

Body-size determinants of niche overlap and intraguild predation within a complex food web

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Summary

1. Body-size may be an important feature of the structure of food webs. Detailed food web data are however scarce, particularly those including ontogenetic dietary shifts within species. We examined the predator guild in a well characterized food web, that of Broadstone Stream (UK), to assess the importance of body-size within and among species in relation to intraguild predation and niche overlap.

2. In agreement with recent food web theory, mutual predation and cannibalism were frequent and occurred in many pairwise permutations. This intraguild predation was strongly asymmetric, being determined by relative body-size within and among species, and seasonal 'ontogenetic reversals' in trophic status arose when generations overlapped.

3. Predator size determined dietary overlap, with ontogenetic shifts often outweighing taxonomic differences. Small predators had the narrowest diets, regardless of species, and were limited to feeding on a restricted subset of the total prey size-spectrum. Niche overlap decreased as pairwise differences in body-size increased among and within species. Overlap in diet also tracked seasonal changes in resource availability, being highest in summer, when prey were abundant and small, and declining progressively over time, as prey became scarcer and/or larger. The small predators also became more detritivorous as prey abundance declined and the larger prey species attained size-refugia.

4. The body-size constraints driving feeding relationships within the predator guild, in terms of both resource partitioning and intraguild predation, lend support to recent niche models of food web structure (Warren 1996; Williams & Martinez 2000). The highly interconnected food web of Broadstone Stream appeared to be structured by relatively simple rules, with seasonal and ontogenetic shifts in the size-spectrum accounting for most of the changes in predator diet and trophic position. Encounter rate in time (prey and predator mobility) and space (microhabitat use) and foraging mode also influenced prey vulnerability and niche overlap, but were secondary to the effect of body-size.

Key-words: cannibalism, coexistence, feeding cycles, food webs, omnivory, polyphagy, mutual predation, size-spectra, trophic status.

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Introduction

Relative body-size of the component species has often been identified as a major determinant of food web structure (Warren & Lawton 1987; Cohen *et al.* 1993a; Memmott, Martinez & Cohen 2000). Size-related constraints on feeding can influence both resource-partitioning and trophic status within food webs, and have been implicated as a potential basis for both the

cascade (Cohen & Newman 1985) and, more recently, the niche model of food web structure (Warren 1996; Williams & Martinez 2000). Detailed data, other than the simple presence/absence of feeding links are however scarce, particularly when assessing the importance of ontogenetic shifts in feeding relationships (Cohen *et al.* 1993b). Because trophic status generally increases with body-size, intraguild predation is often strongly asymmetric and feeding loops may arise both among (mutual predation) and within (cannibalism) species (e.g. Woodward & Hildrew 2001). The size-dependent bias of feeding links within food webs is usually to the detriment of smaller species, whereas larger species may

outgrow potential predators and attain 'size-refugia'. This has important consequences for population dynamics and resource-partitioning within food webs (Chase 1999). Intraguild predation, whereby potential competitors also eat each other, is similarly size-driven and may be viewed as an extreme form of interference competition (Holt & Polis 1997). Once thought to be rare (e.g. Pimm 1982), this mixture of predation and competition appears to be widespread, with many food webs containing an array of polyphagous predators that feed at several 'trophic levels' (Polis 1998).

We examined size-dependent trophic interactions and resource-partitioning among the six dominant predators in a well-characterized food web, that of Broadstone Stream, UK (see Woodward & Hildrew 2001). Because the stream is acid, fish are absent and large predatory insects dominate the community. The common predators can exploit prey heavily between recruitment periods (Hildrew & Townsend 1982; Woodward & Hildrew, in press a), although intergenerational effects may be weaker (Speirs *et al.* 2000). All the predators are generalist omnivores and most prey share at least three predators (Woodward & Hildrew 2001). Despite this broad overlap (at least in terms of the presence or absence of prey in the diet) we might expect body-size asymmetries to determine both the direction and strength of intraguild predation and the differential vulnerability of prey. Most food web models, however, assume constant prey vulnerability over the course of ontogeny, despite the potential importance of size-refugia for prey coexistence (Chase 1999). Further, because the size-spectrum (i.e. the frequency distribution of different body-sizes) of the Broadstone food web varies seasonally, with small individuals predominating in the summer and autumn, we might also expect strong temporal dietary shifts within the predator guild. One such example would be seasonal 'ontogenetic reversals' in trophic status, which can occur when generations overlap (e.g. Polis, Myers & Holt 1989).

The six species examined were, in order of increasing body-size, the larvae of three tanypod midge species (two pentaneurids, *Zavrelimyia barbatipes* (Kieffer) and *Trissopelopia longimana* (Staeger) and *Macropelopia nebulosa* (Meigen)), the caddisfly *Plectrocnemia conspersa* (Curtis), the alderfly *Sialis fuliginosa* Pict., and the dragonfly *Cordulegaster boltonii* Donovan. The predators can also be subdivided into foraging modes: sit-and-wait (*C. boltonii*, *P. conspersa* and *M. nebulosa*) vs. searching predators (*S. fuliginosa* and the two pentaneurid tanypods) and interstitial (*S. fuliginosa* and the tanypods) vs. epibenthic species (*C. boltonii* and *P. conspersa*). *Cordulegaster boltonii* has recently invaded the stream and is now the top predator (Woodward & Hildrew 2001). This large, voracious predator can consume prey to an equivalent of 14% of its own biomass per day and nymphal abundance can exceed 70 m⁻² (Woodward & Hildrew, in press b). Prior

to the invasion, *S. fuliginosa* and *P. conspersa* partitioned food resources when prey were scarce, the latter exploiting an external subsidy of terrestrial invertebrates and also taking a broader size range of prey (Townsend & Hildrew 1979). Because the invader eats the resident predators and their prey, it could play a pivotal role within both the predator guild and the larger community food web.

We asked whether body-size (\approx handling) constraints are a major determinant of predator diet and, if so, how important they are relative to foraging mode. We also assessed the importance of ontogenetic and taxonomic differences among predators and how this influenced resource partitioning and trophic status. Further, because the size-spectrum of predators and prey changes seasonally, we examined temporal diet shifts in response to prey availability. A final objective was to characterize resource partitioning between the invading and resident predators.

