THE ECOLOGY OF CHALK-STREAM INVERTEBRATES STUDIED IN A RECIRCULATING STREAM

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Introduction

Amongst the early investigations on the invertebrate fauna of chalk streams there are only a few detailed studies (Percival & Whitehead 1926, 1929; Whitehead 1935). More recently, attempts have been made to acquire the data necessary to describe the production ecology of species and species groups, particularly those which are normally abundant (Ladle & Baron 1969; Ladle 1971; Ladle et al. 1972; Bass 1976; Welton 1979). More extensive syntheses of the structure of faunal communities in chalk streams have been made by Westlake et al. (1972), Ladle & Bass (1981), Wright et al. (1983) and Wright et al. (1984).

From this and other work it is clear that it is very difficult to determine and quantify the factors influencing interactions between various trophic levels in natural hard-water streams. The complex food webs which incorporate insect larvae in nutrient-rich chalk waters may include primary production of both autochthonous (water plants and algae) and allochthonous (tree leaves and marginal vegetation) plant material (Ladle 1982). Invertebrates may feed directly on the plants themselves or on the organic detritus produced by their death and decomposition. To simplify observation of such interactions, a recirculating stream channel was constructed (Ladle et al. 1977; Ladle et al. 1981). The major advantage of such a structure is that patterns of population change of stream animals are observed under partially controlled physical and chemical conditions, since factors such as catastrophic changes in discharge and variable water quality are eliminated. The trophic system (food web) was comparatively simple because macrophytes were absent, allochthonous input was negligible and a restricted invertebrate community was present. There was also the possibility of sampling enclosed populations of organisms, minimally affected by the processes of drift and upstream migration which complicate investigations in natural streams.

The recirculating channel

The channel is fully described in Ladle et al. (1977). It is race-track shaped, 53 m in length (excluding the pump) and has a trapezoidal cross-section, 1 m wide at the base and 2 m wide at the rim. A substratum gradient of 1 in 250 (similar to that in natural chalk streams) was set up using nominally 40-mm flint gravel to depths of 0·3–0·5 m. The total gravel area available for sampling was 70 m². Water was circulated at a mean velocity of 0·4 m s^{-1} and a continous through-flow of 70 l min^{-1} was introduced by water pumped from a borehole. Outflow was through an overflow notch in the channel side.

The recirculating channel was used to study the quantitative relationships between variations in water chemistry, production of epilithic algae, production of invertebrates and accumulation of mineral and organic sediments. The experimental arrangement permitted detection of small chemical changes by prolonging water retention to the point where such changes became significant (detectable) without progressively altering conditions. The large area of gravel substratum provided a facility for repeated destructive sampling of bottom-living invertebrates.

Estimates of chlorophyll *a* on flint surfaces showed that a growth of diatoms developed rapidly in the early stages (April-May) of experiments carried out in both 1976 and 1977-78 (Marker & Casey 1982). High levels of uptake of dissolved silicate by diatoms from the flowing water were demonstrated to correspond with those which occur progressively as water passes down natural streams (Casey et al. 1981; Marker & Casey 1983).

Invertebrate colonization and diversity

The initial colonization of the substratum by invertebrates in 1976 was chiefly as a result of oviposition by insects (Ladle et al. 1980). A small number of taxa were introduced with the inflow water and with stones removed from an adjacent stream to provide an inoculum of algae. On 5 April 1976, immediately after removal of the covers which were intended to exclude light, organisms and detritus, a total of only ten animals were present in 15 gravel samples; six chironomid larvae, two chironomid pupae and two oligochaetes. Subsequently a succession of taxa was recorded with Chironomidae, notably *Micropsectra* spp. and *Synorthocladius semivirens* (Kieffer), reaching a maximum total density of 68 000±7000 m^{-2} by mid-June (Fig. 1). A second peak occurred in October giving a bimodal seasonal pattern similar to those often observed in studies on natural streams. These chironomid species and others including *Orthocladius* spp., *Nanocladius rectinervis* (Kieffer), *Cricotopus* spp. and *Potthastia gaedii* (Meigen) attained their maximum population densities during the period following the peak of diatoms (chlorophyll *a*) (Fig. 1) (Ladle et al. 1980).

