimental trays). Certain species colonized the trays at a higher rate initially than later, for example, *Baetis rhodani* and *Simulium ornatum*, whilst other species, such as *Caenis*

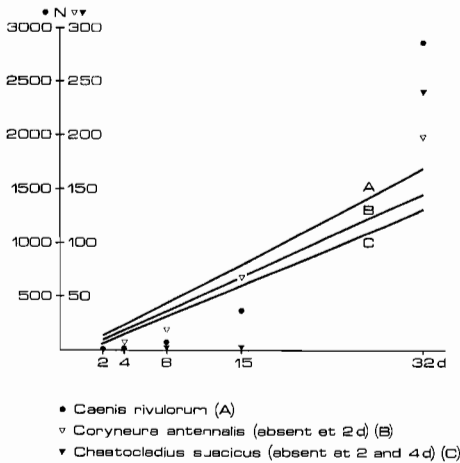


Fig. 2. Numbers of individuals of three species whose rate of colonization increased towards the end of the period. For further explanation, see Fig. 1.

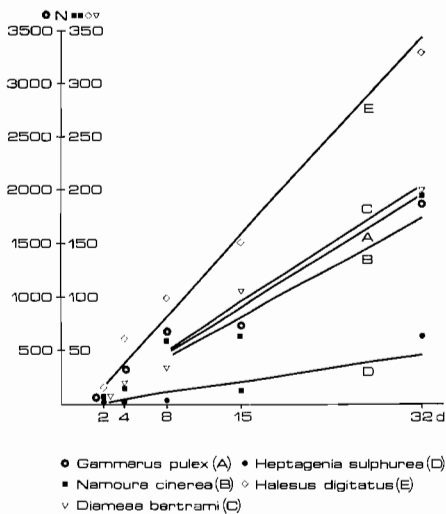


Fig. 3. Numbers of individuals of five species whose rate of colonization did not change appreciably in the course of the period. For further explanation, see Fig. 1.

rivulorum and *Chaetocladus suecicus* appeared in much larger numbers on the last two sampling occasions. The colonization of several species was found to proceed with an approximately even rate throughout the period, for example, *Gammarus pulex* and *Potamophylax cingulatus*.

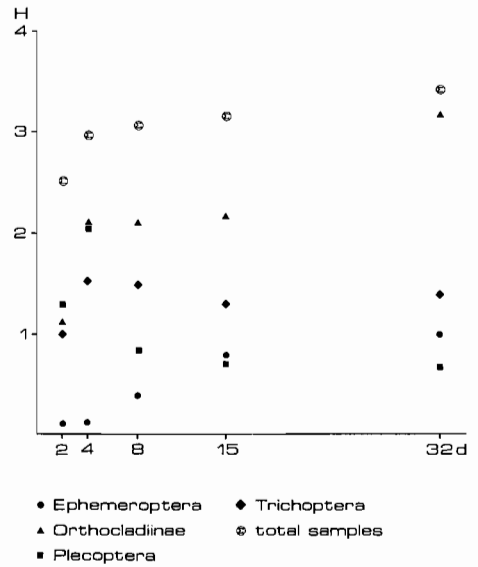


Fig. 4. Changes in species diversity (H) in four insect groups and in the whole samples (including all groups mentioned in Tab. 1) in the course of the experiment.

As shown in fig. 4 the species diversity of the animal collectives populating the trays rose over the first sampling occasions, later to plane out. This pattern can be recognized in each of separate taxa as well as in the total collective, although in the Plecoptera the diversity rose to a peak before sinking back to a lower and more even level.

The relationship between the diversity index values and the numbers of species is examined in fig. 5. The association is close whether the successive samples of each of the four separate taxa (Ephemeroptera, Plecoptera, Trichoptera, Orthocladinae) or values for the whole collective of identified species are used. In fig. 6 the relationship between the diversity index values and the species evenness component is represented. The correlation is weaker, though significant, between these two parameters, as long as the samples of each separate taxon are used, but is not demonstrable for the pooled samples of the entire species collective. The pooled samples of the relatively species-poor Ephemeroptera, Plecoptera and Trichoptera (see Table 1) have relatively low species diversity indices ($H=1.13, 1.47, 1.03$), whilst the speciesricher Orthocladinae attained an H of 2.66. The whole collection of animals

Table 1. The successive colonization of the experimental trays. Each figure represents the total number of animals in a set of four trays removed on the same occasion after having been exposed in the stream for 2, 4, 8, 15 and 32 days, respectively.

