The predatory Chironomidae of an iron-rich stream: feeding ecology and food web structure

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ABSTRACT. 1. Three species of Tanypodinae (Chironomidae) were found in an acid and iron-rich stream in southern England. Maximum abundance was achieved in summer and they were sparse at other times. Individuals were aggregated on the stream bed and were over-represented in accumulations of leaf litter.

2. The diets of all three species consisted of a mixture of prey (prominently detritivorous chironomid larvae) and detritus. More detritus and fewer prey were taken in winter than in summer.

3. When comparing large tanypod species with small and, intraspecifically, late instars with early, the proportion of guts containing prey increased with increasing body size.

4. Stonefly larvae were more prominent in the diet of *Zavrelimyia barbatipes* (Kieffer) in summer than in winter but for the other two species the reverse was true. A bigger proportion of *Trissopelopia longimana* (Staeger) guts contained prey in early summer than in August whereas more *Macropelopia goetghebueri* (Kieffer) guts contained prey in August. This was apparently a consequence of seasonal differences in the distribution of body size among the populations of these two species.

5. The stream contains two further common predators, *Plectrocnemia conspersa* (Curtis) and *Sialis fuliginosa* Pict. These are important predators of tanypod larvae but might also compete with them since they severely deplete populations of prey taken in common.

6. Analysis of the food-web in Broadstone Stream reveals remarkably high values of connectance (C and C_{max}) and of species richness times connectance (SC_{max}). Such characteristics are theoretically associated with fragile and dynamically unstable food webs, and may be found in 'constant' environments. There is also an apparently unusual prevalence of omnivory in the community.

Key words. Tanypodinae, streams, acid, predators, feeding, ecology, food webs.

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Introduction

The macrobenthos of a small, fish-less, acid and iron-rich stream in southern England consists almost entirely of insects, has rather few species and has proved a convenient subject for a community study (Hildrew & Townsend, 1982). Besides a few further species which occur occasionally or are otherwise extremely sparse, Broadstone stream contains five species of predatory invertebrates that fall into two groups on the basis of size. In previous papers we have dealt with the two large species: the net-spinning larvae of the caddis *Plectrocnemia conspersa* (Curtis) and larvae of the alderfly *Sialis fuliginosa* Pict. (Hildrew & Townsend, 1976, 1980, 1982; Townsend & Hildrew, 1979a, b). In the present paper we consider the small predatory larvae of three species of Tanypodinae (Chironomidae). It is unusual to have the opportunity to consider all the major predators in a single community; this was a primary objective of the work discussed here.

In addition, chironomids are an abundant and widespread group of major importance in freshwater systems, with more than 500 species in Britain alone. Recent taxonomic progress in Britain and elsewhere (Pinder, 1978; Wiederholm, 1983) will inevitably promote ecological work on the group but there remains, at present, no information on the ecology of many species. A further objective, therefore, was to provide basic ecological information on three poorly known species of Tanypodinae.

Methods

Broadstone stream is a tributary of the River Medway and the site has been described previously by Hildrew & Townsend (1976). Every 2 months from April 1974 to April 1975, forty randomly dispersed sampling units were taken from a 500 m stretch of stream using a Surber sampler (area 625 cm², mesh 0.33 mm). The substratum in each sample unit was classified subjectively into one of four categories: predominantly stony, predominantly leafy, a roughly equal cover of stones and leaves, or bare bedrock. Water depth was measured at several places within the quadrat area and the

average recorded in one of three ranges: <5 cm, 5–10 cm and >10 cm. Finally, current velocity near the stream bed in each quadrat was classified as <5, 5–10 or >10 cm s^{-1}. During sampling, substratum was removed to about 5 cm depth (except on bare bedrock) and retained in the net. All material was immediately preserved. In the laboratory the mineral fraction was removed by elutriation and animals were sorted from organic debris by hand. These large quantitative samples were supplemented with smaller, qualitative samples taken during the intervening months, mainly for gut content analysis.

Tanypodinae were initially counted into two groups: *Macropelopia goetghebueri* (Kieffer) (Macropelopiini) and Pentaneuriini. Subsequently, the head-capsules and gut contents of samples of larvae were individually mounted on slides in polyvinyl lactophenol. Examination of head capsules enabled two species of Pentaneuriini to be identified: *Trissopelopia longimana* (Staeger) and *Zavrelimyia barbatipes* (Kieffer). In total, the gut contents of 442 *M. goetghebueri*, 455 *T. longimana* and 324 *Z. barbatipes* were analysed. The numbers of guts containing specified prey items or undifferentiated detritus was recorded for second, third and final instars of each species in different seasons. Davies & McCauley (1970) found that some chironomid larvae regurgitate a fraction of their gut contents during preservation. This was not observed in the present study but we cannot exclude it as a possibility. It was not possible, therefore, to estimate rates of consumption on the basis of gut contents, as we did for *Plectrocnemia conspersa* (Hildrew & Townsend, 1982). A further confounding factor in quantitative estimation of feeding rates is the possibility that some prey are not engulfed but their body fluids consumed by piercing and sucking, a behaviour found in some other Tanypodinae (Coffman, 1978).

