

Quantification and Resolution of a Complex, Size-Structured Food Web

GUY WOODWARD, DOUGIE C. SPEIRS, AND
ALAN G. HILDREW

I. Summary	85
II. Introduction	87
A. Connectance Food Webs: Early Patterns and Recent Advances ..	87
B. Quantified Food Webs: From Pattern to Process	90
C. The Broadstone Stream Food Web	92
III. Methods	93
A. Study Site.	93
B. Estimation of Abundance and Biomass of Trophic Elements	94
C. Construction of the Food Webs: Connectance Webs.	95
D. Quantification of Feeding Links	96
E. Construction of the Food Webs: Quantitative Webs	98
IV. Results	100
A. Summary Connectance Web (Including the Permanent Meiofauna).	100
B. Seasonal Connectance Webs (Excluding the Permanent Meiofauna).	103
C. Quantitative Webs	109
D. Annual Production and Ingestion Web	115
V. Discussion.	118
A. Connectance Webs.	118
B. Trivariate Relationships, Ontogenetic Shifts, and Seasonally Quantified Webs	122
C. Food Web Topology and Interaction Strength	125
D. Limitations and Future Directions.	127
Acknowledgments	129
References	131

I. SUMMARY

Previous studies were collated with new data to produce an exceptionally detailed connectance web for Broadstone Stream (UK) that contained 131 species, including the permanent meiofauna (i.e., species that are always passing through a mesh of 500 μm), and 842 links. Despite its apparent

complexity, the structure of this web displayed relatively simple patterns related to body size. For instance, many of the speciose permanent meiofauna were not eaten by the large-bodied, higher predators and thus diet width decreased with increasing predator size. When the permanent meiofauna were excluded from the analysis, however, the opposite was found.

We then assessed body-size relationships within both connectance and quantified webs for the macrofaunal "subweb". The detection of links required considerable sampling effort, especially from the smaller (and intermediate) predators to their prey, suggesting that food web complexity is often seriously underestimated and that this might be further confounded with a potential body-size (and trophic status) bias in less exhaustively sampled webs. Trivariate relationships between body size, abundance, and web structure were apparent, with the majority of links representing consumption of smaller, more abundant prey by larger and rarer predators. In a few instances, this "rule" was broken, largely due to seasonal ontogenetic shifts in body-size distributions. Seasonal changes in resource availability (prey size and abundance) influenced both web complexity and ingestion rates, both of which peaked in summer when generations overlapped, but then declined as prey became scarcer and/or outgrew their potential predators. During summer, connectance in the macrofaunal subweb was high (0.13), and predators ate the equivalent of up to 16.1% of the numerical standing stock per day; by the following spring, however, connectance had halved (0.07) and total consumption had fallen to 5.5% per day. The small predator species ate large numbers of the temporary meiofauna (i.e., mainly insect larvae spending their early instars only in the $<500\ \mu\text{m}$ net mesh size class), especially in summer, whereas the large predators ate the same species but exploited larger size classes. However, because consumption of small predators by larger carnivores accounted for about 10% of the production of the latter, macrofaunal-meiofaunal links could provide important "indirect" energy fluxes to the higher trophic levels.

Finally, we produced a quantified food web with the strength of feeding links expressed as annual ingestion (I) of prey by predators divided by the production (P) of that prey. Body size had strong effects on dynamical aspects of the food web (secondary production and interaction strength), in addition to its marked constraining influence on web structure (connectance, diet width, trivariate relationships). We identified multivariate relationships between body size and associated species traits (e.g., P/B ratio, abundance, trophic status) and the strength of interactions within the quantified web. Most links were weak (I/P, <0.01) and interaction strength scaled with both prey and predator body size: the smallest, more "r-selected" species were those most heavily exploited, with virtually all of their annual production consumed. Among the predators, although the small species ate many prey per unit area, this accounted for a relatively trivial amount of

prey production. The larger predators, however, had more and stronger interactions with the macroinvertebrate prey assemblage, with the strength of links increasing with predator body size.