In chalk streams the quantity and quality of food materials (in the present case represented by diatoms) probably influences the size of orthoclad populations, so that peak numbers often coincide with the spring increase in diatoms (Pinder 1977). Some species, such as *Orthocladius rivulorum* Kieffer, are probably obligate diatom consumers and others merely take facultative advantage of such rich supplies of food (Lindegaard-Petersen 1972).

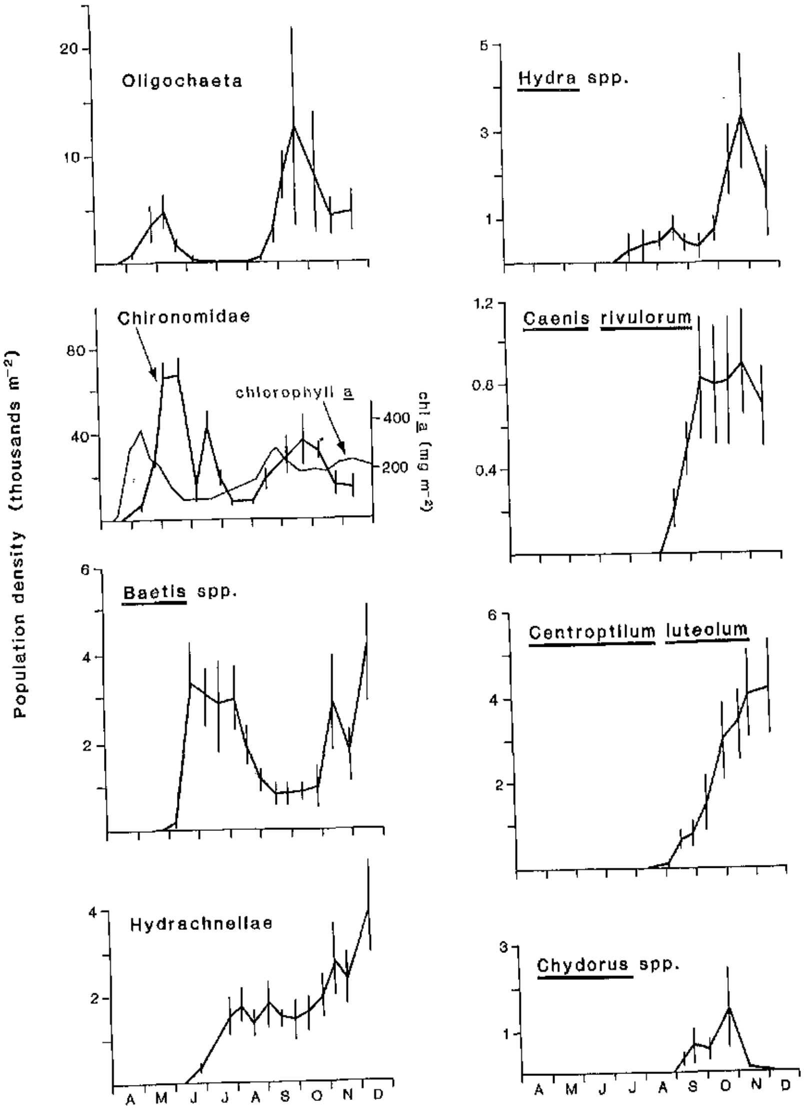

FIG. 1. Changes in population density (means ±95% CL) of invertebrates in the recirculating channel during 1976.

The Oligochaeta, predominantly *Nais communis* Piguet, exhibited peaks in June and October, probably colonizing the channel from stones introduced with the algal inoculum. A species of *Aeolosoma*, originating from the pumped groundwater, accounted for 20% of the June peak.

Five genera of Ephemeroptera were recorded as early as April but numbers remained low until the dramatic increase of *Baetis rhodani* (Pictet) from 240 m^{-2} to 3500 m^{-2} over two weeks (Fig. 1). Numbers remained high until August and similar densities were again attained during November and December. Populations of both *Caenis rivulorum* Etn. and *Centroptilum luteolum* (Müller) did not increase substantially until September with only *C. luteolum* reaching a similar maximum density to that of *B. rhodani* (Fig. 1). Invertebrate predators were established early in the channel reaching 3500 and 4000 m^{-2} in November and December for *Hydra* spp. and Hydrachnellae respectively.