Results

Abundance, size and distribution

Estimates of abundances of tanypod larvae in Broadstone stream (Fig. 1a and b) are certain to be too low because first instars were not taken and second instars were probably somewhat underestimated. *Macropelopia goet-*
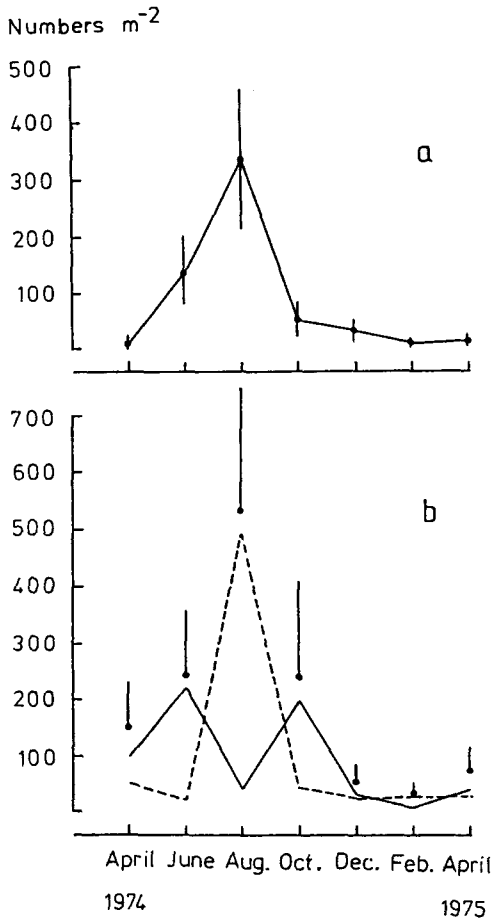
Numbers m^{-2}

FIG. 1. (a) The mean density ($\pm$95% CL) of *Macropelopia goetghebueri*, (b) The unconnected points show the mean density ($\pm$95% CL) of the combined populations of Pentaneuriini; estimates of the density of *Zavrelimyia barbatipes* (- - -) and *Trissopelopia longimana* (—) are also plotted separately.

TABLE 1. Head widths (mm) of instars 2, 3 and 4 of three species of Tanypodinae.

	Instar 2	Instar 3	Instar 4
M.goetghebueri	0.18–0.29	0.34–0.53	0.59–0.92
T.longimana	0.14–0.19	0.23–0.37	0.42–0.62
Z.barbatipes	0.12–0.18	0.22–0.35	0.40–0.56

third and fourth instars to be separated in each case (Table 1). *M.goetghebueri* is the biggest species and *Z.barbatipes* the smallest. First instar larvae of *M.goetghebueri*, occasionally found in the guts of larger tanypods and the other predatory insects, have a head width of about 0.12 mm, and those of the other two species a width of about 0.10 mm.

Reliable interpretations of life cycles of the species cannot be made because they were so sparse for much of the year and because cohorts were not obvious. However, Fig. 2 shows for each species the frequency distributions of instars in June, July and August, when tanypod larvae were most abundant. The sample modal instar for *M.goetghebueri* changed from two to four during this period, probably representing growth of a cohort, whilst that of *T.longimana* changed from four to two, presumably including a period of emergence and recruitment. The modal instar for *Z.barbatipes* changed from four to three during the same period.

The distribution of counts of larvae of *M.goetghebueri* and Pentaneuriini among the sample units was always highly aggregated. Morisita's Index of Dispersion (Morisita, 1962) for both taxa and on each sampling occasion took values >2.27 ($P<0.001$; Elliott, 1977). Values of a simple index of representation (I.R.) of the two taxa among sample units (classified on the basis of substratum, depth and flow regime), are shown in Table 2. I.R. is calculated as $(O-E)/\sqrt{E}$, where O is the observed number of larvae from a given category and E is the expected number (based on the number of sample units falling into that category and the total numbers of larvae in the sample). The index takes a positive value for over-representation and negative for under-representation. The most consistent over-representation for both *M.goetghebueri* and Pentaneuriini was in sample units with a low flow velocity (category 1) and a substratum including leaf litter (categories 1 and 2).
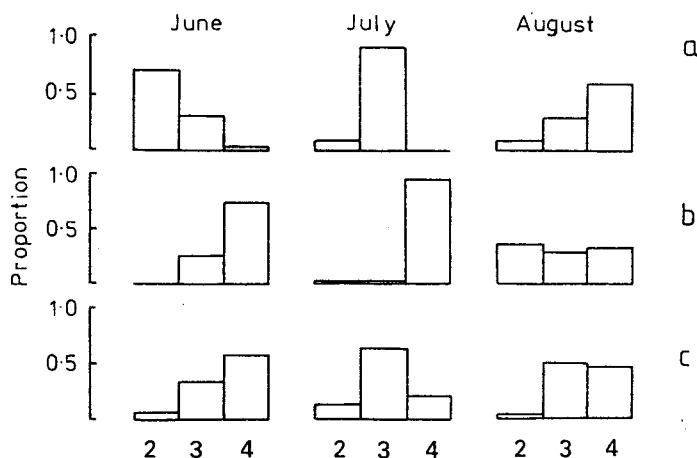
ghebueri was sparse outside the summer months and had a peak mean density in August 1974 of about 350 m^{-2}. The combined population of the two species of Pentaneuriini also reached peak abundance (approximately 530 m^{-2}) in August. Based on the specific identification of larvae in samples used for gut contents analysis, estimates were made of the density of the two species separately. *Zavrelimyia barbatipes* made up more than 90% of the peak August abundance. *Trissopelopia longimana* was the more abundant in June and October.

