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Invertebrate colonisation of the gravel substratum of an experimental recirculating channel

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The development of an invertebrate community in a large scale, experimental stream system is described. Colonisation was chiefly by means of ovipositing adult insects with lesser components introduced with water and stones. A succession of taxa was recorded with large peaks of numbers in the spring and the autumn, comparable to those observed in studies on natural streams. Diversity of the fauna increased quickly at first and then more slowly, possibly because of the reduced availability of ovipositing adults later in the year. Even in the absence of drift and migration, recruitment of insect larvae, which naturally favour gravel substrata in running water, can be rapid and will produce a varied community in which Chironomidae and Ephemeroptera play an important role.

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Introduction

A recirculating experimental stream system was built at Waterston, Dorset, England (National Grid Reference SY 742953) with a view to isolating and controlling some of the factors (e.g. discharge, velocity, temperature and chemical composition of the water) which influence natural chalk streams and thus assessing their importance in these ecosystems. This study investigates the colonisation of the Waterston channel by benthic invertebrates.

There have been a number of studies on colonisation of stream bed habitats by drift (Müller 1954, Waters 1964, Elliott 1967, Bishop and Hynes 1969a) and by upstream movement of invertebrates (Bishop and Hynes 1969b, Hultin 1971, Müller 1974). Both Chutter (1968) and Crisp and Gledhill (1970) concluded that colonisation of depopulated areas of stream substrata, produced as a result of dredging and/or pollution, was primarily due to drift. In a study on an Ontario river, 41.4% of the recolonisation was due to drift and 18.2% to upstream migration (Williams and Hynes 1976a). In the Waterston channel, although drift occurs, there is no gain of invertebrates as it is essentially a closed system and this factor consequently is not operational in colonisation. A similar argument applies to the influence of upstream migration.

There was also significant recolonisation in the Ontario river by vertical movement and recruitment from within the substratum (19.1%). Animals which are presumably able to recolonise superficial substrata have been found at depths of up to 0.7 m (Williams and Hynes 1974). Colonisation after drying of a stream bed may be due, in part, to the presence of resistant eggs in the gravel. Colbo and Moorehouse (1974) studied survival of the eggs of *Austrosimulium pestilens* in a moist stream bed and many chalk stream invertebrates are adapted to ephemeral stream conditions (Casey and Ladle 1976). In the Waterston channel, as gravel was introduced from a terrestrial source, there was no possibility of colonisation from resistant eggs or by vertical migration.

In the absence of the above factors, the only major process operative in the present study was that of aerial colonisation, both by ingress of adults and by oviposition. This method of colonisation is important in some streams (Fernando 1958, Williams and Hynes 1976b, Otto and Svensson 1976), although it is usually

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regarded as of secondary importance (Chutter 1968, Crisp and Gledhill 1970, Williams and Hynes 1976a). Müller (1974) discusses oviposition and its relationship to the natural colonisation cycle of running water. Aerial colonisation must initially be the primary source of stream insects because drift, delayed hatching, and upstream migration all depend on recruitment from eggs.

The object of the present study was to utilise the isolation of this primary colonisation process to determine the magnitude and complexity of resulting populations of benthic invertebrates and the time taken for these to develop.

Materials and methods

The system has previously been described by Ladle et al. (1977). It is a race-track shaped channel of trapezoidal cross-section, 53 m in length with a basal width of 1 m and a top width of 2 m (Fig. 1a). Water is pumped from a borehole in the chalk aquifer to supply the channel and is recirculated by a screw pump at a mean velocity of 0.4 m s^{-1}, before overflowing through a notch. The half life retention of water is normally ca. 12 h. The channel was filled to a depth of 0.3 to 0.5 m with flint gravel from a terrestrial source but of similar character to that found in small chalk streams. In order to provide an inoculation of algae for the system six stones of 100–150 mm diameter, from the adjacent small chalk stream, were introduced at the start of the experiment.