Methods

Broadstone Stream (51°05' N, 0°03' E; 120 m a.s.l.) is an acid headwater (pH 4.7–6.6) of the River Medway, in south-east England (see Hildrew & Townsend 1976 for a detailed site description). A 200-m stretch of stream was sampled in late May/early June, August, October and December 1996, and February and April 1997. On each occasion, 30 randomly dispersed Surber sample-units (25 × 25 cm quadrat; mesh aperture 330 µm) were taken to quantify benthic density. The benthos was sampled to 5 cm depth, the usual vertical extent of the Broadstone hyporheos (Rundle 1988). Samples were preserved immediately in 5% formalin, and subsequently sorted in the laboratory. Invertebrate lengths were measured using an eyepiece graticule and biomass was estimated from length–mass regression equations of the form $\log_{10} y = \log_{10} a + b \log_{10} x$, or the equivalent using natural logarithms (Appendix 1). Oligochaete worms, however, were approximated to cylinders with a specific gravity of 1.05, and a dry : wet mass ratio of 0.15 (after Ramsay *et al.* 1997). Size-spectra were then constructed for the benthic community for each sampling occasion (all individuals were measured in each sample-unit; $n = 43\,514$) by calculating the percentage frequency of individuals within size-classes (\log_{10} dry mass categories). The y -axis was scaled to percentage frequency because of the large seasonal variation (> 1 order of magnitude) in absolute abundance. Dry mass was used as the measure of body-size, rather than length or equivalent spherical diameter, because of large morphological differences among taxa (e.g. 'cylindrical' oligochaetes vs. 'spherical' pea mussels).

Gut contents analysis was performed on all of the predators collected in the Surber samples. In addition, qualitative kick samples were taken to supplement the sample of large *Cordulegaster boltonii* (instars 7–14). In total, 3826 predator guts were analysed (*C. boltonii*,

411; *S. fuliginosa*, 450; *P. conspersa*, 559; *M. nebulosa*, 543; *T. longimana*, 1039; *Z. barbatipes*, 824). Predator foreguts were removed by dissection, mounted in euparal and examined at $\times 400$ magnification. The smaller tanypods, however, were mounted whole. As prey were ingested whole, or in large fragments, most species could be identified relatively easily. Gut contents were identified from reference slides and the biomass of ingested prey was estimated after Hildrew & Townsend (1982). Daily ingestion rates were estimated from equations derived for *P. conspersa*, which assume a mean gut residence time of 9.8 h for stoneflies at 13 °C and a digestion rate of $Q_{10} = 2.3$ (Speirs *et al.* 2000).

'Interaction webs' were constructed to examine intraguild predation and niche overlap among the predators. Feeding links within the subweb of the predator guild were quantified as the numerical standing crop of 'prey' eaten $\text{m}^{-2} \text{24 h}^{-1}$ on each sampling occasion. Links were then expressed as the percentage of each 'prey' population that was consumed per day (i.e. if the abundance of *P. conspersa* and *C. boltonii* were 50 m^{-2} and 10 m^{-2} , respectively, and each *C. boltonii* ate one *P. conspersa* 24 h^{-1} , this link would be assigned a value of 20%). Niche overlap webs were also constructed, using Pianka's Niche Overlap Index:

$$O_{jk} = O_{kj} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where P_{ij} and P_{ik} are the proportions of the i^{th} resource used by the j^{th} and the k^{th} species, respectively (Pianka 1973). This equation generates a single overlap value of between zero (no overlap) and one (complete overlap) for each pairwise comparison. Dietary overlap was calculated for all species pairs on each sampling occasion, and depicted in webs where the thickness of lines connecting pairs of predators represented the degree of overlap. Total overlap within the predator guild was calculated as the mean of all pairwise comparisons.

Predators were subdivided into size-classes for dietary analysis (Table 1). Because the 10 (or more) instars of *S. fuliginosa* could not be separated with certainty, the larvae were divided into five size-classes equivalent to *P. conspersa* instars (after Townsend & Hildrew 1979). Similarly, *C. boltonii*'s size-classes were delimited by groups of instars that gave the closest approximations to *P. conspersa*'s five instars. However, because its 14 instars did not correspond perfectly with those of the other predators, the size-classes used were approximately, rather than exactly, the same as *P. conspersa*'s. Two further size classes, 6 and 7, were also used for late instar *C. boltonii*, which were considerably larger than fifth instar *P. conspersa*. The tanypods were much smaller than the larger predators and were classified by instar number. Consequently, size-class divisions more

Table 1. Size-classes of predators, as delimited by head capsule width (HCW) used in dietary analyses, and the corresponding range of larval instars (see Methods). Note that Instar I was omitted for the tanypods because it is detritivorous

Size-class	HCW (mm)	Predator species	Instar
1	0.4–0.5	<i>Cordulegaster boltonii</i>	1
2	0.5–0.6		2
3	0.6–0.9		3 and 4
4	1–1.7		5–7
5	1.7–3.5		8–10
6	3.5–5.4		11 and 12
7	> 5.5		13 and 14
1	< 0.5	<i>P. conspersa</i> <i>S. fuliginosa</i>	1(?)
2	0.5–0.7		2(?)
3	0.7–1.2		3(?)
4	1.2–1.8		4(?)
5	1.8–3.4		5(?)
2	0.2–0.3	<i>Macropelopia nebulosa</i>	2
3	0.3–0.5		3
4	> 0.6		4
2	0.2	<i>Trissopelopia longimana</i>	2
3	0.3–0.4		3
4	0.5		4
2	0.2	<i>Zavrelimyia barbatipes</i>	2
3	0.3		3
4	> 0.4		4

closely reflected differences among instars, or groups of instars, than among exact size categories, which had less biological relevance: i.e. Size-class 1 was not used as an absolute measure that was identical for each species. Dietary overlap was calculated for comparisons among size-classes. Pairwise differences in the body-size of predators, between both pairs of species and of size-classes within species (estimated as mean individual $\log_{10} \mu\text{g}$ Predator 1 – mean individual $\log_{10} \mu\text{g}$ Predator 2), were plotted against niche overlap to assess size-related constraints on resource partitioning.

STATISTICAL ANALYSIS

Repeated Measures ANOVA was performed using SAS Version 8 to compare the benthic abundance of the six predator species over the six sampling occasions. The $\log_{10}(x + 1)$ transformation was applied, to normalize the data and stabilize variances. Multivariate analysis of the percentage numerical composition of predator diets was performed using CANOCO 4 (ter Braak & Smilauer 1998). Unimodal methods (Detrended Correspondence Analysis) were used for this analysis, rather than linear methods (e.g. Principal Components Analysis), due to the long gradient length of Axis I (> 2 SD).

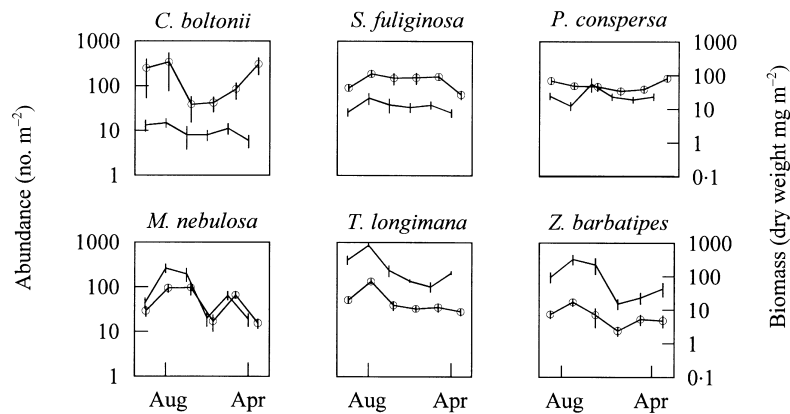


Fig. 1. Seasonal variations in the abundance and biomass (open circles) of the six dominant predator species in Broadstone Stream between 1996 and 1997. Note logarithmic y-axes.