II. INTRODUCTION

A. Connectance Food Webs: Early Patterns and Recent Advances

The notions that species within a community are inextricably linked to one another via their ecological interactions, and that the pattern and strength of these links might reveal fundamental properties of a system, particularly in relation to its stability, are two of the earliest ideas in ecology (Elton, 1927; MacArthur, 1955; May, 1973; McCann, 2000). Because trophic links are relatively easy to document—at least when compared with other, more subtle, interactions (e.g., competitive or mutualistic links)—food webs have been the primary focus of research into ecological networks (Cohen *et al.*, 1993a). Nonetheless, constructing realistic empirical food webs is still extremely difficult; most published webs are qualitative “connectance” webs, which are restricted to simple presence/absence data on species (nodes) and feeding links (vertices). Much of the available data are of poor quality: many webs represent only a subset of the wider community food web, taxonomic resolution is inconsistent and biased towards the higher trophic levels, feeding links are often inferred rather than observed, and some published webs contain biological impossibilities (e.g., predators without prey, ducks as basal species; see Hall and Raffaelli, 1993 for a more detailed critique). Attempts have been made to address these shortcomings in several recent studies by quantifying sampling effort (e.g., Woodward and Hildrew, 2001), improving taxonomic resolution (e.g., Schmid-Araya *et al.*, 2002a,b), and including more quantitative information about species (e.g., body-size and abundance data; Cohen *et al.*, 2003) and links (e.g., the flux of matter between species; Benke and Wallace, 1997). Unfortunately, these improvements are often carried out piecemeal in individual studies on different webs, largely due to the inevitable logistic and financial constraints associated with this labor-intensive work and, as a result, there are no webs that are both fully-quantified *and* highly-resolved for entire communities (McCann, 2000; Berlow *et al.*, 2004). We attempted to address this, at least partially, by exploring the structural properties of one of the most detailed connectance webs currently published, that of Broadstone Stream (Woodward and Hildrew, 2001; Schmid-Araya *et al.*, 2002a), and by subsequently examining relationships between structural patterns and dynamic processes in a quantified subset of the community web, with particular emphasis on the role of body size as a driver of both pattern and process in the food web.

Prior to the mid-1980s, most published connectance webs were very simple, in that they contained few species and/or links (Cohen, 1978; Pimm, 1980, 1982). These webs supported many of the early mathematical models (e.g., May, 1972, 1973) that were in vogue during this period, generally predicting that because the dynamic stability of food webs was inversely related to their complexity, simple webs would predominate in nature and complex webs would be rare (Pimm, 1980). However, many of the early webs were constructed from poor quality data and oversimplified to such an extent that their validity, and hence the theoretical predictions and mathematical models derived from them, have since been questioned and are often roundly criticized (Polis, 1991; Hall and Raffaelli, 1993; McCann, 2000).

Since the mid-1980s, a new catalogue of better quality, data-rich food webs started to emerge, challenging the received wisdom that complexity was the exception rather than the rule (e.g., Hildrew *et al.*, 1985; Warren, 1989; Polis, 1991; Cohen, *et al.*, 1993b, 2003; Closs and Lake, 1994; Tavares-Cromar and Williams, 1996; Benke and Wallace, 1997; Yodzis, 1998; Williams and Martinez, 2000; Woodward and Hildrew, 2001; Schmid-Araya *et al.*, 2002a,b). Many of the apparent discrepancies between the “early and simple” webs and the “recent and complex” webs have now been ascribed to methodological artifacts: the newer webs are far more exhaustively sampled and better resolved taxonomically than many of the earlier webs (Hall and Raffaelli, 1993; Polis, 1994, 1998; McCann, 2000; Woodward and Hildrew, 2002a). For instance, many of the coarse groupings (e.g., algae or meiofauna) that were used previously to lump together supposedly identical “trophic species” (after Sugihara *et al.*, 1997) were now starting to be separated into distinct taxa (e.g., Schmid-Araya *et al.*, 2002a).