At the time of gravel addition 620 invertebrate samplers were placed in the recirculating channel. Each consisted of a cylinder of 5 mm plastic mesh, 200 mm in length with a diameter of 100 mm. Each sampler was fitted with a base of 10 mm marine ply, filled with the introduced gravel and buried level with the surface of the substratum. The samplers were evenly placed in rows of five across the channel (Fig. 1b). All sampling devices were in place by 4 December 1975 and the channel pump was switched on. Covers were positioned over the channel to prevent ingress of light, animals or detritus. The water chemistry was monitored and an account of the preliminary, chemical results is given in Ladle et al. (1977).

The invertebrate fauna was then sampled by removing 15 of these samplers, preselected from random number tables, every two weeks. As each sampler was pulled from the substratum a fine meshed net was held immediately downstream to catch any animals dislodged by the flowing water. Clean gravel was replaced in each depression to prevent subsequent shifting and resettlement of the substratum.

Samples were screened through a 250 μm, sieve and the large stones were washed and removed. All retained fine material and animals were preserved prior to sorting, counting and identification.

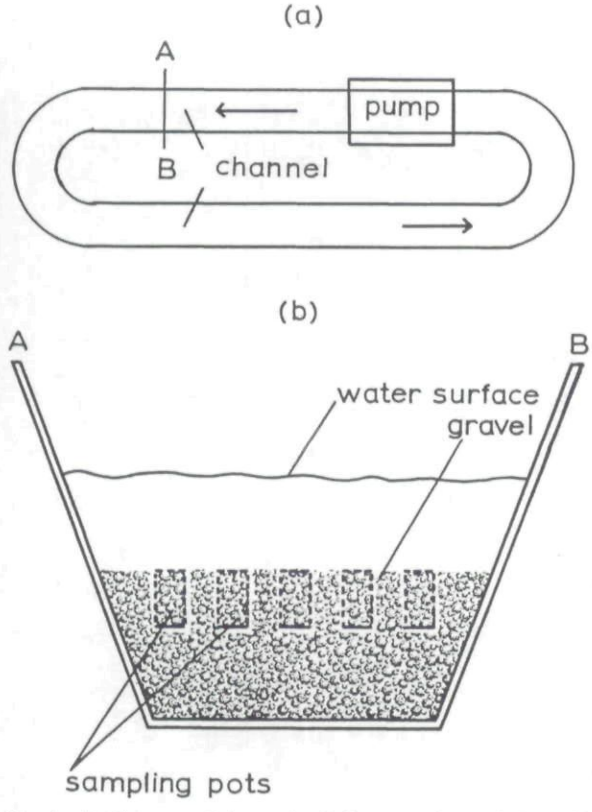

Fig. 1. a) Diagram of the recirculating experimental channel. b) Cross section of the channel showing arrangement of invertebrate samplers.

Results

The covers were taken off on 5 April 1976 and immediately 15 samplers were removed. A total of only ten animals (equivalent to 84 m^{-2}) were found: six chironomid larvae (4 *Micropsectra* sp. and 2 *Brillia modesta*), two unidentified chironomid pupae and two oligochaetes, one *Stylodrilus heringianus* and one *Psammoryctides barbata.* During the following two weeks the diversity increased with *Orthocladius thienemanni, Cricotopus* sp. and *Potthastia gaedii* present. Six oligochaetes were found including *Nais* sp. Other invertebrates at this time included one *Ephemerella ignita,* two simuliid larvae, and two adult aquatic Coleoptera. A complete listing of material identified is presented in Tabs 1a, b.

The Chironomidae increased rapidly in numbers. In the second sample on 19 April 1976 they attained a population density of 458 m^{-2} eventually reaching a maximum of 68000 m^{-2} by mid-June (Fig. 2). Two taxa accounted for 74% of the population at this time; *Micropsectra* 41%, *Synorthocladius semivirens* 33%, with *Eukiefferiella* sp. 8%, *Eukiefferiella calvescens* 5% and *Orthocladius* sp. 2% being the only others contributing

Tab. 1a. List of species, and other taxa, recorded from the recirculating channel in 1976.