Table 2. Repeated measures ANOVA of predator abundance for the six dominant predator species over six sampling occasions (May 1996–April 1997)

	d.f.	F-ratio	P
Month	5	15.61	< 0.001
Species	5	47.49	< 0.001
Species × month	25	3.58	< 0.001

Results

The benthic abundance of the six predators peaked during summer and autumn, following oviposition by adult insects, and then declined over winter (Fig. 1). There were significant differences (all at $P < 0.001$) in predator abundance among species and among months, and the statistical interaction between species and month suggested a degree of within-year temporal separation among the predators (Table 2). Mean abundance and the magnitude of seasonal fluctuations generally decreased with increasing body-size, i.e. pentaneurids (*Z. barbatipes* and *T. longimana*) > *M. nebulosa* > *P. conspersa* > *S. fuliginosa* > *C. boltonii* (Fig. 1). Mean benthic biomass m^{-2} , however, generally increased with body-size (Fig. 1) and was negatively correlated with \log_{10} abundance m^{-2} among the six species ($r = -0.95$; $P = 0.004$): thus, *C. boltonii*, although numerically rare, accounted for a large proportion of total predator biomass.

Detrended Correspondence Analysis of ontogenetic and taxonomic shifts in predator diets revealed a gradient length of 3.8 SD along Axis I, close to the 4 SD that would represent complete species turnover in the diet. Axis I accounted for 22.2% of the species variance, and represented a gradient of decreasing prey and predator size from left to right (Fig. 2). Predator 'foraging modes' were separated along Axis II (which explained 10.2% of the species variance), being of secondary importance to body-size. All size-classes of the epibenthic predators, *C. boltonii* and *P. conspersa*, were located above those of the interstitial predators (tanypods

and *S. fuliginosa*) on Axis II, with only two exceptions: C5 and M3 (Fig. 2). Differential encounter rates influenced prey vulnerability, with mobile, epibenthic prey (e.g. *Nemurella pictetii* Klapalek and cyclopoid copepods) being generally favoured by the epibenthic predators, whereas the interstitial predators (Fig. 2) favoured sedentary, interstitial prey (e.g. chironomids).

All six predators ate virtually every animal taxon smaller than themselves: this created a degree of 'nestedness' in the diet as predator body-size increased. For instance, the tanypods took mainly small prey, particularly other chironomids, whereas *Cordulegaster boltonii* ate these small items in addition to much larger prey, including conspecifics, *S. fuliginosa* and *P. conspersa*. Similarly, the diet of the predators broadened during ontogeny, as progressively larger prey were included (Fig. 3). Even the late instars of the large predator species still took small prey, although relatively infrequently. Consequently, the number of taxa and size-range of prey was greatest for large *C. boltonii* and least for the small tanypods, which were predominantly detritivorous.

Dietary overlap decreased as the size disparity between predators increased (Fig. 4). Significant correlations (at $P < 0.05$) between niche overlap values and pairwise differences in individual predator body-size were found for comparisons both among species (Fig. 4a) and among size-classes within species (Fig. 4b). For the three large predators, where n was sufficiently large for meaningful comparisons to be made, there was no significant difference in the relationship between overlap and body-size among species (ANCOVA $F_{2,33} = 1.71$; $P = 0.197$). The range of overlap values within a species could exceed those comparing across species: for instance, adjacent size-classes of *C. boltonii* had overlap values of nearly 1, compared with nearly zero between the size-classes with the greatest size differences (Fig. 4b).

The mean \log_{10} mass of individual prey ingested increased linearly with \log_{10} predator mass ($r = 0.97$; $P = 0.002$) (Fig. 5). Similar body-size scaling was seen among size-classes within predator species, as illustrated by *C. boltonii* ($r = 0.93$; $P = 0.002$) (Fig. 5). The

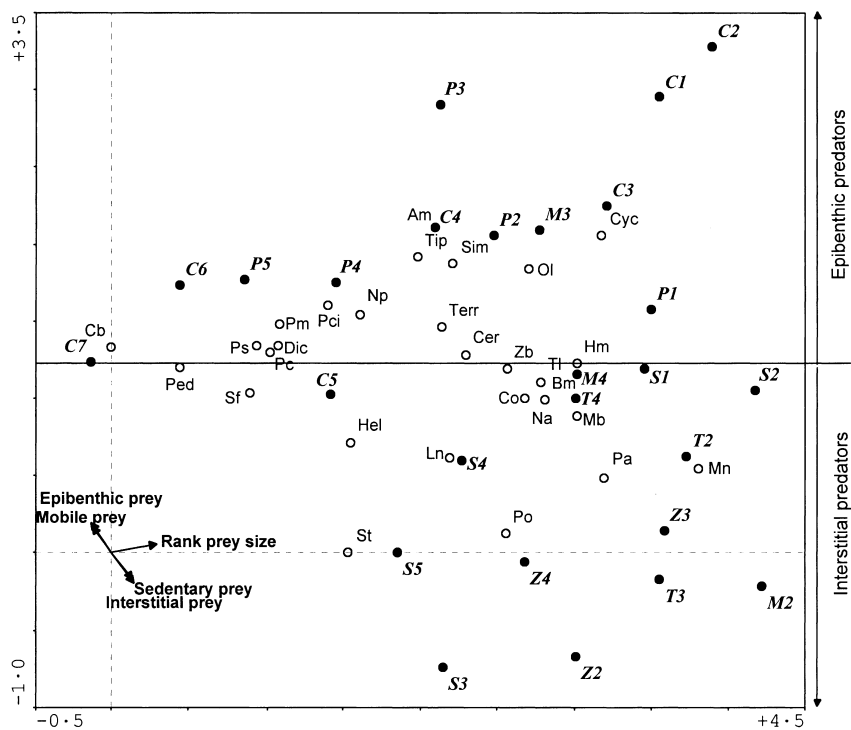


Fig. 2. Detrended Correspondence Analysis of predator diet. Predator species scores are labelled in bold italics as initials, denoting genus, followed by numbers, denoting size-class (details in Table 1). The line parallel to the *x*-axis separates the epibenthic predators from the interstitial predators, barring two exceptions (C5 and M3). Prey are labelled as in Appendix 2.

