The recolonization mechanisms of stream benthos

D. D. WILLIAMS

Pacific Biological Station, British Columbia

H. B. N. HYNES

Department of Biology, University of Waterloo

Williams, D. D. and Hynes, H. B. N. 1976. The recolonization mechanisms of stream benthos. - *Oikos* 27: 265-272.

The animals recolonizing an area of denuded stream substrate are thought to come from four main sources. These are drift, upstream migration within the water, migration from within the substrate, and aerial sources, e.g., oviposition. An experiment in a Canadian stream showed drift to be the most important source of recolonizing animals, contributing 41.4% of the total number that settled on an area of 1800 cm². This compares with 28.2% from aerial sources while upstream migration and movement up from within the substrate contributed about equally (18.2% and 19.1%, respectively). Clearly then, all four directions are important in repopulating bare areas. Further, many groups of organisms were found to have preferred directions from which they recolonize and this, it is argued, may lead to the establishment of separate and distinct faunal assemblages if the other directions are excluded.

D. D. Williams, Dept of the Environment, Pacific Biological Station, Nanaimo, B. C., Canada V9R 5K6. H. B. N. Hynes, Dept of Biology, University of Waterloo, Waterloo, Ontario, Canada N2L 3C1.

Предполагается, что животные, вновь заселяющие участки денудированного течением субстрата, появляются из 4-х главных источников. Это - дрейф, миграции в воде вверх по течению, миграции внутри субстрата и по воздуху, т.е. яйцекладка. Опыт в Канадской реке показал, что дрейф - наиболее важный источник животных при реколонизации, поставляющий 41,4% животных от общего количества, поселившегося на площади 1800 см². В сравнении с этим, 28,2% поступает из воздушной среды, а миграции вверх по течению и приток из субстрата дают примерно равные количества животных /18,2 и 19,1%, соответственно/. Ясно, что все 4 источника имеют значение в заселении незанятых территорий. Далее установлено, что многие группы организмов проявляют избирательность к способу заселения субстрата, и это, как аргументируется, может привести к формированию отдельных, отличающихся друг от друга фаунистических комплексов, при исключении других способов заселения.

Accepted 12 January 1976

© OIKOS

Introduction

Mayr (1964) defined colonization as "the invasion of species into disturbed and newly created habitats." Obviously, a certain amount of colonization of a disturbed habitat will be by original species, or recolonizers, which had been wiped out by the perturbations.

Recolonization studies on running water benthos have shown that animals quickly re-appear in the affected areas (e.g. Müller 1954, Waters 1964). However, former taxonomic diversity and population densities may not be re-established for quite some time, depending upon the severity and duration of the stress and the availability of undamaged areas to serve as sources for recolonization (Cairns et al. 1971).

In the light of these studies and our own observations, it became apparent that denuded areas of substrate on a stream bed would be open to recolonization from four main sources. These are: downstream drift, upstream migration within the water, vertically upward migration from within the substrate, and aerial sources, e.g., oviposition by adult insects. In this paper, we propose to illustrate the relative importance of each of these four sources to the fully recolonized state.

The four sources

Drift is a very important aspect of life in running water (see Waters 1972) and has been found to be an important source of recolonizing organisms. However, Elliott (1967a, b) showed that this importance varies seasonally, being a reflection of the life cycles of the animals involved.

Upstream migration of benthos within the water is a not so well documented, and perhaps a somewhat underestimated process in running water. It has been argued that it acts to compensate for the drift, although few studies have been able to prove this. Bishop and Hynes (1969) found that upstream movement in the Speed River, Ontario, accounted for only 6.5% by numbers and 4% by weight of the drift, and Brusven (1970) found it to be "insignificant" as a means of recolonizing insect-denuded riffles and offsetting drift.