	24 May	8 Jun	21 Jun	5 Jul	19 Jul	2 Aug	16 Aug	1 Sep	13 Sep	27 Sep	11 Oct	25 Oct	8 Nov	22 Nov	13 Dec
Hydrazoa															
Hydra sp.					+	+	+	+	+	+	+	+	+	+	+
Tricladida															
Polycelis tenuis Ijima		+													
P. felina (Dalyell)										+					
Dugesia sp.													+		
Dendrocoelum lacteum (Müller)						+									
Nematoda		+	+						+	+	+	+		+	
Oligochaeta															
Enchytraeidae	+		+												
Eiseniella tetraedra (Savigny)			+												
Aelosoma spp.	+		+			+									
Stylaria lacustris (L.)										+					
Pristina foreli Piguet															
Nais spp.	+											+			+
N. elinguis Müller			+												
N. communis Piguet	+									+		+			+
N. variabilis Piguet	+		+			+									
Psammoryctides barbata (Grove)	+														
Rhyacodrilus coccineus (Vejdovsky)	+														
Stylodrilus heringianus Clap.	+														
Copepoda	+	+	+		+	+	+	+	+	+	+	+	+	+	+
Harpacticidae															+
Cladocera															
Alona affinis Leydig											+	+	+	+	
Chydorus ovalis Kurz			+		+	+		+	+	+	+	+	+	+	
Ostracoda										+	+	+	+	+	+
Isopoda															
Asellus aquaticus (L.)															+
Ephemeroptera															
Caenis rivulorum Etn.								+	+	+	+	+	+	+	+
Ephemerella ignita (Poda)	+	+	+				+	+	+	+	+	+	+	+	+
Ecdyonurus sp.												+			
Heptagenia sulphurea (Müller)								+							
Paraleptophlebia sp.										+	+	+	+	+	+
Centroptilum luteolum (Müller)							+	+	+	+	+	+	+	+	+
Baëtis muticus (L.)								+							
B. niger (L.)								+							
B. rhodani (Pictet)		+	+		+	+	+	+					+		
B. vernus (Curtis)		+													
B. spp.	+	+	+		+	+	+	+	+	+	+	+	+	+	+
Plecoptera		+							+			+	+	+	
Megaloptera															
Sialis lutaria (L.)	+									+					
Trichoptera															
Rhyacophila dorsalis (Curtis)			+		+	+	+	+		+		+	+	+	+
Agapetus fuscipes Curtis						+		+	+			+			+
Polycentropus flavomaculatus (Pictet)									+	+	+	+	+	+	+
Hydropsyche sp.						+	+	+	+		+	+			
Hydroptilidae			+								+	+	+	+	+
Halesus radiatus (Curtis)										+					
Hemiptera															
Velia caprai Tamanini		+													
Corixa dorsalis Leach								+							
Coleoptera															
Dytiscidae			+												
Hydroporus angustatus Sturm										+					
H. marginatus (Duftschmid)										+					
Elmis aenea (Müller)					+				+	+	+	+	+	+	
Limnius volkmari (Panzer)											+				
Staphylinidae	+	+								+					
Gastropoda															
Valvata cristata Müller		+				+	+		+	+	+		+		
Physa fontinalis (L.)													+		+
Planorbis contortus (L.)															+

Tab. 1b. List of Diptera recorded from the recirculating channel in 1976.