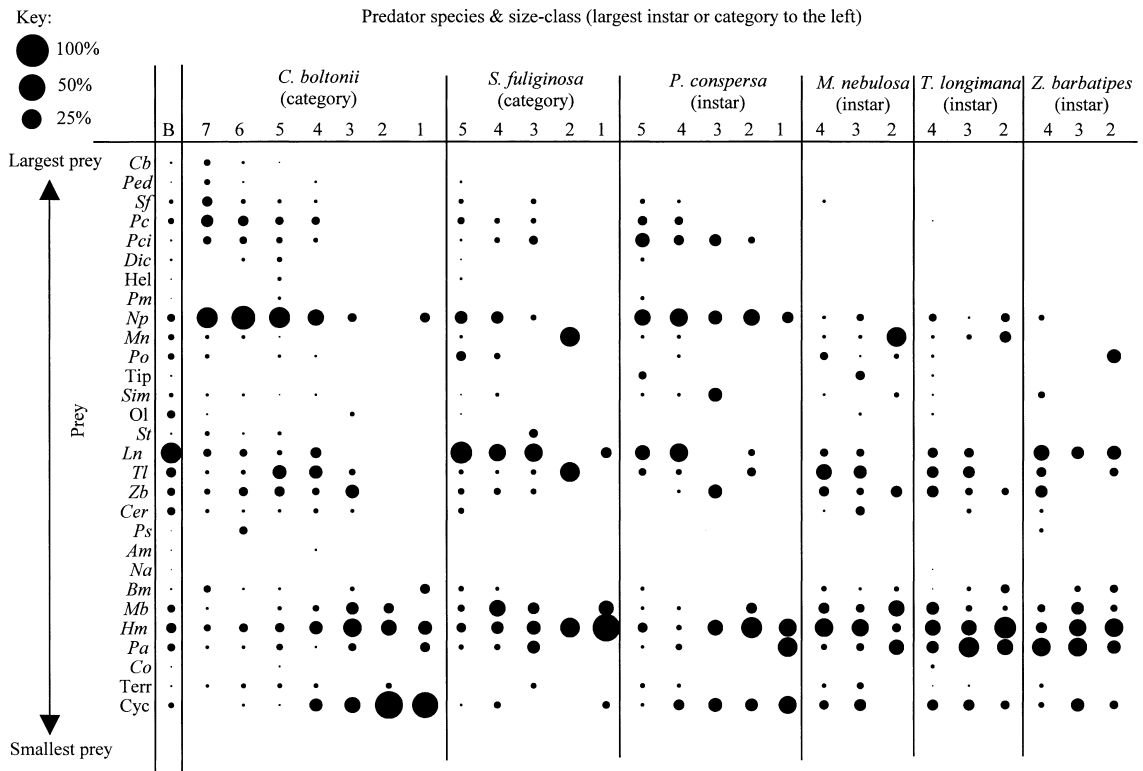


Fig. 3. Taxonomic and ontogenetic shifts in predator diets pooled over six sampling occasions between 1996 and 1997 ($n = 3826$ guts). 'Prey' are arranged vertically, in descending order of body-size. Predator species are arranged in order of maximum body-size from left to right and, within species, in decreasing order from left to right. Dark circles represent the relative numerical abundance of each species in the diet of each size-class (i.e. circles in each column add up to 100%). The column labelled B represents the composition of the benthos. Keys for species codes and predator size-classes are given in Appendix 1 and Table 1, respectively.

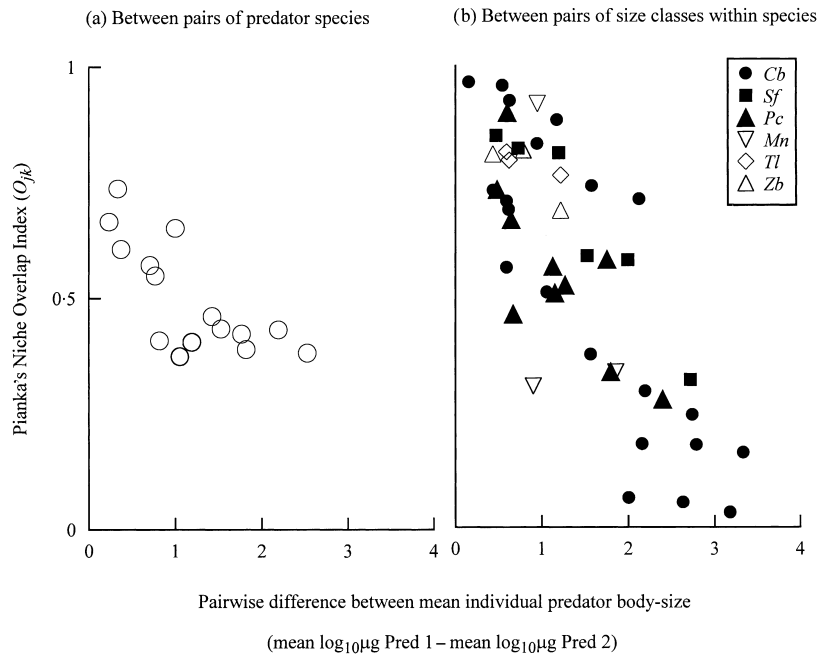


Fig. 4. Pairwise differences in individual predator body-size (Mean \log_{10} dry mass μg Predator 1 – Mean \log_{10} dry mass μg Predator 2) against niche overlap (a) among the six predator species and (b) among size-classes within each species.

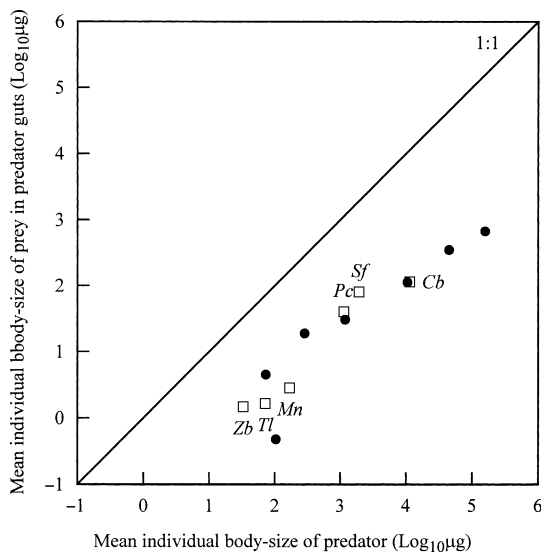


Fig. 5. Mean biomass of individual prey items present in the guts against mean individual predator body-size among the six predator species (\square) and among the seven *C. boltonii* size-classes (\bullet).