Because connectance webs make no distinctions between rare or common species and links, many food web statistics (e.g., connectance, linkage density) are sensitive to resolution and sampling protocol, which are rarely standardized across webs (Cohen *et al.*, 1993a; Hall and Raffaelli, 1993; Martinez *et al.*, 1999). If the guts of most predators are empty, or nearly so (e.g., Woodward and Hildrew, 2001), then links to rare or less-favored prey will be missed, unless sample sizes are very large. However, many studies have used relatively small sample sizes for describing links (Goldwasser and Roughgarden, 1997). For instance, Tavares-Cromar and Williams (1996), Townsend *et al.* (1998) and Thompson and Townsend (1999) analyzed ten guts per taxon on each sampling occasion. Further, sampling effects were potentially autocorrelated with web size, because speciose communities tend to contain more rare species (Tokeshi, 1999), and species are generally more likely to be detected in the community than their food web linkages characterized adequately (e.g., Goldwasser and Roughgarden, 1997; Woodward and Hildrew, 2001). The publication of

yield-effort curves for links and species would alleviate this problem, but such curves are rarely shown (Cohen *et al.*, 1993a). Thompson and Townsend (1999) produced curves for species but not for links, whereas Goldwasser and Roughgarden (1997) produced curves for links, but not for individual predator species. Woodward and Hildrew (2001) found that, in a summary web, curves for links varied markedly among species and with trophic status, and that asymptotes were reached only after several hundred guts had been examined. These studies suggest that the small sample sizes used in many of the early studies were unlikely to be sufficient to capture the true complexity of real food webs. None of these studies, however, considered the seasonal variations in yield-effort curves that we address here, which might account for the purported temporal shifts in web structure. Also, little attention has been given to how the strength of a link might be related to the frequency of its detection. Essentially, how important is it to catalog rare links?

The new catalog of highly complex, data-rich empirical webs has driven recent important advances in ecological theory (Polis, 1998; McCann, 2000; Williams and Martinez, 2000), including the recognition of the role of body-size as a structuring force in food webs (Warren, 1996; Cohen *et al.*, 2003; Woodward, *et al.*, in press). A notable and recurrent feature of many of the more recent food webs is the existence of nested hierarchies of dietary niches, such that a given predator's potential diet is effectively a subset of that of the next largest predator (e.g., Cohen *et al.*, 1993b; Woodward and Hildrew, 2002b). Because this generates upper-triangular food web matrices, a central assumption of the cascade model of food web structure (Cohen and Newman, 1985), body size provides one plausible biological explanation for this assumption (Warren and Lawton, 1987; Cohen, 1989).

Subsequent refinements of this type of model have resulted in the development of niche-based food web models (Warren, 1996; Williams and Martinez, 2000). Warren (1996) demonstrated that plausible predictions of web features (e.g., food chain length) could be made when body size was used as a single niche dimension in a model of biological constraints on food web structure. The niche model of Williams and Martinez (2000) also uses a single, general niche dimension (which could represent body size) but the strict hierarchy used in the cascade model is relaxed, so that up to half of the consumer's trophic niche can include species with a niche value higher than itself. This simple model successfully reproduces many of the complex patterns seen in real food webs—such as the prevalence of omnivory—and suggests that community niche space can be collapsed into a single dimension (potentially body size), at least when considering static structural patterns (Williams and Martinez, 2000). Recently, attempts have been made to include greater ecological detail in connectance webs, beyond simple presence/absence data. For instance, Cohen *et al.* (2003) have identified strong trivariate relationships between food web structure, species abundance, and

body size. They found that small species were abundant but low in the food web, and that large species were rarer, higher in the food web, and possessed a greater number of links. Despite the fact that these patterns have yet to be examined explicitly in a range of other systems, many of the component univariate or bivariate patterns they report have already been described elsewhere, such as inverse relationships between body size and abundance (Schmid *et al.*, 2000) and upper triangularity (Williams and Martinez, 2000; Woodward and Hildrew, 2001; Schmid-Araya *et al.*, 2002a), suggesting that they might be of general applicability.

B. Quantified Food Webs: From Pattern to Process

One of the major criticisms leveled at connectance webs is that they provide only static representations of the trophic scaffolding within a community, but supply no information about the relative importance of the different links or the dynamic processes (e.g., energy flux; Lotka-Volterra population dynamics) operating within the web (Paine, 1988; Hall and Raffaelli, 1993; Benke and Wallace, 1997). Notwithstanding these objections, connectance webs, despite their many limitations, have undoubtedly provided some invaluable insights into real ecological phenomena; pattern and process are likely to be inextricably linked in real food webs. Increasingly, attempts are being made to unite the static (e.g., Williams and Martinez, 2000) and dynamic (e.g., May, 1972) approaches to food web ecology, and there are suggestions that body size might constrain both the patterning and strength of trophic interactions (e.g., de Ruiter *et al.*, 1995; Emmerson and Raffaelli, 2004).