	5 Apr	26 Apr	10 May	24 May	8 Jun	21 Jun	5 Jul	19 Jul	2 Aug	16 Aug	1 Sep	13 Sep	27 Sep	11 Oct	25 Oct	8 Nov	22 Nov	13 Dec
Pericoma sp.															+			
Bezzia sp.																+		
Apsectrotanypus trifascipennis (Zetterstedt)						+	+	+						+				
Procladius sp.						+												
Potthastia gaedii (Meigen)		+	+	+	+													
P. longimana (Kieffer)						+	+	+		+		+		+		+		+
Brillia modesta Meigen)	+						+					+		+		+		+
Cricotopus sp.		+	+	+	+	+												
C. bicinctus (Meigen)					+	+												
Eukiefferiella sp.					+	+	+	+				+		+		+		+
E. calvescens (Edwards)					+	+	+	+		+		+		+		+		+
E. claripennis (Lundbeck)				+														
E. ilkleyensis (Edwards)				+	+	+												
Heterotrissocladius marcidus (Walker)						+												
Orthocladius sp.			+	+	+	+						+		+		+		+
O. thiennemanni Kieffer			+	+	+										+			
O. rivulorum (Kieffer)		+		+	+													
Synorthocladius semivirens (Kieffer)			+	+	+	+	+	+		+		+		+		+		+
Corynoneura sp.										+				+		+		
Thienemanniella sp.				+	+	+	+	+		+								
Chironomus sp.				+	+													
Microtendipes sp.						+	+											
Paratendipes sp.														+		+		+
Polypedilum (Laetum type)							+	+				+						
Micropsectra sp.	+		+	+	+	+	+	+		+		+		+		+		+
M. aristata Pinder					+	+		+										
Tanytarsus sp.					+	+	+	+				+		+		+		+
T. arduennensis Goetgebhuer						+												
T. brundini Lindeberg						+	+											
Paratanytarsus sp.				+	+	+	+							+				+
Rheotanytarsus sp.																+		
Tanypodini							+	+		+				+		+		+
Macropelopia sp.						+	+	+										
Rheocricotopus sp.			+	+														
Nanocladius rectinervis (Kieffer)			+	+	+	+	+	+		+		+				+		+
Thienemannimyia sp.							+	+										
Simulium ornatum Meigen					+			+	+	+		+		+				
S. angustipes Edwards											+							

more than 1%. Following a rapid decline in numbers in late June there was a further increase in population density reaching a peak of 42000 m^{-2} in mid-July. This peak was almost entirely composed of *Synorthocladius semivirens*, 80% and *Micropsectra* sp., 10%. Numbers declined following the second peak to a low density of only 7000 m^{-2} in mid-August after which the population again increased steadily to 33000 m^{-2} by early November with the same two species still predominant; *Synorthocladius semivirens* 84%, *Micropsectra* sp. 7%, *Tanytarsus* sp. 4% and *Potthastia longimana* 2%.

The Oligochaeta, predominantly *Nais communis* exhibited peaks in June and October (Fig. 2). Following a peak of 5000 m^{-2} in June the population density remained low (<500 m^{-2}) in July, August and early September, before increasing rapidly to 12500 m^{-2} coinciding with the autumnal peak of Chironomidae. With the exception of *Nais communis* only *Aelosoma* sp. was collected in appreciable numbers and this small worm constituted about 20% of the oligochaete population on 10 April 1976.

Ephemeroptera were present in very small numbers from as early as April when five genera were recorded but numbers remained low until June when there was a dramatic increase in *Baëtis rhodani* from 240 m^{-2} to 3500 m^{-2} in two weeks (Fig. 3). The population density then remained almost constant until early August after which there was a decline through September and October due to the gradual emergence of the cohort. This is confirmed by measurement of head capsule lengths (Fig. 3).

Population densities of both *Caenis* sp. and *Centroptilum* sp. remained low until early September. Subsequently both increased rapidly during September and in the case of *Caenis* reached a maximum density of 900 m^{-2} during October and November (Fig. 4). Numbers of *Centroptilum* rose steadily during October and November and were 4200 m^{-2} in mid-December (Fig.