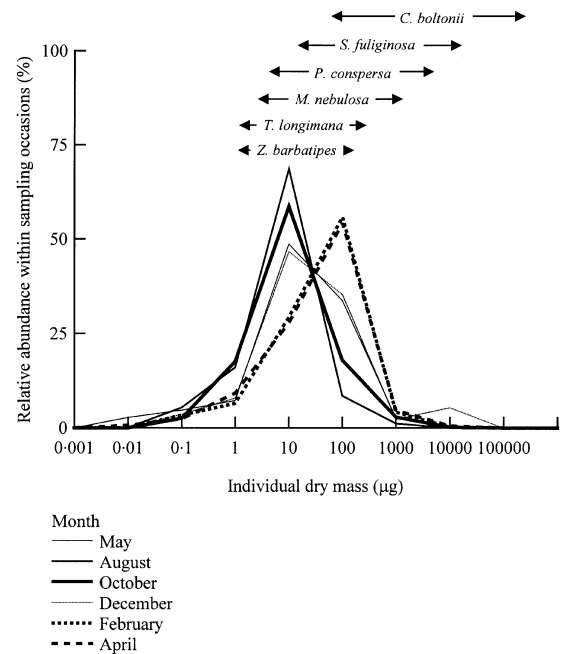


Fig. 6. Relative abundance size-spectra of the Broadstone Stream macroinvertebrate benthos on six sampling occasions (1996–97). The double-headed arrows indicate the size-ranges of the six predator species.

increase in the geometric mean of predator size was however less than proportional to the increase in prey size, when compared with the 1 : 1 line.

The size-spectrum of the community underwent strong and progressive temporal shifts, from being dominated by small individuals in summer and autumn, to being dominated by much larger individuals in spring (Fig. 6). This is attributable both to changes in species composition (chironomids were most abundant in summer and autumn, whereas the larger stoneflies were most common in winter and spring) and to individual growth.

Intraguild predation occurred when there were strong body-size asymmetries: large predators ate smaller predators, regardless of taxonomy (Fig. 7 upper panel). Predation on small species by large species could be intense at certain times. For instance, in October, *M. nebulosa* ate an equivalent of up to 46% of the numerical standing crop of the *Z. barbatipes* population per 24 h. 'Bottom-up' predation, where large species were preyed on by small species (arrowed links

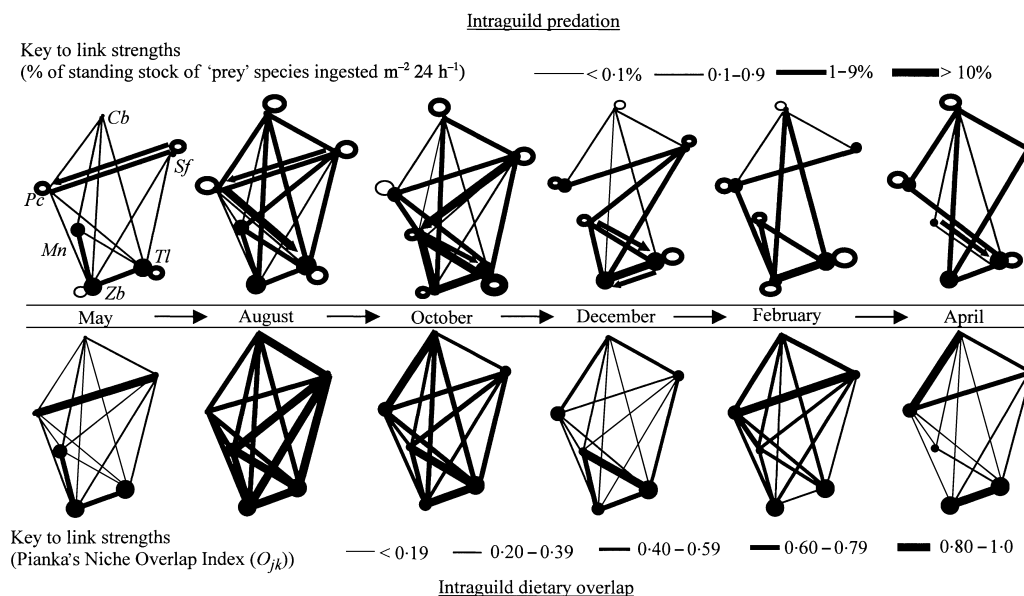


Fig. 7. Interaction webs for the Broadstone Stream predator guild (1996–97). Intraguild food webs are shown in the upper panels, niche overlap webs in the lower panels. The area of each circle is proportional to benthic abundance within sampling occasions. The positions of the predators in the webs are ranked vertically, in order of decreasing body-size from *C. boltonii* to *Z. barbatipes* (see labels in top left-hand panel). Arrow heads in the intraguild food webs show where predation occurs 'downwards' (i.e. species of a larger mean size are consumed by species of a lower mean size), links without arrows represent the usual consumption of smaller species by larger species. Cannibalism is represented by circular loops.

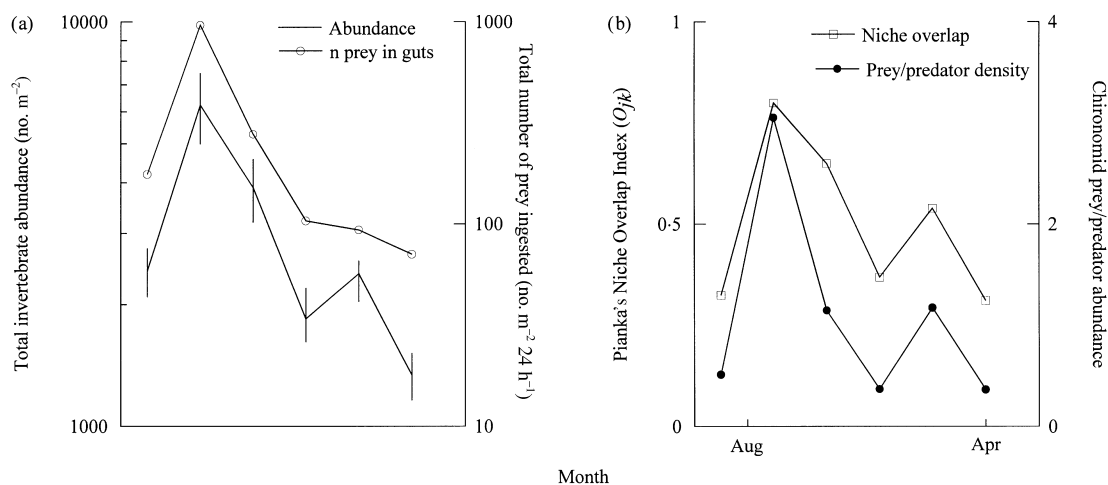


Fig. 8. Seasonal shifts in (a) total invertebrate density (mean \pm 1 SE) and total predation pressure (as number of prey ingested $\text{m}^{-2} \text{24 h}^{-1}$) and (b) predator dietary (niche) overlap and the quotient of chironomid density to predator density for the six dominant predators in Broadstone Stream (May 1996–April 1997). Niche overlap values are the means of pairwise comparisons among predator species.

in the upper panel of Fig. 7), however, was relatively weak when considered over the entire year, and was strongest when small instars of 'large' species coexisted with large instars of 'small' species. The number and intensity of intraguild feeding loops was highest during the summer and autumn, when generations overlapped, but declined subsequently, as interspecific size differences increased. Dietary niche overlap among the predators was highest among species of similar average size (Fig. 7 lower panel), but varied considerably over time, being relatively high in the summer and autumn, even between the largest and smallest species, but low

in winter and spring. The total number of prey ingested and the quotient of non-predatory chironomids to predator density exhibited similar seasonality (Fig. 8). These seasonal changes in overlap tracked resource availability, in terms of both total abundance and shifts in the size-spectrum of the benthos (Figs 8 and 6).