An initial, relatively high, invertebrate diversity on 26 April 1976 was associated with the presence of only eleven more or less equally represented taxa. Subsequently, the diversity of the fauna increased to a level which, even on 13 December 1976, was still less than that of most natural streams (Pinder 1982). In a simple experimental system such as the channel, it is not surprising that relatively few species should assume dominance in the early stages.

It was demonstrated that even in the absence of drift and upstream migration, both of which are involved in colonization of the substrata of natural streams, the recruitment of insect larvae to the gravel beds of flowing water can be rapidly accomplished by oviposition and will produce an association of species in which Chironomidae and Ephemeroptera are abundant.

Depth distribution of invertebrates

For many years there has been debate regarding the depth to which invertebrates penetrate river-bed sediments, particularly gravel substrata. Replenishment of populations by recruitment of young animals from deeper interstitial layers has been suggested and there is some evidence for such recruitment, particularly from streams with loose stony beds (Hynes 1983). In the present study, experiments with sampling devices which extended to depths of either 100 mm or 200 mm beneath the gravel surface demonstrated that, with the exception of six taxa, there were no significant differences between the numbers of animals in the 100 mm and 200 mm samplers. These six taxa were all more numerous in the shallower samplers (Welton et al. 1981). These observations are contrary to most published work on the depth distribution of river-bed fauna. Hynes (1983) suggested that this apparent anomaly may have been due to the absence of upflowing ground water with its associated organic matter from the channel system. However, the channel was continually replenished with pumped ground water which exchanged freely with the interstitial water throughout the gravel bed. In natural chalk-stream gravels which usually include large quantities of finer sediment in the interstices, it is doubtful whethere most invertebrates normally live much deeper than 100 mm with the exception of circumstances where upwelling or through-flow of ground water occurs (Welton et al. 1981).

Growth and production studies

In 1977, the experiments of 1976 were repeated following removal of the superficial layers of gravel; complete replacement of sampling devices was also necessary to permit improved and sustained sampling for more than 12 months. As in the previous year, Chironomidae (24 taxa in all) colonized the gravel substratum in 1977. Three species were particularly abundant: *Chaetocladius melaleucus* (Meigen) which represented 60% of the larvae present in late May with a maximum density of 72 000 m^{-2}; *Synorthocladius semivirens*, again prominent, attaining 64 000 m^{-2} in August; and *Micropsectra aristata* Pinder with 48 000 m^{-2} in June (Fig. 2) (Ladle et al. in press).

C. melaleucus was univoltine, being present in samples for only 4 weeks, and estimates of growth rate of the larvae, assuming exponential growth, were 9·76% and 5·08% length day^{-1} for the first and second fortnight respectively. From the mean growth rate and the length of larvae, it was predicted that the recruitment period was c. 33 days and that the total cohort presence was c. 66 days with the length of life of an individual being 33 days. The maximum biomass recorded was c. 1 g m^{-2} and the production was 10·9 g dry wt m^{-2}.

Synorthocladius semivirens occurred throughout the study period with no clear patterns of progressive increase in body length discernible during the summer months. The mean growth rate for September and October was 1·88% length day^{-1} and the calculated duration of larval life was 93 days. Annual production was estimated at 2 g dry wt m^{-2}.

Micropsectra aristata was again present on every sampling occasion and a bimodal length distribution occurred throughout the summer. Development was rapid with estimates of growth rate from 3.22–5·98% length day^{-1}. This fast growth was confirmed by the presence of pupal exuviae from mid-June to end of July indicating the emergence of adults. The maximum larval length decreased during the summer showing that pupation occurred at a smaller size. There was a close relationship between the percentage rate of growth in length and water temperature. From this and the sizes of larvae, the duration of larval life was calculated