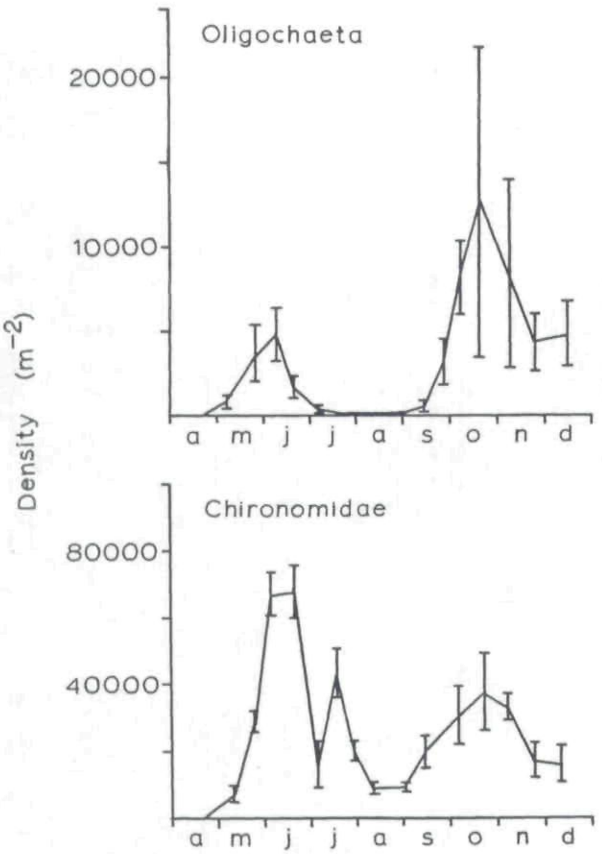

Fig. 2. Changes in population density (means ± 95% C.L.) of Oligochaeta and Chironomidae in the recirculating channel in 1976.

4). *Ephemerella ignita* was present throughout but at no time was there a marked increase in numbers and densities remained below 250 m^{-2} at all times. *Paraleptophlebia* sp. was present in even smaller numbers (< 50 m^{-2}).

Cladocera, particularly *Chydorus* sp., were present throughout the summer and began to increase in density during September, reaching a peak of 1500 m^{-2} in late October (Fig. 5). This density is probably an underestimate because small individuals may have passed through the 250 μm sieve. This may also be true of the Copepoda which were present in very low numbers during the summer and autumn.

Invertebrate predators were established early in the channel but were slow to build up in numbers. Hydrachnellae appeared in June and increased steadily to a maximum of 4000 m^{-2} in mid-December (Fig. 5). Hydra, present in small numbers from August to October, peaked at 3500 m^{-2} in November and subsequently declined (Fig. 5). The flatworm, *Polycelis* sp. was present but the population density was very low and the predatory trichopteran *Rhyacophila*, present throughout the summer, showed a slight increase to about 500 m^{-2} in November and December.

Indices of diversity (Shannon and Weaver 1949) and of dominance (Simpson 1949) were calculated for the fauna on each sampling date (Tab. 2). The initial high level of diversity on 26 April 1976 was associated with the presence of only eleven, more or less equally represented taxa. The subsequent colonisation, predominantly by chironomids of the genera *Orthocladius* and *Potthastia* resulted in a minimum diversity index of just under 0.6 on 10 May 1976 after which there was an increase to almost 1.7 by 1 September 1976. A short period of levelling or decrease took place in September, with chironomids increasingly dominant, followed by a rising index value which continued to a maximum of 2.6