Movement up from within the substrate must also be important, as the hyporheos has been shown to consist of the larvae of many stream insects, and also the adults and immature stages of non-insects (Williams and Hynes 1974). This aspect has been little studied, although certain researchers have noted remarkably quick recoveries of benthos (not from drift or upstream migration and too rapid for aerial recolonization) after catastrophes such as spates, erosion, chemical spills and insecticide application.

Colonization from aerial sources, via oviposition, too, is important (see Otto and Svensson 1976) but it is obviously limited to the spring and autumn months in temperate latitudes, although it may occur all the year round in the tropics (Fernando 1958).

The stream

The experimental area was located on a tributary of the Nith River, Wilmot Township, Ontario (43°30'N; 80°30'W). This is a slow-flowing (10 to 20 cm s⁻¹ during the summer), meandering, silty stream, fed mostly from agricultural drainage. On average, it is about 4 m wide and 30 cm deep in the riffle areas, but some pools may be as wide as 8 m and 50 cm deep. Its course alternates through open pasture and deciduous woodland. The substrate consists of a 30 cm layer of mixed gravel with some large rocks (10 to 30 cm in diameter) underlain by sand and clay. During the period of the experiment (June) the water temperature remained around 20°C.

Material and methods

Four types of trap were designed to isolate each of the faunal fractions contributing to the recolonization of stream substrates. They are shown in Fig. 1.

Trap A was designed to screen out all access to the substrate than by drift. A sterilized substrate similar in composition to that of the stream bed was placed in the bottom wooden tray (60 cm × 30 cm) to a depth of 5 cm. A rectangular, 0.5 cm thick, perspex cover was attached to the sides of the trap, and a sheet of polyethylene was stuck to the upstream end so as to touch the surface of the water and thus prevent adult insects from flying in and ovipositing. The downstream end of the trap had two vertical slots between which a 1 m long drift net of 135 µm mesh could be placed, and a sheet of wood sealed off the end of the box above the net frame. A rectangular metal funnel was fitted inside the mouth of the drift net in order to prevent animals from crawling back once they had passed into the net. Positioning on the stream bed required the removal of the top 5 cm of substrate and the trap was sunk into this space. It was held stationary by pegs driven through eye-bolts at the corners. Because of the small mesh the net was brushed off at least once daily, to remove silt, and it was emptied once every 2 or 3 days.

Trap B was constructed to allow entry only to benthic organisms moving upstream. It too, had a perspex-covered wooden tray base, but this was divided in half by a thin wooden strip so that the two halves could be compared. The downstream side was open to the current but again polyethylene sheet sealed off the air-space above the water. The upstream side of the box was screened with three layers. The first of these was 1 cm mesh chicken-wire which prevented large debris from accumulating on the two layers of nitex netting placed immediately behind. The first of these had 250 µm openings and the second 135 µm; both were stretched on rectangular wooden frames (3 cm wide) which fitted into vertical slots just behind the wire. All joints were tight so that no animals could move around the screens. The trap was set into the stream bed in similar fashion

Fig. 1. The four types of recolonization traps:

- A. Drift
- B. Benthic upstream migration
- C. Vertical upward migration
- D. Aerial

(Arrows indicate the direction of entry of animals into each trap; direction of current is from left to right.)

to Trap A, but with the open end facing downstream. The screens were cleaned once daily.

Trap C allowed access to only those organisms moving vertically up from the lower levels of the substrate. Again, the perspex-covered wooden tray formed the frame, but this time the tray had a 1 cm mesh chicken-wire base through which animals could pass. The upstream end was again screened by three layers, and, in addition, the downstream end had one screen of 135 μm nitex. In this case, the substrate was added after the trap was in position on the stream bed.

Trap D allowed colonization by aerial forms only. It consisted of a 60 × 30 cm × 15 cm (deep) box made entirely of perspex sheet. The upstream end has 250 μm and 135 μm nitex screens, while the downstream end had only one of 135 μm. A rectangular block of polystyrene foam was glued to each of the top outside edges of the box to serve as floats; for camouflage purposes they were painted green. Guy ropes attached the trap to the stream bank and in this way the trap was free to move up and down with the water level. Substrate was added until the whole thing floated with approximately 7 cm of the trap projecting above the waterline.