	2 d	4 d	8 d	15 d	32 d	Σ
HIRUDINEA						
<i>Acanthobdella peledina</i> Gr.	—	—	1	—	—	1
<i>Erpobdella octoculata</i> L.	—	—	—	2	—	2
<i>Glossiphonia complanata</i> L.	—	2	3	4	20	29
<i>G. heteroclita</i> L.	—	—	—	—	3	3
<i>Haemopsis sanguisuga</i> L.	—	—	—	—	1	1
<i>Helobdella stagnalis</i> L.	1	2	1	—	—	4
<i>Hemiclepsis marginata</i> O. F. M.	—	—	—	—	1	1
<i>Theromyzon tessellatum</i> O. F. M.	—	—	—	1	—	1
Total:	1	4	5	7	25	42
DECAPODA						
<i>Astacus astacus</i> L.	—	—	2	1	—	3
ISOPODA						
<i>Asellus aquaticus</i> L.	1	1	6	3	3	14
AMPHIPODA						
<i>Gammarus pulex</i> L.	52	338	673	727	2006	3796
EPHEMEROPTERA						
<i>Baetis pumilus</i> Burm.	—	—	—	—	8	8
<i>B. rhodani</i> Pict.	180	522	1106	1238	938	3984
<i>B. sp. A</i>	—	—	4	4	—	8
<i>Caenis rivulorum</i> Etn.	1	7	68	287	2871	3234
<i>Ephemera danica</i> Müll.	—	—	3	4	25	32
<i>Heptagenia fuscogrisea</i> Retz.	—	—	—	—	1	1
<i>H. sulphurea</i> Müll.	1	3	5	13	64	86
Total:	182	532	1186	1546	3907	7353
PLECOPTERA						
<i>Amphinemura borealis</i> Mort.	—	—	—	1	12	13
<i>Capnia bifrons</i> Newm.	—	3	3	—	—	6
<i>C. nigra</i> Pict.	—	—	—	1	—	1
<i>Isoperla grammatica</i> Pod.	2	3	1	1	15	22
<i>Leuctra hippopus</i> Kmp.	—	2	—	—	1	3
<i>Nemoura cinerea</i> Retz.	5	13	60	63	194	335
<i>N. flexuosa</i> Aub.	—	3	8	7	—	18
<i>Nemurella picteti</i> Klp.	—	—	—	—	1	1
<i>Protonemura meyeri</i> Pict.	1	1	—	—	—	2
Total:	8	25	72	73	223	401
TRICHOPTERA						
<i>Rhyacophila fasciata</i> Hag.	3	2	3	2	3	13
<i>Hydropsyche</i> sp.	—	9	22	16	82	129
<i>Plectrocnemia conspersa</i> Curt.	—	3	5	7	28	43
<i>Polycentropus</i> sp.	—	2	—	1	—	3
<i>Limnephilus flavicornis</i> Fbr.	—	—	—	—	1	1
<i>L. rhombicus</i> L.	1	—	1	1	5	8
<i>Limnephilus</i> sp.	1	6	10	9	8	34
<i>Glyphotaelius pellucidus</i> Retz.	—	—	1	—	2	3
<i>Halesus digitatus</i> Schrk.	20	60	99	151	330	660