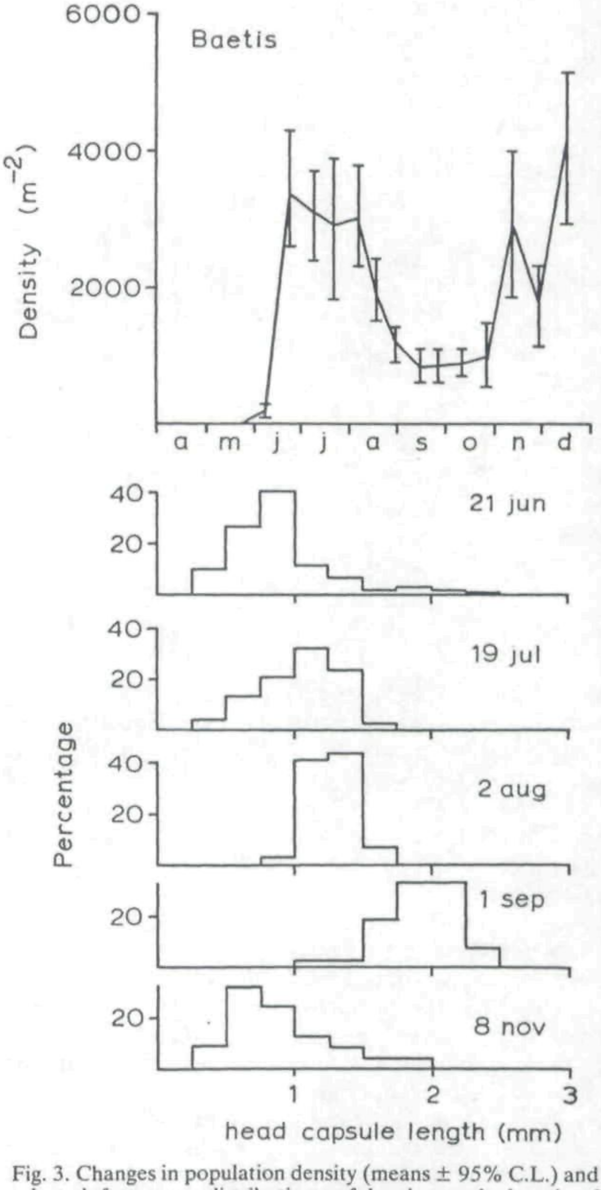

Fig. 3. Changes in population density (means ± 95% C.L.) and selected frequency distributions of head capsule length of *Baëtis rhodani* in the recirculating channel in 1976.

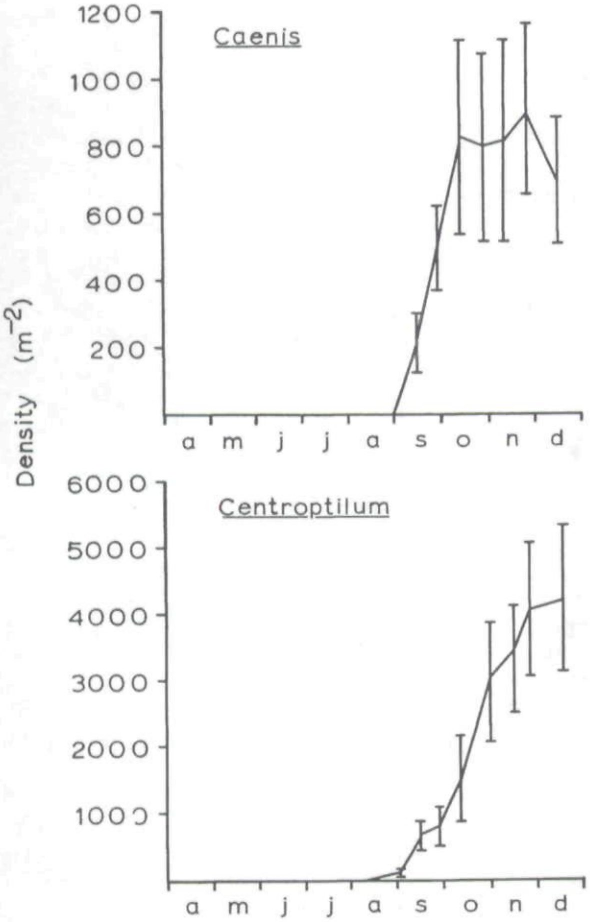

Fig. 4. Changes in population density (means ± 95% C.L.) of *Caënis* sp. and *Centroptilum* sp. in the recirculating channel in 1976.

on 13 December 1976, the last sampling date, when 26 taxa were represented.

Discussion

In a comparatively simple running water system such as that under discussion it is not surprising that relatively few species should assume dominance in the early stages, nor that these species should produce clear cut generations and marked recessions.

Oligochaetes of the genera *Nais* and *Aelosoma* colonised the channel in the early stages. The former was probably introduced with the algal inoculum and the latter was found in small numbers in the borehole water used to fill the channel.

The early chironomid colonisers were *Orthocladius thienemanni, O. rivulorum, Nanocladius rectinervis, Cricotopus* sp. and *Potthastia gaedii.* Each of these species attained its maximum population density over

Tab. 2. Indices of diversity and dominance for the benthic fauna of the circulating channel in 1976.