Head width measurements of large samples of larvae identified to species allowed second,

FIG. 2. The proportion of samples of (a) *M.goetghebueri*, (b) *T.longimana* and (c) *Z.barbatipes* made up of second, third and fourth instar larvae in June, July and August 1974.

TABLE 2. Indices of representation {I.R.$=O-E/\sqrt{E}$) of larvae of *Macropelopia goetghebueri* and Pentaneuriini among sample units classified according to substratum (categories 1–4; leafy, leafy/stony, stony, bedrock), depth (1–3; 0–5 cm, 5–10 cm, >10 cm) and flow (1–3; 0–5 cm s^{-1}, 5–10 cm s^{-1}, >10 cm s^{-1}). Positive values indicate over-representation and negative values under-representation.

	Substratum				Depth			Flow		
	1	2	3	4	1	2	3	1	2	3
Macropelopia goetghebueri										
April 1974	5.9	−1.2	−3.6	−1.8	−0.9	−1.8	2.5	1.3	0.1	−2.0
June	−0.7	3.8	0.2	−6.6	−5.6	4.5	2.2	4.2	0.1	−7.0
August	3.2	10.0	−5.5	−8.2	−5.9	4.9	1.4	7.2	−6.0	−8.0
October	8.2	3.8	−5.3	−4.3	−2.8	3.6	−0.5	7.0	2.9	6.7
December	8.8	0.1	−3.6	−3.1	−3.5	0.9	1.9	4.1	−2.5	−3.2
February 1975	3.6	4.2	−2.1	−2.2	−2.3	2.9	−0.3	7.5	−0.1	−3.4
April	9.7	0.5	−3.0	−2.2	3.6	−3.2	0.2	3.8	−0.7	−3.3
Pentaneuriini										
April 1974	17.5	−4.0	−10.7	−4.7	−3.0	−8.6	10.4	4.8	−0.5	−6.0
June	17.7	−6.5	2.4	−8.4	−12.9	−6.8	16.7	10.7	−9.1	−10.3
August	3.7	1.2	−0.5	−5.8	−5.4	2.4	4.2	6.3	−3.0	−10.8
October	21.3	−1.9	−8.4	−9.2	−5.6	−4.4	5.7	21.3	−7.6	−11.7
December	9.9	1.0	−4.2	−3.7	−2.4	0.4	1.6	3.9	−2.2	−3.0
February 1975	6.1	1.2	0.5	−3.7	−4.4	−1.5	4.4	4.5	4.6	−5.2
April	0.0	9.0	−4.6	−4.8	−4.9	−6.1	8.7	4.9	0.7	−5.7

Diet

Overall, the diets of the three species were similar and all categories of food were found in all species (Fig. 3a). The prey included both harpacticoid and cyclopoid benthic Copepoda, detritivorous chironomid larvae, predatory chironomid larvae, stonefly larvae, terrestrial litter mites and a very small proportion of other items, mainly small terrestrial insects. There were also a number of spherical cocoons, about 150 μm in diameter, whose identity is unknown but which may be those of rhabdocoels.