A control trap was also used. This consisted merely of the standard area wooden frame with a 1 cm mesh wire bottom. It was thus open to all the various means of recolonization.

The use of screens caused a certain reduction (approximately 25%) of the water velocity in the traps. This

was unavoidable, but with the exception of the controls it was the same for each.

The arrangement of two of each type of these traps along the stream bed was such that no one trap would interfere with the colonization of another. Fig. 2 shows their positions along a section of uniform riffle during June 1972 in the Nith tributary. The drift traps were the furthest upstream and the upstream migration traps the furthest downstream, with the others in pairs in the space between. All the traps were located in midstream so as to minimize faunal distribution effects. They were left for 28 days – which seemed to be a reasonable average of the time thought to be required for complete recolonization (Coleman and Hynes 1970, Mason et al. 1967, Crowe 1970). At the start of the experiment the substrates were seeded with nutrients consisting of a ground-up mixture of dried elm, alder and maple leaves equal in weight to the amount of total organic matter, in the stream substrate, determined beforehand, and measured by a high temperature (450°C for 24 h) weight reduction method. At the end of the experiments each trap, with the exception of type C and the control, was loosened from the substrate and slowly lifted to the water surface allowing water to drain out quietly through the screens. The substrates were then emptied into polyethylene bags and 10% formalin was added. In the case of the other traps, once they had been loosened from the bed, a large nitex hand net was slid under the base to prevent any animals from dropping back through

Fig. 2. The positions of recolonization traps as laid out in the Nith tributary during June 1972. (Arrows indicate the direction of entry of animals into each trap.)

the wire onto the stream bed. The trap and net were then lifted out together. In the laboratory, the samples were floated with saturated calcium chloride solution and subsampled to one-quarter. The animals were then sorted and counted using the counterstaining technique of Williams and Williams (1974).

Results

The numbers and percentages of the total trap contents for the various taxa found in each trap are shown in Tabs 1 to 5. Replication of the numbers in each taxon in the two drift traps, and their percentages of the total trap contents is, in most cases, good (Tab. 1). Therefore, it seems reasonable to merely take an average of the two values for each taxon and to consider this. Also, as the chironomids far outnumbered all the other taxa combined (chironomid/non-chironomid ratio = 4.1/1), they will be dealt with separately. Of the non-chironomid fauna, the nematodes and oligochaetes were the most numerous, constituting 37.2 and 43.8% of the colonizers respectively. It is conceivable to think of nematodes as

Tab. 1. The numbers of each taxon present in drift traps 1 and 2. Average number and percent of each taxon per trap are also given.

	Drift trap 1 no. present	Drift trap 2 no. present	Average no. per trap	Average % per trap
Nematoda..	680	1456	1068	37.2
Oligochaeta..	1224	1292	1258	43.8
Gastropoda..		8	4	0.1
Hirudinea..	72		36	1.3
Cladocera..	80	128	104	3.6
Ostracoda..	72	48	60	2.1
Cyclopoida..	88	112	100	3.5
Harpacticoida....	8	8	8	0.3
Decapoda..	16		8	0.3
Acari.....	24	8	16	0.6
Ephemeroptera.....	64	88	76	2.6
Trichoptera..	16	40	28	1.0
Coleoptera..	80	16	48	1.7
Other				
Diptera...	16	64	40	1.4
Terrestrial..	32		16	0.6
No of non-chironomids..	2472	3268	2870	100
No of Chironomidae....	13104	9304	11204	
Total/trap..	15576	12572	14074	

being common in the drift, but the oligochaetes probably arrived by downstream movement along the surface of the stream bed. Next in numerical importance were the cladocerans (3.6%), cyclopoids (3.5%), mayfly nymphs (2.6%), ostracods (2.1%), and aquatic beetles (1.7%). Most of the remaining taxa comprised an average of 1% or less of the total. Trap 1 had been colonized by 15576 animals and Trap 2 by 12572. The average was 14074, and it is this value which we shall use in later calculation of the relative importance of each source of recolonization to the fully recolonized state.