Date	Diversity (Shannon)	Dominance
26 Apr	1.58	0.58
10 May	0.60	0.80
8 Jun	0.69	0.80
21 Jun	0.72	0.81
19 Jul	0.82	0.77
2 Aug	1.18	0.62
16 Aug	1.43	0.53
1 Sep	1.69	0.49
13 Sep	1.33	0.64
27 Sep	1.51	0.58
11 Oct	1.79	0.46
25 Oct	1.77	0.46
8 Nov	1.98	0.42
22 Nov	2.26	0.33
13 Dec	2.56	0.26

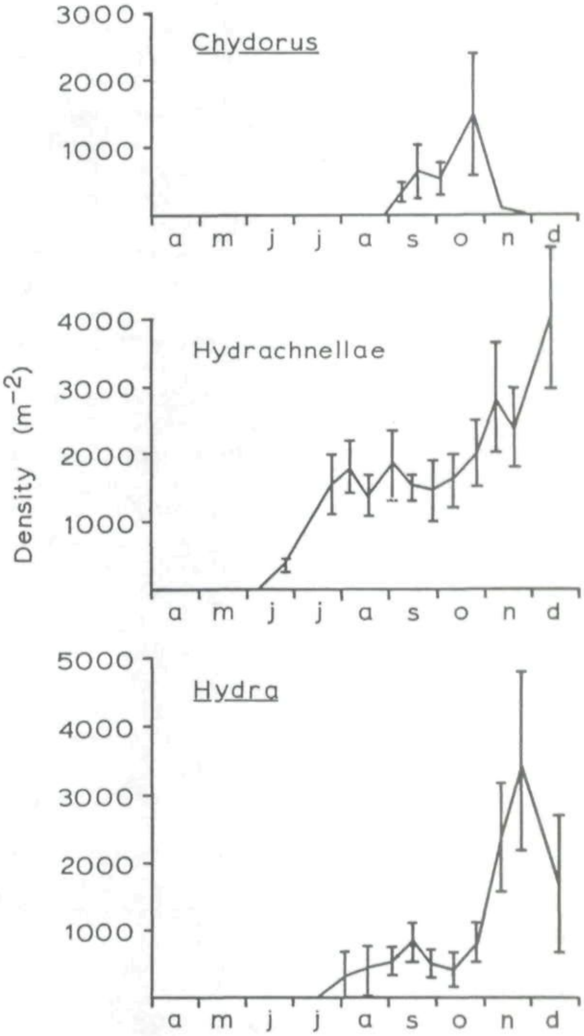

Fig. 5. Changes in population density (means ± 95% C.L.) of *Chydorus* sp., Hydrachnellae and *Hydra* sp. in the recirculating channel in 1976.

the period of greatest abundance of benthic diatoms, which reached 400 mg m^{-2} chlorophyll *a* in mid-May (Marker and Casey 1977). For example, *O. rivulorum*, which naturally inhabits stony substrata and constructs gelatinous tubes, feeds on the spring 'bloom' of diatoms in a fast current (Lindegaard-Petersen 1972). *Potthastia gaedii*, which normally produces a series of generations annually in chalk stream situations (Pinder pers. comm.) was present briefly and also peaked early in the study, when large numbers of diatoms were present on the bed of the channel. Many species of chironomids are known to oviposit in open waters (Williams pers. comm.). *P. gaedii*, however, prefers water velocities slower than those found in the channel and this may account for the low population density and reduced number of generations of this species. Subsequently *P. gaedii* was replaced by the related *P. longimana* which was present in small numbers from June through to December.

Apart from those species which were present sporadically in small numbers, the other major pattern was one of a summer peak followed by a lesser autumn and winter increase. An instance of this is *Synorthocladius semivirens*, which commonly inhabits stones in current and has spring and autumn generations (Brundin 1949). This species was the predominant organism throughout the period of study but many others, although present in lesser numbers, were sufficiently frequently represented to suggest that oviposition takes place over a substantial part of the year and that, given appropriate conditions, populations or cohorts of larvae could be established at different times. To a lesser extent the following species showed a similar pattern to *S. semivirens: Micropsectra* sp., *Eukiefferiella* sp., of which some species normally have continuous recruitment and oviposition and an indeterminate number of generations; *Eukiefferiella calvescens, Potthastia longimana* which has been demonstrated to show generations in June and October (Lindegaard-Petersen 1972) and *Tanytarsus* sp. *Orthocladius* sp., although colonising early, also showed a secondary peak in October.

A study on the 'flint-zone' of the River Thames (Mackey 1976) indicated peak numbers of Chironomidae in July and December (1500 and 600 m^{-2}). In the Tadnoll Brook peaks of Orthocladinae in early June and September (11200 and 2000 m^{-2}) and of Chironominae in June (5200 m^{-2}), late August and December were demonstrated in bottom sediments, while 100000 m^{-2} were recorded from a macrophyte substrate in early May (Pinder 1977).