The stream had five common species of Chironomidae with detritivorous larvae (Townsend & Hildrew, 1979a) and all were, on occasion, found in the guts of all three predatory species. *Heterotrissocladius marcidus* (Walker) and *Micropsectra bidentata* (Goetghebuer) were most commonly taken. Both species of stonefly (Plecoptera) present in Broadstone stream (*Leuctra* spp., mainly *L.nigra* Oliver, and *Nemurella picteti* Kla-
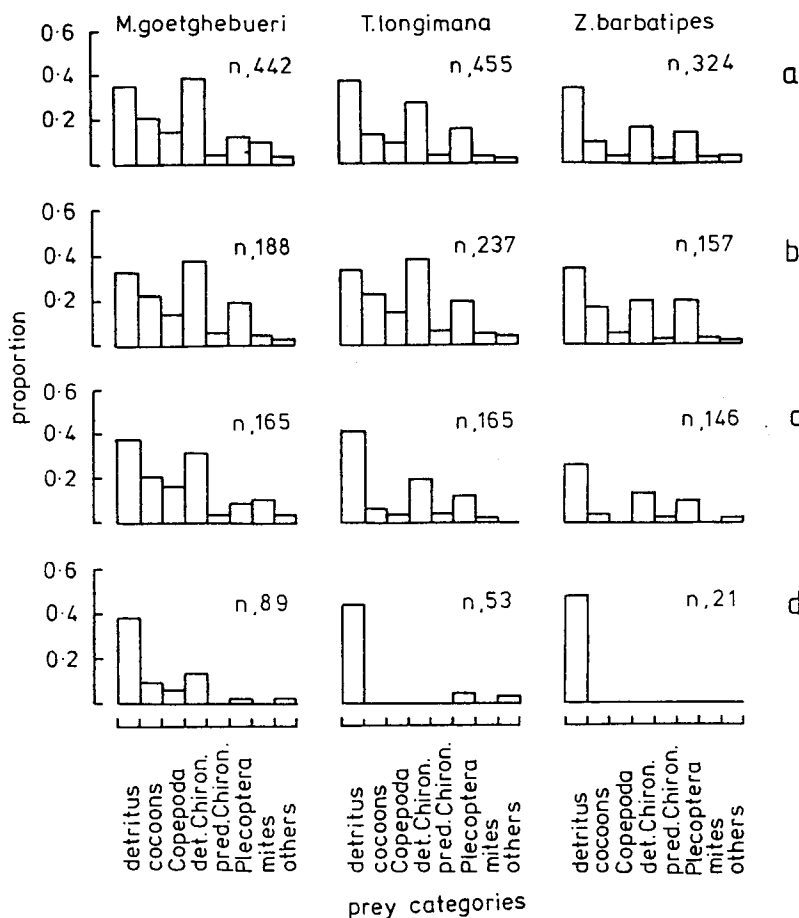
FIG. 3. The proportion of larvae of *Macropelopia goetghebueri*, *Trissopelopia longimana* and *Zavrelimyia barbatipes* containing particular food items: (a) all larvae, (b) fourth instars, (c) third instars, (d) second instars.

palek) were included in the diet of the predatory chironomids. Whole stonefly head capsules were rare in the guts and remains were characteristically fragmented. The pattern of occurrence of detritus indicates clearly that it was consumed directly and did not merely represent the gut contents of prey animals.

The percentage of empty guts was 13.3%, 23.8% and 41.8% for *M.goetghebueri*, *T.longimana* and *Z.barbatipes*, respectively, and there was a highly significant association between the numbers of guts containing recognizable items or not and species (χ^2 test on a 3×2 contingency table, $P<0.001$). This difference between the species was a consequence of progressively smaller numbers of guts containing Copepoda, detritivorous Chironomidae

and cocoons, in the sequence *M.goetghebueri*, *T.longimana* and *Z.barbatipes* (χ^2 tests for each prey category, $P<0.001$). There were no significant differences in the numbers of guts containing stonefly larvae or detritus.

A comparison of specific larval instars reveals important differences (Fig. 3b–d). In the two smaller species, *T.longimana* and *Z.barbatipes*, there was a decline with instar in the numbers of guts containing prey of all categories. Indeed *Z.barbatipes* was not predatory in the second instar (nor presumably in the first), and the second instar of *T.longimana* was also overwhelmingly detritivorous. For the largest species, *M.goetghebueri*, many categories of prey also declined with decreasing instar, although some prey were present in the guts of

second instar larvae. There were significant differences among the instars of *M.goetghe-bueri* in the representation of detritivorous chironomids, stoneflies and cocoons (χ^2 tests, all $P<0.001$) and copepods ($P<0.05$). Note that for none of the species was there a significant difference among instars in the number of guts containing detritus.