Tab. 2 shows the data for the upstream migration traps. It will be remembered that the bottom trays of these traps were divided into two. This was to see if any of the organisms, by rheotactic movements, would accumulate in the upstream halves. The results show this to be unlikely; whereas in Trap 1, 3016 animals were found in the upstream half (A) compared with 2777 in the downstream half, in Trap 2, 3153 had colonized the upstream and 3444 the downstream section. The average percentages of the trap contents showed the upstream colonizers to have been primarily nematodes, oligochaetes, cyclopoids and chironomids – although the chironomid/non-chironomid ratio was only 0.64/1 – followed by cladocerans, ostracods and leeches. The average number of animals per tray was 6195.

Tab. 3 gives the data for the traps colonized by animals moving vertically upwards from the lower layers of

Tab. 2. The numbers of each taxon present in upstream migration traps 1 and 2. Average number and percent of each taxon per trap are also given. For each trap A is the upstream and B the downstream half.

	Upstream trap 1 no. present		Upstream trap 2 no. present		Average no. per trap	Average % per trap
	A	B	A	B		
Coelenterata.....			8		4	0.1
Nematoda.....	656	592	504	584	1168	30.9
Oligochaeta.....	536	432	688	572	1114	29.5
Pelecypoda.....		32	32	40	52	1.4
Hirudinea.....	56	80	8	56	100	2.7
Cladocera.....	80	80	88	120	184	4.9
Ostracoda.....	104	80	72	96	176	4.7
Cyclopoida.....	472	336	392	488	844	22.4
Harpacticoida.....		16	8		12	0.3
Amphipoda.....	8				4	0.1
Decapoda.....			1		0.5	0.01
Acari.....		8			4	0.1
Ephemeroptera.....	8	8	8	24	24	0.6
Trichoptera.....	16		8		12	0.3
Coleoptera.....	24	16	40	16	48	1.3
Other Diptera.....	8				4	0.1
Pisces.....		1			0.5	0.01
Terrestrial.....	8	16	24		24	0.6
No. of non-chironomids.....	1976	1697	1881	1996	3775	100
No. of Chironomidae.....	1040	1080	1272	1448	2420	
Total/trap.....	3016	2777	3153	3444	6195	

the substrate. The cyclopoids, leeches and chironomids (chironomid/non-chironomid ratio, 1.7/1) were the most important groups involved, followed by the nematodes, oligochaetes, cladocerans and beetles. The total trap contents were 6058 and 6952 (a difference of less than 15%) giving an average of 6505 animals per trap.

The data for those animals colonizing the aerial traps are shown in Tab. 4. Larval Chironomidae were dominant (chironomid/non-chironomid ratio, 113/1), followed by the collembolans (29.4%), adult and larval aquatic beetles (12.5%), gastropods (12.5%) and leeches (12.5%). The latter two groups must have moved up the outside of the trap, out of the water and over the lip and then down the inside. Therefore, as far as this study is concerned, they have been classed as aerial colonizers. Most of the insects found were immature, but whereas the slower growing species such as *Hydropsyche* sp. were represented by small larvae, the faster growing ones, e.g., *Microtendipes* sp. were present as both early and late instars. These facts together with careful monitoring of the screens for entry of eggs and young larvae, and observed oviposition, strongly suggest that the animals collected come solely from eggs laid directly in the traps. The only surprising group found was the cyclopoids, eight of which were found in each trap. These might be explained by nauplii having been carried in water accidentally splashed into the trap at some stage. The traps contained an average of 9557 animals.