	2 d	4 d	8 d	15 d	32 d	Σ
<i>H. radiatus</i> Curt.	—	—	—	—	2	2
<i>H. tessellatus</i> Ramb.	—	—	—	1	—	1
<i>Micropterna sequax</i> McL.	—	2	1	7	2	12
<i>Silo pallipes</i> F.	—	—	—	—	1	1
Total:	25	84	142	195	464	910
DIPTERA SIMULIIDAE						
<i>Simulium ornatum</i> Mg.	24	65	84	82	29	284
<i>Simulium</i> sp. A	—	1	—	15	8	24
<i>Simulium</i> sp. B	—	—	2	—	7	9
Total:	24	66	86	97	44	317
DIPTERA CHIRONOMIDAE						
ORTHOCLADIINAE						
<i>Brillia longifurca</i> K.	—	1	—	1	—	2
<i>B. modesta</i> Mg.	1	8	21	26	48	104
<i>Chaetocladius suecicus</i> K.	—	—	3	1	239	253
<i>Coryneura</i> cf. <i>antennalis</i> K.	—	7	17	60	196	280
<i>Cricotopus</i> sp. A	—	1	3	123	74	201
<i>Cricotopus</i> sp. B	—	—	—	1	16	17
<i>Diamesa</i> cf. <i>bertrami</i> Edw.	7	17	34	134	200	392
<i>D.</i> cf. <i>hygropetrica</i> K.	—	1	—	—	—	1
<i>Diamesa</i> sp. A	1	—	6	10	3	20
<i>Diplocladius cultriger</i> K.	—	1	4	1	—	6
<i>Epoicocladius ephemerae</i> K.	—	—	1	1	40	42
<i>Eukiefferiella bavarica</i> G.	—	—	5	—	1	6
<i>E. cyanea</i> Th.	—	—	—	—	1	1
<i>E.</i> cf. <i>discoloripes</i> G.	1	10	45	81	7	144
<i>E. potthasti</i> Lehm.	—	—	3	2	—	6
<i>Euorthocladius rivicola</i> K.	1	4	—	—	33	38
<i>E. rivulorum</i> K.	13	46	114	256	139	568
<i>Heterotrissocladius marcidus</i> Walk.	—	—	—	3	4	7
<i>Limnophyes</i> sp. A	—	2	2	5	9	18
<i>Metriocnemus hygropetricus</i> K.	—	4	2	—	—	6
<i>Metriocnemus</i> sp. A	—	—	1	—	—	1
<i>Microcricotopus rectinervis</i> K.	—	11	41	159	444	655
<i>Parakiefferiella bathophila</i> K.	—	1	1	—	—	2
<i>Parametriocnemus stylatus</i> K.	—	2	8	17	32	59
<i>Paraphaenocladius impensus</i> Walk.	—	—	2	1	32	35
<i>P. pseudirritus</i> Str.	—	—	—	—	1	1
<i>Potthastia longimana</i> K.	—	—	—	—	4	4
<i>Prodiamesa olivacea</i> Mg.	1	—	—	3	4	8
<i>Psectrocladius</i> sp. A	—	—	—	1	—	1
<i>Pseudorthocladius curtistylus</i> G.	—	1	—	—	—	1
<i>Rheocricotopus chalybeatus</i> Edw.	6	102	599	1461	252	2420
<i>Rheorthocladius saxicola</i> K.	—	—	27	—	—	27
<i>R.</i> eg. <i>rubicundus/majus</i>	135	322	1000	2043	1068	4568
<i>Synorthocladius semivirens</i> K.	—	1	1	2	71	75
<i>Thienemanniella</i> cf. <i>clavicornis</i> K.	—	4	32	86	63	185
<i>Trissocladius distylus</i> K.	—	1	—	—	—	1
Unident. species A	1	3	19	26	7	56
Total:	167	550	1991	4514	2989	10211
Total, all taxa:	460	1600	4163	7163	9661	23047

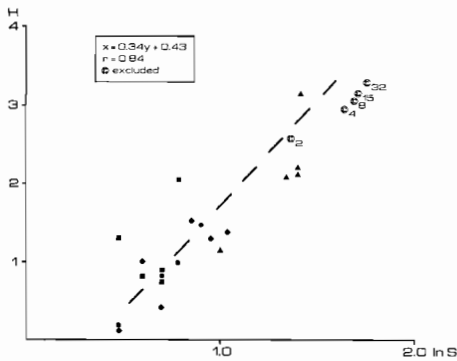


Fig. 5. Relationship between species diversity (H) and number of species (ln S) in four insect groups. Omitted from the regression calculation but shown for comparison are the corresponding values referring to the total samples (based on Tab. 1). Symbols are explained in Fig. 4.

(80 identified species) has an H of 3.49 and an E of 0.55.

Discussion

When the trays were placed in the stream, they represented patches or islands of alien habitat. They were surrounded by bottom areas with a great deal of detritus accumulations, whilst the trays initially contained no such material. Therefore, it seems hardly surprising that, both in terms of species and of individuals, the colonization rate was comparatively low during the first days of exposure. Under natural conditions naked stones have been found to harbour fewer species than detritus (e.g. Mackay & Kalff, 1969). The process of detritus sedimentation increased the similarities between the trays and the surrounding bottom, and the species composition of the trays presumably approached the natural situation. However, some species clearly found the trays more suitable to live in soon after their implantation than later. This applied to *Simulium ornatum* and *Baetis rhodani* (fig. 1), whose rates of colonization decreased markedly during the later part of the experiment, presumably because more animals departed than arrived per time unit. As demonstrated in fig. 2, some species, of which *Caenis rivulorum* is a good example, completely

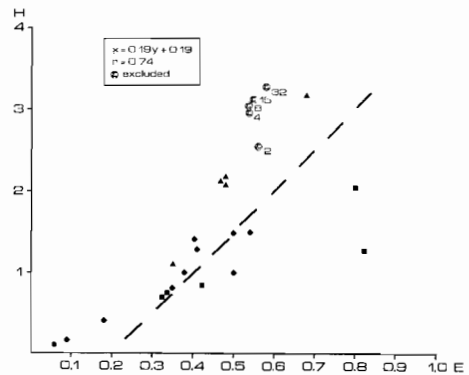


Fig. 6. Relationship between species diversity (H) and the evenness component (E) in four insect groups. Omitted from the regression calculation but shown for comparison are the corresponding values referring to the total samples (based on Tab. 1). Symbols are explained in Fig. 4.

refused to colonize the trays during the first week, but later inhabited them in huge numbers. Since there is no reason to believe that the numbers of *C. rivulorum* entering the trays drastically changed in the course of the experiment, this probably is a result of the species' habitat selection.