There were also, in each of the species, strong seasonal differences in diet (Fig. 4). To maintain adequate sample sizes, data have been grouped into those from the important summer period (June to August) and those from October to April (hereafter called 'winter'). To demonstrate that seasonal differences in diet are not simply due to the specific seasonal representation of particular instars, Fig. 4 also retains a division into fourth instar and third plus second instar larvae. The most obvious feature to emerge was a dramatic
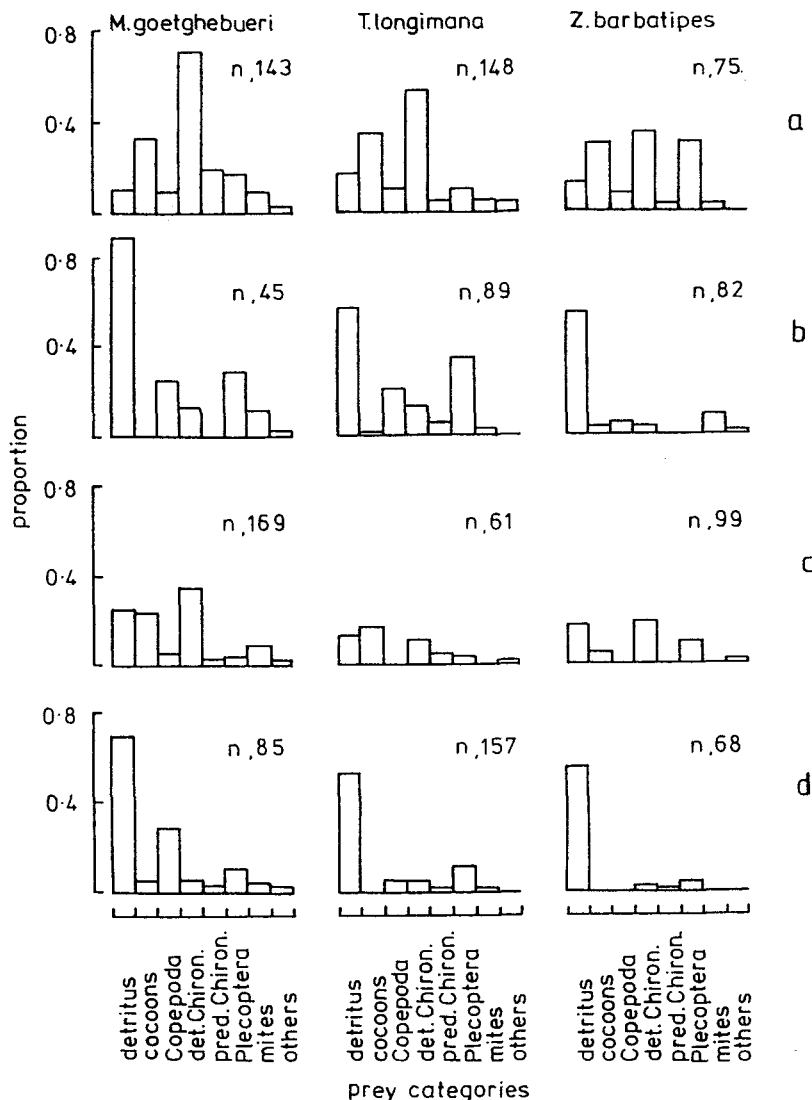

FIG. 4. The proportion of larvae of *Macropelopia goetghebueri, Trissopelopia longimana* and *Zavrelimyia barbatipes* containing particular food items: (a) fourth instars summer, (b) fourth instars winter, (c) second and third instars summer, (d) second and third instars winter.

increase in the representation of detritus in winter compared with summer ($P<0.001$ for each species). Also, cocoons were rarely present in the guts of any species outside the summer months. Another major seasonal difference in common is that all species took far more detritivorous chironomids in summer than winter ($P<0.001$ in each case).

Further seasonal patterns exist which reveal differences, rather than similarities, between the species. For instance, *M.goetghebueri* took significantly more copepods in winter than summer (Fig. 4, $P<0.001$). The pattern in *T.longimana* was similar but not statistically significant and *Z.barbatipes* took very few copepods at any time. Also, the timing of consumption of stoneflies was clearly different between *Z.barbatipes*, on the one hand, and *M.goetghebueri* and *T.longimana* on the other (Fig. 4). For the latter pair of species, there were significantly more guts containing stoneflies in winter than summer (both $P<0.005$) whilst *Z.barbatipes* took significantly more in summer than winter ($P<0.005$). There were thus significant associations between predator species and the number of guts containing stoneflies or not ($P<0.005$ in both winter and summer).