Tab. 5 shows the data for the two control traps. Chironomids and oligochaetes were the most abundant colonizers (chironomid/non-chironomid ratio, 9.3/1), followed by leeches, hydropsychid caddisflies, cyclopoids and beetles.

Tab. 3. The numbers of each taxon present in vertical upward migration traps 1 and 2. Average number and percent of each taxon per trap are also given.

	Vertical trap 1 no. present	Vertical trap 2 no. present	Average no. per trap	Average % per trap
Coelenterata.....	8		4	0.2
Nematoda.....	346	448	397	16.1
Oligochaeta.....	416	520	468	19.0
Gastropoda.....	16	8	12	0.7
Hirudinea.....	648	712	680	27.8
Cladocera.....	96	48	72	3.0
Ostracoda.....	8	16	12	0.5
Cyclopoida.....	696	744	720	29.4
Harpacticoida.....		24	12	0.5
Decapoda.....		16	8	0.3
Acari.....	8		4	0.2
Ephemeroptera.....		16	8	0.3
Coleoptera.....	48	64	56	2.3
No of non-chironomids.....	2290	2616	2453	100
No of Chironomidae.....	3768	4336	4052	
Total/trap.....	6058	6952	6505	

Discussion

Theoretically, if complete recolonization was not achieved until the end of the 28-day period, the control traps should have contained the greatest densities of animals, as they were open to all four directions of

Tab. 4. The numbers of each taxon present in aerial traps 1 and 2. Average number and percent of each taxon per trap are also given.

	Aerial 1 no. present	Aerial 2 no. present	Average no. per trap	Average % per trap
Gastropoda.	8	16	12	12.5
Hirudinea ..	8	16	12	12.5
Cyclopoida .	8	8	8	9.8
Collembola .	24	24	24	29.4
Plecoptera ..		8	4	2.7
Ephemeroptera		8	4	2.7
Trichoptera .		24	12	7.9
Coleoptera .	8	16	12	12.5
Other				
Diptera . . .		16	8	5.3
Terrestrial . .		16	8	5.3
No. of non-chironomids	56	152	104	100
No of Chironomidae	8926	9980	9453	
Total/trap ..	8984	10132	9557	

colonization. Further, perhaps their total contents should approximate the sum of those from the other four types of traps. In fact, this summation produces a figure of 36351 animals colonizing a 60 × 30 cm section of stream bed, which compares well with the average density from the two control traps of 34016. However, if we take 34016 to be the more accurate value for the fully recolonized substrate, then the percentage contribution of each of the four sources may be calculated as follows:

	Trap average	Contribution expressed as percentage of the actual control trap average
Drift	14074	41.4%
Upstream	6195	18.2%
Vertical	6505	19.1%
Aerial	9577	28.2%
Actual control	34016	100.0%
Theoretical control	36351	

It seems, therefore, that so far as the total number of animals is concerned, during the month of June 1972 in the Nith tributary, drift was the most important source of recolonizing animals. This was followed by aerial sources, with upstream migration and movement up from within the substrate each contributing 18–19%. Doubtless these values would differ from season to season as, e.g., there would be no aerial colonizers during the winter. It is interesting to note that in each case, the numbers colonizing each of the four types of traps was less than (and add up to) those in the control traps. Why the numbers in the drift traps, e.g., did not reach the

maximum density of the controls, when large numbers of potential colonizers (74.7% in Trap 1 and 86.2% in Trap 2) passed on over the substrate to be caught in the drift nets, is uncertain.