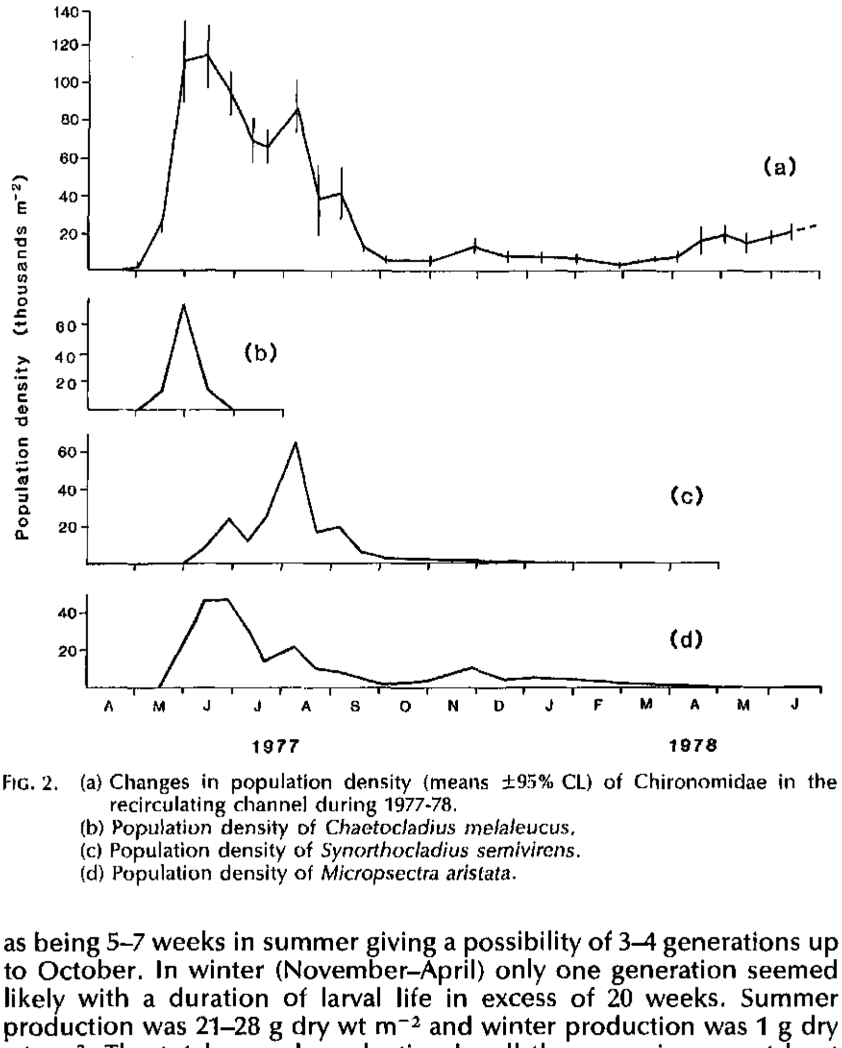

FIG. 2. (a) Changes in population density (means ±95% CL) of Chironomidae in the recirculating channel during 1977-78.
(b) Population density of *Chaetocladius melaleucus*.
(c) Population density of *Synorthocladius semivirens*.
(d) Population density of *Micropsectra aristata*.

as being 5–7 weeks in summer giving a possibility of 3–4 generations up to October. In winter (November–April) only one generation seemed likely with a duration of larval life in excess of 20 weeks. Summer production was 21–28 g dry wt m^{-2} and winter production was 1 g dry wt m^{-2}. The total annual production by all three species was at least 35 g dry wt m^{-2}.

The most abundant ephemeropteran which colonized the channel was *Baetis rhodani*, a multivoltine species (Humpesch 1979; Welton et al. 1982) which attained a maximum population density of 29 000±1·7 m^{-2} in August 1977. This is far in excess of values usually reported in other situations, possibly because of the absence of fish and the restricted number of invertebrate predators. The summer maximum in the Waterston stream adjacent to the channel was only 1120 m^{-2} (Ladle & Bass 1981). From size-frequency histograms, there were clear cases of a shift in the mean size of recognizable groups in which there was little likelihood of their being affected by recruitment of young larvae and emergence of adults (Welton et al. 1982). From these groups, values of mean percentage growth rate (G) were calculated (range 1·07–2·45% length day^{-1}) for different water temperatures (T °C). Using the regression relationship of G against T (r^2 = 78·9%) to interpret the results of sequential size–frequency data, five cohorts were identified (Fig. 3) (Welton et al. 1981). Erroneous conclusions may result if the time interval between samples is long relative to the cohort life span. In an attempt to overcome this, the study incorporated a shorter sampling interval (14 days) in the summer months when growth was expected to be rapid.