Figure 9 represents several assumed measures of 'food quality', which decreases from Fig. 9a–e. Figure 9a–c includes exclusively animal prey of progressively smaller body-size. Among the non-animal food, algae are generally a richer food source than FPOM (see Benke & Wallace 1997). Many predator

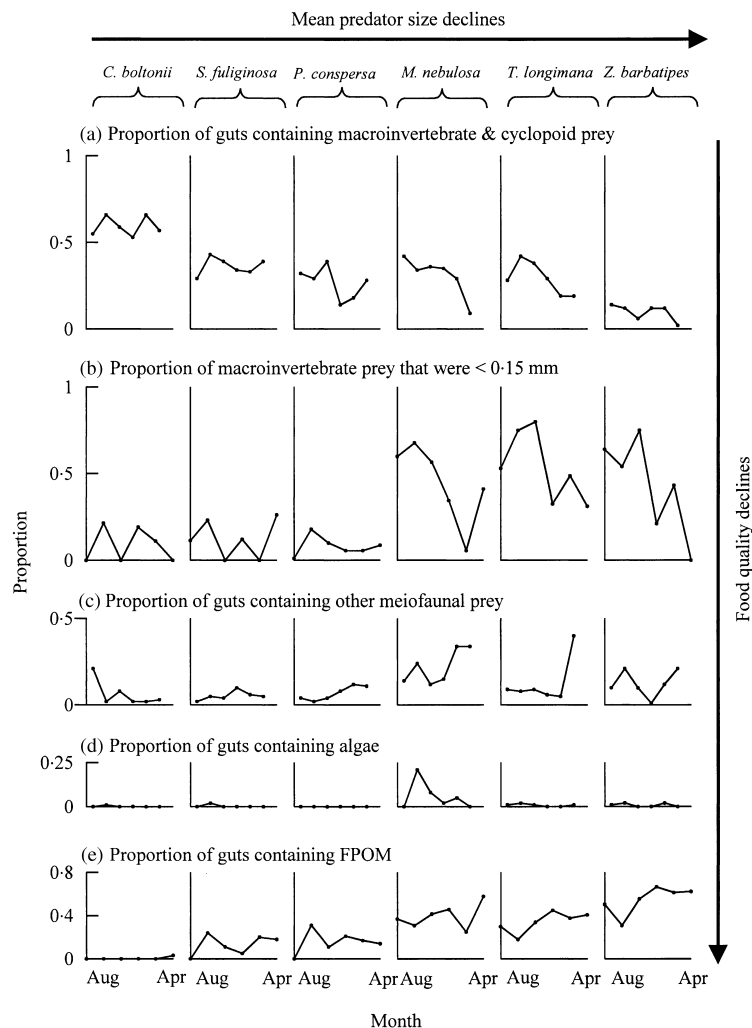


Fig. 9. Seasonal shifts in feeding among the predator assemblage of Broadstone Stream between May 1996–April 1997. Food categories are arranged vertically in decreasing order of ‘food quality’ (see Methods).

guts contained no macroinvertebrate or cyclopoid prey, especially during winter and among the smaller species (Fig. 9a). Among guts that did contain these prey, the proportion of prey that were small (< 0.15 mm) increased with decreasing predator size and peaked in summer and autumn (Fig. 9b), when the benthic size-spectrum was dominated by small individuals (Fig. 6). The proportion of guts containing other meiofauna (haracticoids, cladocera, ostracods, protozoa and unidentified ‘cocoons’) was higher in the tanypods than in the larger predators (Fig. 9c). Algae were found only rarely in predator guts, except for *M. nebulosa*, which consumed diatoms frequently, especially in the summer (Fig. 9d). FPOM found in the guts of the large predators probably reflected the gut contents of prey (the attack response of these predators is triggered by prey movement), whereas its far greater frequency in tanypod guts, especially in the smallest size classes, suggested active and direct consumption (Fig. 9e). The tanypods took large numbers of small chironomids in the summer and autumn, when these prey were abundant, but became increasingly detritivorous as chironomid abundance fell.

Discussion

Body-size constraints clearly played an important role in determining both niche overlap and trophic status within the predator guild of Broadstone Stream. In addition, population size fell, but biomass per unit area rose, as body-size increased (Fig. 1; see also Schmid, Tokeshi & Schmid-Araya 2000). Thus, although the top predator was up to two orders of magnitude rarer than the smallest species, it accounted for a large portion of total predator biomass. Shared feeding links were common, with the taxonomic composition of a predator’s diet being effectively a subset of the diet of the next largest predator. Nested hierarchies of feeding niches within guilds might be common in nature. This is suggested by their occurrence in apparently disparate systems including, for example, terrestrial mammals in the Siberian taiga (Churchfield, Nesterenko & Shvarts 1999), midge larvae in an Austrian stream (Schmid & Schmid-Araya 1997) and the predator, pathogen and parasitoid community associated with broom, *Cytisus scoparius* (L.) (Memmott *et al.* 2000). In Broadstone, nestedness produced size-based asymmetries in

resource use among and within species, with the large predators having increasingly more 'free' niche space because they exploited a broader size-range and therefore a greater number of prey species, than were available to the small predators. Despite this asymmetry, however, the large predators might be negatively affected by the other species over protracted time-scales: because most prey were univoltine, those eaten when young by the smaller predators would be unavailable to the larger species later.

The high proportions of empty guts, especially during winter (Fig. 9; see also Hildrew, Townsend & Hasham 1985), supports experimental and modelled data that suggest that the Broadstone predators' consumption rates are far below their potential maximum (see Speirs *et al.* 2000; Woodward & Hildrew in press b). Low prey availability might favour opportunism, such that the predators attack any item encountered and of a suitable size, and this could account for the unusually complex food web (see also Woodward & Hildrew 2001). The expansion and contraction of dietary overlap with prey abundance reflected seasonal changes in the relative sizes of predators and prey, with much higher overlap in summer and autumn, when prey were small, compared with winter and spring, when prey were much larger (Figs 6–8). Potentially, competition for food might occur within the predator guild, as indicated by this increased differentiation of dietary niches as food became scarcer (cf. Pianka (1973) and Lawlor (1980)), although these suggestions are tentative and need to be tested experimentally.

Seasonal changes in invertebrate abundance reflected peak recruitment during summer oviposition, followed by a progressive decline until spring. This decline has been previously attributed to predation (Hildrew & Townsend 1982), as prey do not appear to be resource-limited for either food or suitable habitats (Dobson & Hildrew 1992). In addition, field experiments have demonstrated that the Broadstone predators can deplete prey between recruitment periods (Lancaster, Hildrew & Townsend 1991; Lancaster 1996; Woodward & Hildrew in press a). The marked decline in tanypod abundance following the summer suggested that intraguild predation might have particularly dramatic effects on these smaller species, which were common prey of the larger predators.