The various taxonomic groups seemed to favour different directions of colonization, and Tab. 6 shows the average numbers of animals present in the four types of traps together with the percent distribution of each group throughout these traps. Some of the numbers present are small (e.g. coelenterates, amphipods and stone flies) and therefore little importance can be attached to their distributions. Also, it must be understood that these interpretations are based on the colonization directions of a particular assemblage of species during only part of a year. Consequently, members of the same taxa may well show preferences for different directions under other circumstances. However, the following assumptions seem valid. Nematodes and oligochaetes mostly invaded by moving downstream and upstream, the importance of either direction being about equal. Cladocerans and ostracods also moved downstream but were more numerous moving upstream. Mayfly nymphs primarily invaded from the drift although a few did move upstream. Cyclopoids colonized equally by moving upstream and from the lower substrate levels but the leeches came predominantly from the substrate. The chironomids came mostly from the drift and aerial

Tab. 5. The numbers of each taxon present in control traps 1 and 2. Average number and percent of each taxon per trap are also given.

	Control trap 1 no. present	Control trap 2 no. present	Average no. per trap	Average % per trap
Coelenterata	16		8	0.2
Nematoda ..	96	128	112	3.4
Oligochaeta.	904	1504	1204	36.4
Gastropoda.	96	64	80	2.4
Pelecypoda .	70	134	102	3.1
Hirudinea ..	626	480	553	16.7
Cladocera ..	16		8	0.2
Ostracoda ..	32	64	48	1.5
Cyclopoida .	232	256	244	7.4
Harpacticoida	16	32	24	0.7
Decapoda ..	24	8	16	0.5
Acari	32	32	32	1.0
Plecoptera ..		8	4	0.1
Ephemeroptera	144	96	120	3.6
Trichoptera .	538	416	477	14.4
Coleoptera .	168	224	196	5.9
Other				
Diptera . . .	104	64	84	2.5
No. of non-chironomids	3114	3510	3312	100
No of Chironomidae	28320	33088	30704	
Total/trap ..	31434	36598	34016	

Tab. 6. Average numbers of animals present in the four types of traps together with the percentage distribution of each taxon throughout these traps.

	Drift		Upstream		Vertical		Aerial	
	Av. no.	Av. %	Av. no.	Av. %	Av. no.	Av. %	Av. no.	Av. %
Coelenterata	0	0	4	50.0	4	50.0	0	0
Nematoda	1068	40.6	1168	44.4	397	15.1	0	0
Oligochaeta	1258	44.3	1114	39.3	468	16.5	0	0
Gastropoda	4	14.3	0	0	12	42.9	12	42.9
Pelecypoda	0	0	52	100.0	0	0	0	0
Hirudinea	36	4.3	100	12.1	680	82.1	12	1.4
Cladocera	104	28.9	184	51.1	72	20.0	0	0
Ostracoda	60	24.2	176	70.9	12	4.9	0	0
Cyclopoida	100	6.0	844	50.5	720	43.1	8	0.5
Harpacticoida . . .	8	25.0	12	37.5	12	37.5	0	0
Amphipoda	0	0	4	100.0	0	0	0	0
Decapoda	8	48.5	0.5	3.0	8	48.5	0	0
Acari	16	66.7	4	16.7	4	16.7	0	0
Collembola	0	0	0	0	0	0	24	100.0
Ephemeroptera . .	76	67.9	24	21.4	8	7.1	4	3.6
Trichoptera	28	53.9	12	23.1	0	0	12	23.1
Plecoptera	0	0	0	0	0	0	4	100.0
Coleoptera	48	29.3	48	29.3	56	34.2	12	7.3
Chironomidae . . .	11204	41.3	2420	8.9	4052	14.9	9453	34.8
Other Diptera . . .	40	76.9	4	7.7	0	0	8	15.4
Pisces	0	0	0.5	100.0	0	0	0	0
Terrestrial	16	33.3	24	50.0	0	0	8	16.7

invasion although movement from the substrate and upstream were also important. Beetles were equally numerous in the drift, moving upstream and from the gravel whereas caddis larvae came mainly from the drift. The drift. The bivalves appeared to be entirely restricted to moving upstream.