Ephemerella ignita (Poda) which normally produces a resting egg stage and completes its single annual generation of larvae in spring and

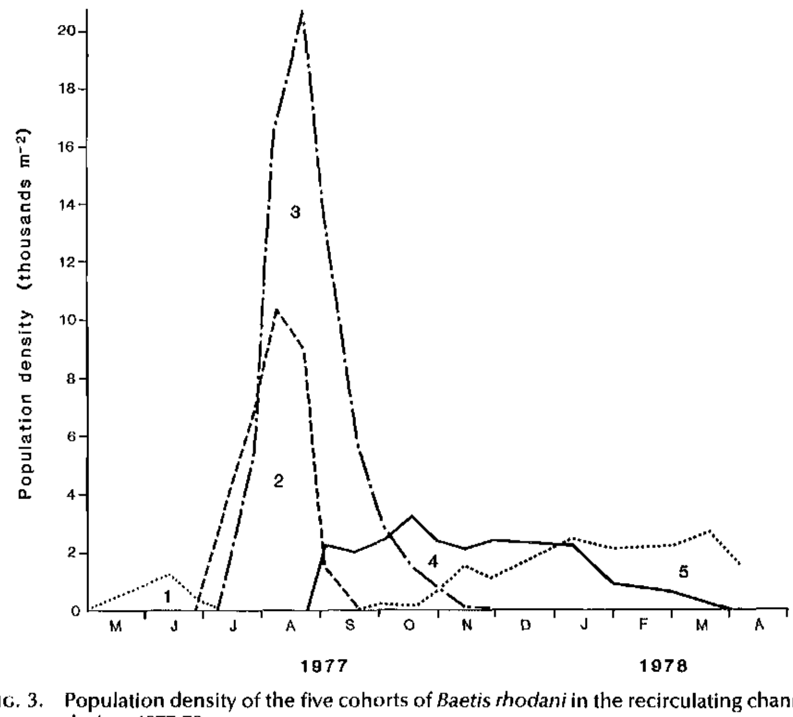

FIG. 3. Population density of the five cohorts of *Baetis rhodani* in the recirculating channel during 1977-78.

summer (Bass 1976) reached the high density of 13 000 m^{-2} in spring with a maximum growth rate of 3·3% length day^{-1}.

Nineteen species of Ephemeroptera occurred in the channel during 1977–78 although most were present intermittently at low population densities (Welton et al. 1982). The total annual production by the abundant species of Ephemeroptera, 10·2 g dry wt m^{-2} was only about one third of that by Chironomidae.

The larvae of the caddis *Polycentropus flavomaculatus* (Pictet) attained the high population density of 20·5 m^{-2}. There was an annual cycle involving a small fast-growing summer generation which was detectable only because of the absence of substantial numbers of larvae from the preceding winter (Fig. 4) followed by a more productive overwintering generation with extended periods of recruitment and pupation (Bass et al. 1982). The interpretation of the life cycle differs from those of Elliott (1968) and Macan & Maudsley (1968) who found a single generation. The differences may simply reflect differing environmental conditions, the rapid growth of the summer generation being at a time when temperatures were high and food was abundant.

Discussion

The results of work in the prototype experimental channel have now provided information on, and initiated studies into, many aspects of chalk-stream ecology including the crystallization kinetics of calcite from calcium bicarbonate solutions (House 1981a, b; Cassford, House & Pethybridge 1983; House 1984), silicon concentrations in chalk streams (Casey et al. 1981) and their relationships with the growth of algae (Marker & Casey 1982) and production and grazing rates of invertebrates.

Other experimental flowing-water studies have shown substantial effects of grazing invertebrates on epilithic diatom associations (Eichenberger & Schlatter 1978). Grazing is clearly more relevant in the present situation than nutrient depletion which is frequently a cause of declining phytoplankton growth in lakes (Reynolds 1982). The total annual production of grazing invertebrates (Chironomidae and Ephemeroptera) in the channel of >45 g dry wt m^{-2} can be related to consumption of epilithon in various ways. By combining the numerical abundance and size distribution of each species on each sampling date with the relative weights of gut contents and rates of passage of food through the guts, an estimate of total ingestion should be possible. Until the data for such calculations has been processed, a minimum estimate of ingestion based on an assimilation efficiency of about 10% would suggest a total ingestion of epilithic material of >450 g dry wt m^{-2}. Ingestion would be at its highest rate during peaks of invertebrate biomass which follow closely the peak numbers of total diatoms. Over the 14-day period of peak diatom production a total of 210–420 g dry wt m^{-2} (figure derived from Marker &