Trophic status was clearly determined by body-size, with the largest predator, *C. boltonii*, being preyed on only by larger conspecifics, and the smallest, *Z. barbatipes*, being eaten by all five of the larger species and by conspecifics (Fig. 7). The direction of intraguild predation could change, however, particularly when early instars of large species coexisted with late instars of small species. These 'ontogenetic reversals' (Polis *et al.* 1989; p. 304) occurred seasonally and, at times, represented potentially strong predation pressure, although their effects were probably weak when averaged over the entire year. Similarly, each of the six species was cannibalistic when small and large larvae coexisted.

Potentially, trophic status could shift from that of prey, to potential competitor, to predator over the course of ontogeny, both within and among species. Traditional food web theory predicts that feeding loops should be rare because they supposedly destabilize web structure (Pimm 1982), although more recent data suggest that they are in fact common (Williams & Martinez 2000) and may even be stabilizing under certain conditions (Polis *et al.* 1989). Seasonal ontogenetic reversals might facilitate predator coexistence in Broadstone by reducing the survival of larger predators (e.g. *P. conspersa*) to later instars, which could then have preyed upon the smaller species (e.g. tanypods). Ontogenetic reversals occurred in many combinations among the Broadstone predators (Fig. 7), but were particularly frequent among pairs of predators with different foraging modes. Such loops were detected in seven instances but, intriguingly, only once between predators with the same foraging mode (*Z. barbatipes* ↔ *T. longimana*). Our data suggest that the *a priori* exclusion of loops, as in the cascade model (e.g. Cohen & Newman 1985), may be inappropriate and that a less rigid hierarchical ordering of dietary niches may be more realistic, as in more recent models of food web structure (Warren 1996; Williams & Martinez 2000). Body-size constraints have been suggested as a potential structuring force behind the niche model (Williams & Martinez 2000), and ontogenetic reversals, due to shifts in the size-spectrum, such as occur in Broadstone, might account for the frequency of looping interactions and the apparent plasticity of 'trophic levels' in real food webs.

Although large prey in Broadstone attained size-refugia from the tanypods, these small predators were extremely omnivorous and exploited food refugia (algae and FPOM) not readily available to the larger predators (Fig. 9). During winter, when macroinvertebrate prey are rare and/or large, the tanypods also have more feeding links to the permanent, soft-bodied meiofauna (e.g. rotifers) (Schmid-Araya *et al.* 2002), although the energetic importance of this food source is unknown and difficult to quantify. The tanypods were able to feed higher in the food web at other times (e.g. late instar *T. longimana* preyed on early instar *P. conspersa* during summer). The relative switch from carnivory to detritivory when potential prey were scarce, reduced niche overlap with the larger predators and could have been triggered by a change in feeding behaviour (see also Hildrew *et al.* 1985), perhaps to reduce vulnerability to predation.

The invasion of a food web by a new species is often modelled, but rarely described empirically (McCann 2000; Woodward & Hildrew 2001). Because the predators in Broadstone were generalist omnivores whose diet and trophic status were dependent on body-size, the invasion of a new, larger species could, potentially, have strong negative impacts on the residents, via both predation and competition. *Cordulegaster boltonii* had the potential to exert such effects because it preyed on

all the other predators, was eaten only by conspecifics, and its diet overlapped extensively with the other predators. The previous top predator, *Plectrocnemia conspersa*, was a favoured prey item and had an almost identical diet to *C. boltonii* and, consequently, might be especially vulnerable to the new predator. These suggestions are supported by field and laboratory experiments, in which *C. boltonii* depleted both *P. conspersa* and the caddis' favoured prey (Woodward & Hildrew in press a,b). In addition, prior to the invasion, *P. conspersa* partitioned resources with its potential competitor, *S. fuliginosa*, when food was scarce by taking terrestrial prey and large stoneflies (Townsend & Hildrew 1979). The invader, however, also exploited these food sources, encroaching on *P. conspersa*'s feeding niche and reducing the resident's ability to partition resources with *S. fuliginosa*. Consequently, both direct and indirect consequences of intraguild predation might explain the marked decline in *P. conspersa* as *C. boltonii* has increased (Woodward, Jones & Hildrew 2002).

So far we have focused on resource use and trophic relations among the predators but, because predation can be intense (Hildrew & Townsend 1982), apparent competition might also be important in structuring the prey assemblage. Sixty-two percent of macroinvertebrate taxa in the food web were preyed on by all six predator species, and no prey shared fewer than three predators with any other species (Woodward & Hildrew 2001). Recent food web models that take size structuring of the prey assemblage into account suggest that small prey will suffer disproportionately, because of the lack of size-refugia, in the presence of predators and larger prey (Chase 1999). This might explain the dramatic seasonal declines in chironomid abundance in Broadstone, when compared with the much weaker depletion of the larger stoneflies (Woodward *et al.* in press). Also, because the Broadstone predator guild includes both sit-and-wait and searching modes, and epibenthic and interstitial predators, prey face a variety of risks from predators, in addition to any size-related effects (cf. Peckarsky & McIntosh 1998).

Increasingly, body-size is seen as a crucial determinant of food web pattern and process (Warren 1996; Chase 1999; Williams & Martinez 2000), although data are still limited (but see Memmott *et al.* 2000) and tend to focus on qualitative, rather than quantitative, patterns (Cohen *et al.* 1993b). Further, ontogenetic dietary shifts can exceed taxonomic differences but are rarely included in food webs, despite the early recognition of their importance (e.g. Hardy 1924). More high quality empirical data on the role of body-size, both within and among species, are needed if we are to further develop realistic theoretical frameworks and to parameterize and validate models. We hope that our study, although limited to one system, has gone some way towards addressing this important lacuna.

At a larger, 'macroecological' scale, examination of body-size in relation to the trophic structure of com-

munities (e.g. Jennings *et al.* 2001) offers a promising avenue for further research. Three-table ordination techniques (e.g. Doledec *et al.* 1996) could be used to assess how community (\approx food web) structure and species traits (e.g. body-size, trophic status) respond to major environmental gradients (e.g. productivity, pH and fishing intensity). Large species, such as top predators, appear to be particularly vulnerable to extinction and the loss of these could have serious consequences for the wider community food web. For instance, acidification alters the community size-spectrum in freshwaters, with fish being replaced by invertebrates as top predators (Woodward & Hildrew 2002). If invertebrate predators have stronger interactions with prey than vertebrate predators, as has been suggested (e.g. Sih, Englund & Wooster 1998), this could have potentially dramatic effects on the food web. Predicting how natural systems respond to perturbation is a major goal in ecology and is central to attempts at conserving biodiversity (McCann 2000); an improved understanding of the role of body-size in food webs might enable ecologists to move closer to achieving that objective.