The diets of *M.goetghebueri* and *T.longimana* appear to differ only when account is taken of their contrasting size distributions in summer (Fig. 2). *Trissopelopia longimana* was larger in June and, since the occurrence of prey in guts seems to be strongly related to
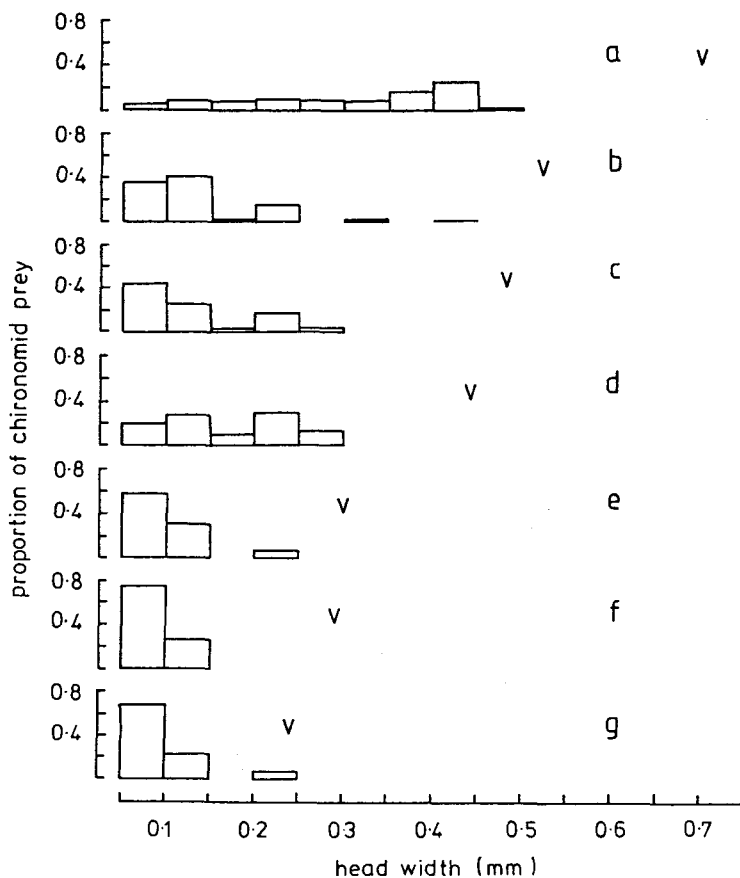

FIG. 5. The relationship between predator size (single instars of the three tanypod species, mean predator head width marked V) and prey size (frequency distribution of chironomid prey head width): (a) *M.goetghebueri*, fourth instar (n, 192); (b) *T.longimana* fourth instar (n, 177); (c) *Z.barbatipes*, fourth instar (n, 38); (d) *M.goetghebueri*, third instar (n, 80); (e) *T.longimana*, third instar (n, 36); (f) *Z.barbatipes*, third instar (n, 36); (g) *M.goetghebueri*, second instar (n, 13).

body size, it is not surprising that it took significantly more detritivorous chironomids and cocoons at that time than *M.goetghebueri*. Of the June sample of 68 *M.goetghebueri* and 143 *T.longimana*, 16 and 66 larvae, respectively, contained detritivorous chironomids (*P*<0.005) and 15 and 51, respectively, contained cocoons (*P*<0.05). In August the size difference was reversed (Fig. 2) and *M.goetghebueri* then took far more chironomids (from 234 *M.goetghebueri* and 32 *T.longimana*, 141 and 9, respectively, contained detritivorous chironomids; *P*<0.001).

Finally, the size distribution of the head capsules of chironomid prey (both detritivorous and predatory) is shown in Fig. 5, along with the mean head widths of the predators taking them. Chironomidae were the only prey items which were sufficiently numerous for such an analysis. Not surprisingly, larger predators included larger prey in their diet, although small chironomid head capsules (about 0.05 mm) were also frequently found in the guts of fourth instar *M.goetghebueri* larvae (the largest tanypod predators).

Discussion

The species of Tanypodinae found in Broadstone stream are described as characteristic of the cool, rather unproductive, upland waters of northern Europe by Fittkau (1962). In addition, *Macropelopia goetghebueri* was found in the acid streams of the New Forest by Hall (1951a, b), and by Morgan (1949) at a variety of sites on the Isle of Man and in northern England. It was also found, along with *Zavrelimyia barbatipes*, in a cool, iron-rich, Danish stream by Lindegaard-Peterson (1972). There is little further information on any of the three species. More generally, the fauna and flora of the Ashdown Forest, a southern English heath, includes many species more characteristic of northern and western Britain (Townsend *et al.*, 1983) and the occurrence of these chironomids is a further example.

There have been a moderate number of accounts of the diets of tanypods although most deal with a single genus from standing waters, *Procladius*. Authors have frequently found a mixed diet of small, aquatic animals

with detritus and algae (Izvekova, 1967, 1971; Armitage, 1968; Roback, 1968; Mackey, 1977, 1979; Dusoge, 1980; Vodopich & Cowell, 1984). A few have suggested that larvae are less predatory when small (Izvekova, 1967; Armitage, 1968) and, indeed, Baker & McLachlan (1979) found no animal remains in the guts of three species, including *Macropelopia goetghebueri*, although their samples, of unspecified instar, were very small. Izvekova (1971) reported that *Psilotanypus imicola* Kieffer could develop on algae alone but Mackey (1977) and Vodopich & Cowell (1984) found that the growth of *Ablabesmyia monilis* L. and *Procladius culiciformis* (L.), respectively, was very slow when larvae were denied animal food, and the latter species did not moult beyond the third instar when fed on algae and detritus alone. On no previous occasion has the diet of a complete, albeit small, assemblage of Tanypodinae from a single site been described and rarely have samples been sufficiently large to permit comparison both between instars and seasons.