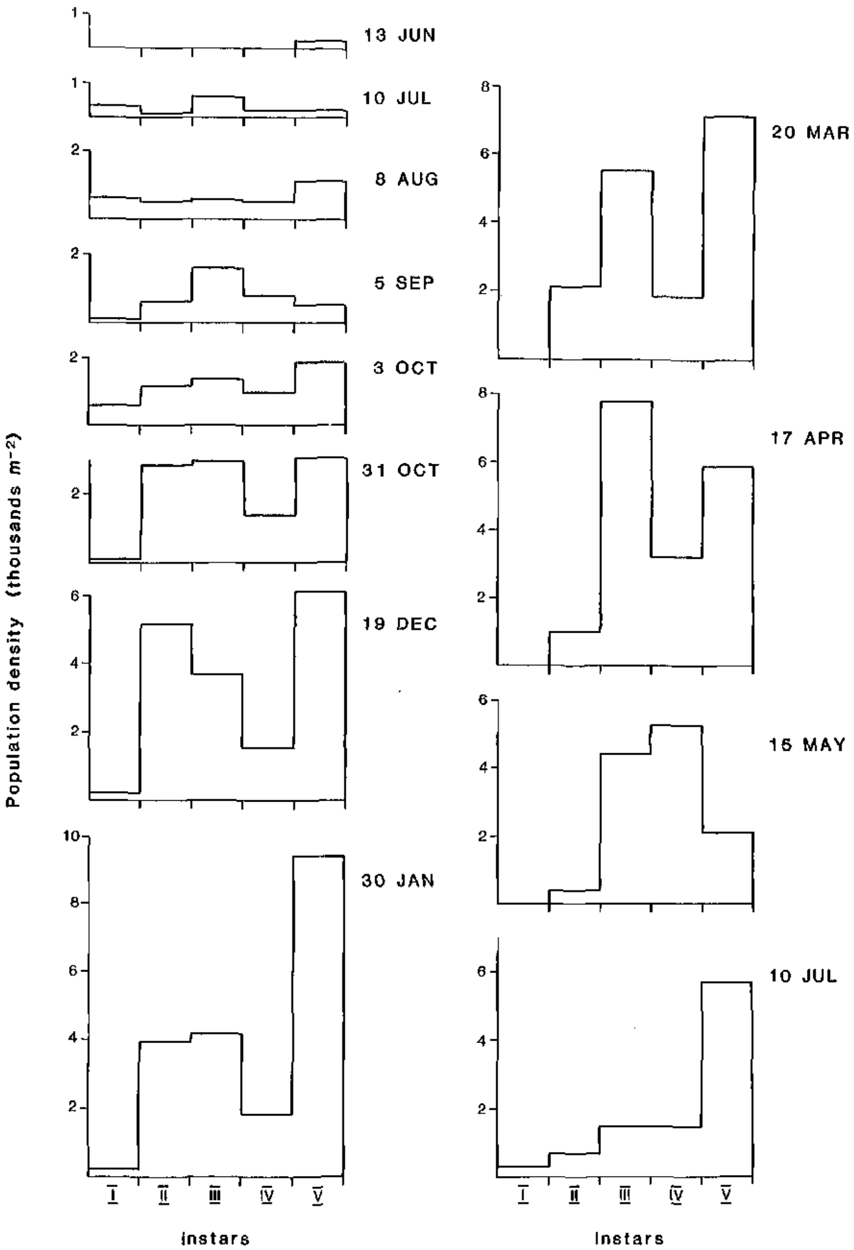

Fig. 4. Instar analysis of *Polycentropus flavomaculatus* in the recirculating channel during 1977-78.

Casey 1982) was consumed and/or sedimented into the gravel interstices. In the absence of more detailed information, the fact that these values are well within the same order of magnitude is not inconsistent with the existence of a causal relationship between the diatom decline and the removal of these organisms by the grazing activities of the invertebrates.

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