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Appendix 1

Regression equations used to predict dry mass of taxa within Broadstone Stream. W, Head capsule width; L, Body length. Morphometrically similar taxa, shown in parentheses, were used where data were unavailable for the Broadstone taxa. Letters at the end of rows denote the source of equations (see key below). r^2 values are given where available

Taxon	y	x (mm)	Equation	r^2	
<i>Cordulegaster boltonii</i> (Donovan)	Log ₁₀ (mg)	Log ₁₀ W	$y = -0.20 + 2.85(x)$	0.95	f
<i>Sialis fuliginosa</i> Pict.	Log ₁₀ (µg)	Log ₁₀ W	$y = 2.68 + 2.90(x)$	0.88	b
<i>Plectrocnemia conspersa</i> (Curtis)	Log ₁₀ (µg)	Log ₁₀ W	$y = 2.58 + 2.80(x)$		e
<i>Pedicia</i> sp. and <i>Dicranota</i> sp. [<i>Dicranota</i> sp.]	Ln(mg)	LnL	$y = -5.53 + 1.91(x)$	0.54	g
<i>S. torrentium</i> (Pictet) [<i>Siphonoperla</i> sp.]	Ln(mg)	LnW	$y = -0.27 + 2.70(x)$	0.80	g
<i>Platambus maculatus</i> (Pictet) [Coleoptera larvae]	Ln(mg)	LnW	$y = 2.15 + 3.80(x)$	0.55	g
<i>Macropelopia nebulosa</i> (Meigen)	Log ₁₀ (µg)	Log ₁₀ W	$y = 3.12 + 3.86(x)$	0.73	d
Pentaneurini (and <i>Corynoneura lobata</i> Edwards)	Log ₁₀ (µg)	Log ₁₀ W	$y = 3.13 + 3.06(x)$	0.48	d
<i>Bezzia</i> sp.	Log ₁₀ (mg)	Log ₁₀ L	$y = -3.39 + 2.73(x)$	0.56	a
<i>Potamophylax cingulatus</i> (Stephens) [Trichoptera]	Ln(mg)	LnW	$y = 0.50 + 2.91(x)$	0.58	g
Other Tipulidae [<i>Tipula abdominalis</i> (Say)]	Ln(mg)	LnL	$y = -5.30 + 2.36(x)$	0.93	c
<i>Nemurella pictetii</i> Klapalek	Log ₁₀ (µg)	Log ₁₀ W	$y = 2.71 + 3.13(x)$	0.80	d
<i>Leuctra nigra</i> Olivier (and <i>L. hippopus</i> Kempny)	Log ₁₀ (µg)	Log ₁₀ W	$y = 2.54 + 2.23(x)$	0.64	d
<i>Prodiamesa olivacea</i> (Meigen)	Log ₁₀ (µg)	Log ₁₀ W	$y = 3.50 + 2.97(x)$	0.69	d
<i>Heterotrissocladius marcidus</i> (Walker)	Log ₁₀ (µg)	Log ₁₀ W	$y = 3.17 + 2.30(x)$	0.36	d
<i>Micropsectra bidentata</i> (Goetghebuer)	Log ₁₀ (µg)	Log ₁₀ W	$y = 3.07 + 1.75(x)$	0.45	d
<i>P. submarginata</i> (Stephens) [Leptophlebiidae]	Ln(mg)	LnW	$y = -0.83 + 4.25(x)$	0.86	g
Oligochaetes	g		$(y = \pi r^2 (1.05))/4$		h
<i>Simulium</i> sp.	Ln(mg)	LnW	$y = 0.20 + 3.32(x)$	0.93	g
Helodidae (larvae) [Elmidae (larvae)]	Ln(mg)	LnW	$y = 2.15 + 3.80(x)$	0.55	g
<i>Niphargus aquilex</i> (Schiödte) [<i>Gammarus fossarum</i> Koch]	Ln(mg)	LnL	$y = -4.95 + 2.83(x)$	0.90	g
<i>Asellus meridianus</i> Racovitza [<i>A. aquaticus</i> L.]	Log ₁₀ (mg)	Log ₁₀ W	$y = -3.13 + 1.32(x)$	0.34	i

Key to sources of regression equations: a, L. Greenberg (personal communication); b, J.H. Winterbottom (personal communication); c, Smock (1980); d, Hildrew & Townsend (1982); e, Hildrew & Townsend (1976); f, Woodward (1999); g, Burgherr & Meyer (1997); h, Ramsay *et al.* (1997); i, J.I. Jones (personal communication).

Appendix 2

Codes used to denote invertebrate taxa, given in parentheses, and associated ecological traits, given in brackets. Mobile and sedentary taxa are denoted by m and s, respectively. Detritivorous chironomids (*P. olivacea* to *P. albicorne* grp) are also divided into tube-dwellers (t) and free-living taxa (f). P.E. Schmid (personal communication) supplied species traits of chironomids. Epibenthic and interstitial taxa are denoted by e and i, respectively.

Predators:	[Cb] <i>Cordulegaster boltonii</i> (s,e); [Sf] <i>Sialis fuliginosa</i> (m, i); [Pc] <i>Plectrocnemia conspersa</i> (m, e); [Mn] <i>Macropelopia nebulosa</i> (s, i); [Tl] <i>Trissopelopia longimana</i> (m, i); [Zb] <i>Zavrelimyia barbatipes</i> (m, i); [Ped] <i>Pedicia</i> sp. (m, i); [Dic] <i>Dicranota</i> sp. (m, i); [St] <i>Siphonoperla torrentium</i> (m, e); [Cer] Ceratopogonidae (m, i); [Pm] <i>Platambus maculatus</i> (L.) (m, e)
Prey:	[Pci] <i>Potamophylax cingulatus</i> (m, e); [Ar] <i>Adicella reducta</i> MacLachlan (m, e); [Np] <i>Nemurella pictetii</i> (m, e); [Ln] <i>Leuctra nigra</i> (s, i); [Lh] <i>Leuctra hippopus</i> (s, i); [Ps] <i>Paraleptophlebia submarginata</i> (m, e); [Hel] Helodidae (m, e); [Tip] Tipulidae (s, i); [Po] <i>Prodiamesa olivacea</i> (f, i); [Bm] <i>Brillia modesta</i> (Meigen) (f, i); [Mb] <i>Micropsectra bidentata</i> (t, i); [Hm] <i>Heterotrissocladius marcidus</i> (f, i); [Cl] <i>Corynoneura lobata</i> (f, i); [Pa] <i>Polypedilum albicorne</i> grp (f, i); [ChPu] Chironomid pupae (s, i); [Sim] <i>Simulium</i> sp. (s, e); [Am] <i>Asellus meridianus</i> (m, e); [Cyc] Cyclopoids (m, e); [Na] <i>Niphargus aquilex</i> (m, i); [Ol] Oligochaetes (s, i); [P] <i>Pisidium</i> sp. (s, e); [Terr] Terrestrial invertebrates (n/a); [Ac] <i>Acari</i> (oribatid litter mites) (n/a).