It is interesting that one of the species colonizing the trays at a constant rate regardless of their changing conditions is *Gammarus pulex*, a euryoecious and usually abundant species. Because of its prolonged period of reproduction, local populations of this species very often consist of a mixture of individuals ranging from newly born to mature. The great range of individual body sizes may contribute to an effective resource exploitation by the population; this subject is being pursued presently.

Our colonization experiments illustrate the active element in the process of habitat selection of the species involved (see survey by Meadows & Campbell, 1972). A very close dependency on narrowly circumscribed environmental conditions has been demonstrated in several lotic invertebrates, for example in Trichoptera by Edington (1965) and Williams & Hynes (1973). Our experiments also demonstrate the great extent of drift in many populations and point to its ecological significance. It is true that sudden spates have been known to inflict heavy losses in benthic populations,

but apart from such accidents drifting with the current provides a means of energy-saving locomotion enabling individuals to reach more favourable places than those from which they set out. We agree with Lehmkuhl & Anderson (1972) that drift normally leads to dispersal rather than depletion.

Naturally, the rate of colonization of our trays may have changed over time for reasons other than the changing substrate conditions. The animals may fluctuate with respect to their reactions to environmental stimuli leading to different drift and/or colonization rates. It has been repeatedly shown for various animals that certain age or size classes take part in population movements out of proportion to their share of the benthic population (see Otto, 1971, for *Potamophylax cingulatus*). This possibility is probably important for certain chironomids that have a very rapid development, but for other taxa we believe it to be of minor importance.

At the start of the experiments the trays offered a pure hard bottom substrate with no organic debris. After a brief time they became covered with so much organic debris that, like the surroundings, they provided a biotope of very mixed substrates. The process was so rapid that there are indications of an equilibrium being approached at the end of the experiment, both in terms of species number and diversity. This emerges from a comparison of the diversity indices after 15 and 32 days, respectively (fig. 4). This equilibrium clearly was due to colonization rates of different populations changing in different directions, so that increases and decreases approximately outweighed each other.

The only taxon deviating from the general pattern with respect to diversity changes is Plecoptera (fig. 4). This may be due partly to the small number of individuals in the samples, partly to the circumstance that, whilst several species initially colonized the trays, only *Nemoura cinerea* found them suitable for the whole period, so that this species became almost alone. This of course depressed the diversity in this group.

The colonization of substrates implanted in a stream (or any other biotope) has many resemblances to the colonization of islands and to the succession of communities on denuded areas. Early stages of colonization are characterized by a low number of species and rapid rates of turnover and gradually develop into

a stage of greater stability, provided the colonizable substrates are not too simplified in which case the characteristic features of early colonization stages may persist over considerable periods (Dickson & Cairns, 1972). Under certain circumstances an overshoot may precede the equilibrium phase. In our case, the transformation of the implanted substrates into an almost natural complexity was such a fast process that equilibrium was approached within a few weeks.

Unfortunately there are very few studies dealing with the macroinvertebrate species assemblages in lotic environments with which we can compare our findings. It is interesting that Mathis (1968) obtained diversity values similar to ours from what appears to be corresponding biotopes in North America. Great caution, however, is called for in such comparisons since, among other things, taxonomic scope and sampling procedures of different investigations will lead to different results.

The significance of the diversity concept has been discussed mainly on the basis of species collectives of terrestrial environments and, more particularly, of avian communities (recent review by MacArthur, 1972). In the present study the species richness of the samples played the primary role for the diversity value. As the samples were pooled and thus a more complete representation of the natural species collectives was acquired, the evenness component became nearly constant and no longer affected the diversity value. Further work is clearly required to examine these relationships in closer detail. Some special features of lotic ecosystems, such as their pronounced dependency on imported energy and the prevalence of saprophagous food chains in them (Mackay, 1969; Cummins et al., 1966, 1973) suggest that particularly useful information may be derived from work in this biotope.

Acknowledgements

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