Large quantities of sedimentary detritus accumulated in the bed of the channel in June. Much of this food material being derived from the fragmentation and settlement of benthic diatoms (Welton and Ladle 1979). The quantity and quality of available food may influence the size of orthoclad populations in chalk streams (Pinder 1977) so that peak numbers often coincide with the spring increase of diatoms. Some, like *Orthocladius rivulorum*, are probably obligate diatom consumers (Lindegaard-Petersen 1972) and others merely take a facultative advantage of this supply of food.

The successions of taxa from the initial colonisation by chironomids and oligochaetes to baëtids in the summer months is similar to that often observed in natural chalk streams. Chironomids, many species of which are multivoltine, are quick to take advantage of a newly exposed stream bed. The basic succession is governed by the oviposition strategies of the species involved. *Baëtis* oviposit underwater on submerged stones in rapidly flowing water (Elliott 1972, Kimmins 1972). Eggs were found in October–December and March–July by Elliott (1972) and the timing of the first generation in the channel was presumably dependent on the presence of adult females and not delayed hatching of eggs. At the temperatures found in the channel in April–June (8°C–20°C) eggs of this species would hatch in 1–3 weeks.

The very low densities attained by *Ephemerella ignita* were due to the fact that the channel was not operational at the time of oviposition. The eggs of this species are normally laid in summer in open water (Kimmins 1972) and hatch in the spring of the following year (Bass 1976).

Centroptilum luteolum is reported to have a quick summer and long winter generation (Bretschko 1965). The increase in population of this species observed in September–December in the present work is, presumably, due to hatching and recruitment of this winter generation. Oviposition in this species, is by dropping eggs or dipping the abdomen in open water (Kimmins 1972).

Caenis rivulorum has a single winter generation (Thibault 1971) accounting for the increase in density observed in the channel in September–December.

Most of the species which colonised were those normally present in small chalk streams but a few were not typical. The larva of the caddis *Brachycentrus subnubilus* normally occurs only in the lower reaches of large chalk streams and beetles of the genus *Helophorus*, which occur in slow flowing waters were presumably attracted by the large, open water surface. Some organisms which might have been expected to colonise the fast flow effectively, for example Simuliidae, were never present in large numbers, presumably because conditions for oviposition by the species which normally live in small chalk streams (i.e. the presence of overhanging marginal vegetation) were not satisfied. Other species which are known to oviposit directly on the flowing water surface (e.g. *Simulium lineatum*) do not occur in small streams near the channel. In addition, most of the simuliids which inhabit chalk streams live on 'streamer weed' (*Ranunculus, Oenanthe*, etc.) and the only attachment surfaces in the channel were the stones and the glass reinforced plastic walls of the channel itself.

Most of the predatory organisms attained their maximum numbers late in the study period. Hydracarina were probably introduced continually at first, in the parasitic stage, on ovipositing chironomid hosts. *Hydra* sp. was almost certainly introduced on the few stones used to 'seed' the system with algae and reached a peak after that of the microcrustacea which may have entered in the same way. This method of introduction probably accounts for the presence of *Polycelis* sp. An increase in the population density of *Rhyacophila dorsalis* late in the year was probably due to the hatching of eggs laid between June and October (Elliott 1968).

The diversity of the fauna was less than that recorded from the gravel beds of natural chalk streams (Pinder pers. comm.) although, by the end of the study, in December, the Shannon index was 2.56. The lower diversity indices recorded were during the initial stages of colonisation when one or two species of Chironomidae were predominant. The high initial Shannon index was due to the presence of low densities of a small number of species. Later, in September, when a number of organisms showed secondary peaks of abundance, the diversity index decreased slightly.

Invertebrate population densities were quite comparable to those recorded in natural streams. 'Aerial' colonisation is clearly adequate to rapidly establish depleted stream faunas, in numerical terms if not in structure, even in the absence of drift, upstream migration, delayed hatching or recruitment from within the substratum.

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