Conclusion

In the light of these experiments, it now becomes apparent that all four sources of recolonizers are important in repopulating denuded areas of substrate. Isolating each of these four sources leads to the establishment of separate and distinct faunal assemblages, which differ both quantitatively and qualitatively the former possibly depending on the latter. It is possible for this reason that colonization equal to that in the control traps could not have been achieved by any of the four other types of trap. However, as regards the percentage contribution of each of the sources of colonizers to the fully recolonized state, we think that it is still justifiable to use the total numbers of animals for this, provided that we keep in mind that there may well be qualitative differences between the assemblages colonizing each type of trap due to the species preferred direction of colonization.

The implications of this study are that caution should be applied when attributing total recolonization of benthic organisms to one means, e.g., drift and that any one isolated source may take far longer in allowing re-establishment to previous taxonomic diversity and density levels.

Acknowledgements – We would like to thank Mrs N. E. Williams for helping with the field work, Mrs D. Pisarczyk for sorting many of the samples and Mr M. A. Moser for kindly allowing us access to his property. The work was supported by a National Research Council of Canada operating grant to H.B.N.H. for which we are grateful.

References

- BISHOP, J. E. and HYNES, H. B. N. 1969. Upstream movements of the benthic invertebrates in the Speed River, Ontario. – *J. Fish. Res. Bd Can.* 26: 278–298.
- BRUSVEN, M. A. 1970. Drift periodicity and upstream dispersion of stream insects. – *J. Ent. Soc. B. C.* 67: 48–59.
- CAIRNS, J. JR., CROSSMAN, J. S., DICKSON, K. L. and HERICKS, E. E. 1971. The recovery of damaged streams. – *Ass. South-eastern Biol. Bull.* 18: 79–106.
- COLEMAN, M. J. and HYNES, H. B. N. 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. – *Limnol. Oceanogr.* 15: 31–40.
- CROWE, J. M. E. 1970. The use of rock-filled basket samplers to survey the aquatic invertebrates of the Saskatchewan River. – Paper presented at the 18th Midwest Benth. Soc. Meeting, 1970. (Unpubl.)
- ELLIOTT, J. M. 1967a. Invertebrate drift in a Dartmoor stream. – *Arch. Hydrobiol.* 63: 202–237.
- 1967b. The food of trout (*Salmo trutta*) in a Dartmoor stream. – *J. Appl. Ecol.* 4: 59–71.
- FERNANDO, C. H. 1958. The colonization of small freshwater habitats by aquatic insects. I. General discussion, methods and colonization in the aquatic Coleoptera. – *Ceylon J. Sci. Biol. Sci.* 1: 117–54.
- MASON, W. T., ANDERSON, J. B. and MORRISON, G. E. 1967. A limestone-filled artificial substrate sampler float unit for collecting macroinvertebrates in large streams. – *Prog. Fish-Cult.* 29: 74.
- MAYR, E. 1964. Summary. – In: Baker H. G. (ed.). *The genetics of colonizing species.* – Academic Press, N.Y.: 553–556.

- MÜLLER, K. 1954. Investigations on the organic drift in north Swedish streams. - Rep. Inst. Freshwat. Res. Drottningholm 35: 133-148.
- OTTO, C. and SVENSSON, B. W. 1976. Consequences of removal of pupae for a population of *Potamophylax cingulatus* (Trichoptera) in a South Swedish stream. - Oikos 27: 40-43.
- WATERS, T. F. 1964. Recolonization of denuded stream bottom areas by drift. - Trans. Am. Fish. Soc. 93: 311-325.
- 1972. The drift of stream insects. - Ann. Rev. Ent. 17: 253-272.
- WILLIAMS, D. D. and HYNES, H. B. N. 1974. The occurrence of benthos deep in the substratum of a stream. - Freshwater Biol. 4: 233-256.
- and WILLIAMS, N. E. 1974. A counterstaining technique for use in sorting benthic samples. - Limnol. Oceanogr. 19: 152-154.