Among the tanypods of Broadstone stream there were clear differences when comparing seasons and instars. All three species were less predatory in winter and when they were small. A problem in the interpretation of such patterns is that we have no quantitative information on the availability of very small prey such as benthic crustacea and other micro-invertebrates or of cocoons. However, it is known that the density and biomass of detritivorous chironomids and stoneflies fluctuates markedly through the year. For instance, total chironomid biomass declined from August 1974 to February 1975 by almost 400 times, attributed to intense predation by *Plectrocnemia conspersa* and *Sialis fuliginosa* (Hildrew & Townsend, 1982). The decline in stonefly biomass, although less extreme, was nonetheless marked. It is clear, therefore, that the predatory chironomids face very great changes in prey abundance.

Perhaps not surprisingly, therefore, there was an obvious switch, for tanypod larvae of all sizes, from a largely predatory diet in summer to an overwhelmingly detritivorous one in winter, presumably involving a great reduction in food quality. Such a change must involve a switch in foraging behaviour, since detritus is available throughout the year.

All three species take large numbers of small detritivorous chironomid larvae in summer, when the latter are abundant. Tanypod larvae are then to be found crawling over the gelatinous egg masses of chironomids (A. Box, pers. comm.) and perhaps take hatchlings as they emerge. The stonefly *Nemurella picteti* also produces a gelatinous egg-mass in Broadstone stream and it would be interesting to discover whether *Zavrelimyia barbatipes,* apparently a specialist on stoneflies in summer, can locate and feed upon hatchlings in such situations.

There was an overall decline, with decreasing predator size, in the number of guts containing food and this was attributable to a reduction in all the various prey categories in the diet, though not of detritus. This observation is true when making comparisons both interspecifically, between larger tanypod species and small, and intraspecifically, between instars. Presumably, small predators have limited abilities to handle relatively large prey and there may also be a shortage of suitably small items. It is clear from the relationship between predator and chironomid prey size that the smallest categories of prey available (first instar larvae) are taken by even the biggest tanypod predators. The guts of large tanypods contained prey in all size categories and large predators simply included a wider range of prey in their diet. Thus, small instars of the predators did not have a food refuge in the form of small prey invulnerable to larger predators,

We have been able to demonstrate differences between the diets of these three coexisting species, based on seasonal prey specialization and life-cycle differences. There is no obvious way, however, to judge the significance of such differences either against any degree of difference expected by chance or as 'coexistence mechanisms' of potentially competing species. There is some circumstantial evidence that food is limiting to predator populations in Broadstone stream, since the predators cause such obvious reductions in prey throughout the year. This might suggest that any competition would be important among predators but not among prey. Resource partitioning has, indeed, been found between the two large insect predators in the stream, *Plectrocnemia conspersa* and *Sialis fuliginosa* (Townsend & Hildrew, 1979a, b) and

was most apparent in winter when prey were sparse. In the case of Tanypodinae, however, interspecific differences were most obvious in summer, when prey were abundant, whilst in winter all three species were detritivorous.

Scrutiny of the food web in Broadstone stream shows that *P.conspersa* and *S.fuliginosa* share all the same major prey categories with the three tanypods (Fig. 6). However, the two large species also prey heavily on the smaller predators; indeed, the pronounced declines in tanypod densities after the summer peaks are attributable to this predation (Hildrew & Townsend, 1982). Thus *P.conspersa* and *S.fuliginosa* each have a dual interaction with the tanypods; a direct predatory effect and, indirectly, as consumers of common resources.

There has recently been a good deal of theoretical interest in the structure and stability of food webs and their relationship with environmental fluctuations (Cohen, 1978; Pimm, 1982; Briand, 1983; Briand & Cohen, 1984). Descriptions of more real webs are needed, and that in Broadstone stream appears to be about the most detailed available, at least for a freshwater community. A number of its features, in relation to theoretical predictions and previous observations, may be mentioned here. The number of predator/ prey links, as a proportion of possible pairwise links, between all the species in the community yields a minimum value of connectance (C_{min}) whereas the calculations of C_{max} includes, in addition, all potentially competitive interactions (where two species share at least one resource; Yodzis, 1980). In our calculations, dual interactions (where a species pair have both a predator/prey and a competitive interaction) have been counted only once. C_{min} and C_{max} take values of 0.35 and 0.76, respectively, in Broadstone and SC_{max} (where S is the number of interacting 'species') is 18.2. Connectance and SC_{max} are both very high (only two and one, respectively, out of the forty webs considered by Briand (1983) had higher values). Such high values are theoretically associated with fragile and dynamically unstable food webs and were found to be characteristic of 'constant' environments by Briand (1983). However, we know of no unambiguous measure of 'constancy' for streams.

There is also a great deal of omnivory in Broadstone (defined as a species feeding at
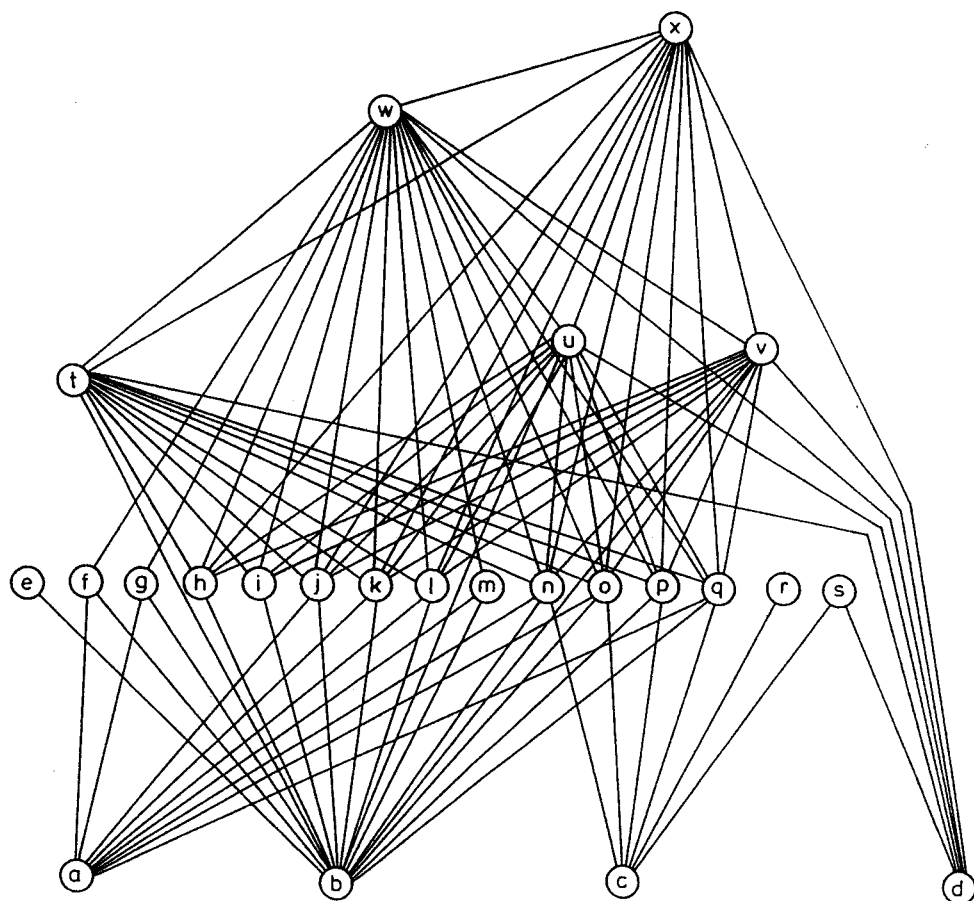
FIG. 6. The food web in Broadstone stream. The species are arranged according to the maximum number of links from the base (mean maximum food chain length is 4.14); basal resources: (a) iron bacteria; (b) fine particulate organic matter; (c) coarse particulate organic matter; (d) terrestrial invertebrates: primary consumers; (e) *Pisidium* sp.; (f) Simuliidae; (g) *Niphargus aquilex* Schiodte; (h) microcrustacea; (i) other microinvertebrates; (j) *Heterotrissocladius marcidus*; (k) *Micropsectra bidentata*; (l) *Prodiamesa olivacea* (Meigen); (m) Oligochaeta; (n) *Leuctra nigra*; (o) *Nemurella picteti*; (p) *Brillia modesta* (Meigen); (q) *Polypedilum albicornis* (Meigen); (r) Tipulidae; (s) *Potamophylax cingulatus* (Stephens): primary carnivores; (t) *Macropelopia goetghebueri*; (u) *Trissopelopia longimana*; (v) *Zavrelimyia barbatipes*: secondary carnivores; (w) *Plectrocnemia conspersa*: tertiary carnivores; (x) *Sialis fuliginosa*.

more than one trophic level; Pimm, 1982). The three tanypod species feed on two 'trophic levels', *P.conspersa* feeds on three and *Sialis fuliginosa* on four (Fig. 6). Omnivory, however, was predicted to be scarce by Pimm (1982). The apparent differences between the food web described here and others is probably partly due to the unusually detailed information available for Broadstone stream. However, omnivory could also be associated with very unproductive systems if, as a con-

sequence of a meagre food supply, all possible items are included in the diet of component species. Reliable interpretation of such patterns, however, will certainly require similarly detailed information from distinct but comparable communities. Finally, the ratio of the number of predator species to prey was estimated at 0.33, close to the middle of the range found for freshwater invertebrate communities in Britain and North America by Jeffries & Lawton (1985).

Acknowledgments

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