When considering dynamic processes, the equal weighting of links implicit in connectance webs is unlikely to reflect the true distribution of interaction strengths, which are often highly skewed (Hall and Raffaelli, 1993; McCann, 2000). Species rank-abundance curves typically follow either log-normal or geometric series (Tokeshi, 1999) and there is increasing evidence that, within a web, most links are weak with only a few being strong (e.g., Paine, 1992; de Ruiter *et al.*, 1995; Raffaelli and Hall, 1996; Emmerson and Raffaelli, 2004). Recent models have shown that an abundance of weak links can increase a web's stability (e.g., McCann *et al.*, 1998), forcing ecologists to reassess the long-held paradigm that complex webs are unstable (e.g., May, 1972, 1973; Pimm, 1982). Despite their evident importance in aiding our understanding of community dynamics, interaction strengths are nearly always estimated, rather than measured, and empirical data with which to test the assumptions of models are scarce (but see Emmerson and Raffaelli, 2004).

Attempts to quantify webs can be divided into two broad categories, with the first focusing on population/community dynamics (e.g., Power, 1990; Wootton *et al.*, 1996) and the second on the flux of energy or matter (the

“ecosystem approach,” e.g., Benke and Wallace, 1997), with virtually none combining the two (but see Hall *et al.*, 2000). The former approach can itself be subdivided into questions about overall community dynamics (e.g., the complexity-stability debate), and those seeking predictions about the dynamics of focal species populations (Berlow *et al.*, 2004). The ecosystem approach has often been used to view food webs from a mass-balance perspective; the recent emergence of stoichiometric analysis, which can be seen as a natural extension of this viewpoint, has led to a closer union with the community approach by recognizing the role of species populations in driving nutrient dynamics (see Elser and Urabe, 1999 for a more detailed review).

There is a small but growing number of quantified (or semi-quantified) food webs in existence (e.g., Power, 1990; Paine, 1992; de Ruiter *et al.*, 1995; Benke and Wallace, 1997). However, there is little or no standardization between these webs, with the strength of links being expressed in many different ways. Berlow *et al.* (2004) list 11 definitions of “interaction strength” in use in the ecological literature. Inevitably, this lack of standardization mitigates against the detection of generalities, or the lack of them, when comparing among webs (McCann, 2000). This rather loose use of the term reflects, at least partially, the contingent nature of the field and the historical schism between the parallel schools of the ecosystem and community approaches. The important question for food web ecologists is: are these different definitions somehow related, such that they refer to similar phenomena? For instance, are population dynamics and energy flux linked? Interaction strengths defined or measured in different ways are not *necessarily* related, so comparisons between quantified webs constructed using the different approaches should be made with caution, unless some form of cross-validation can be carried out. For instance, while a single prey species might account for much of a predator’s production, the population size of the prey may itself be unaffected. Conversely, a predator may consume a large proportion of the production of one prey species, while that prey contributes little to the overall production of the predator (e.g., if predators are subsidized by alternative food sources).

Producing quantified webs is extremely labor-intensive, and finding a single measure of interaction strength that is acceptable to both modellers and empiricists has yet to be achieved (Berlow *et al.*, 2004). For instance, it has been argued that energy flow webs cannot reveal whether consumers have negative effects on their food supply or competitors (e.g., Paine, 1988) and that field experiments are therefore required to unravel such causal relationships (e.g., Paine, 1992). However, conducting manipulations that include even a small fraction of the pairwise interactions within a web is unfeasible in all but the simplest systems. Even the relatively “simple” community of our study site (Broadstone Stream), which has a very restricted fauna due to its

acidity, has over 700 links when both the macrofauna (animals retained on a 500 μm mesh) and meiofauna (animals that pass through a 500 μm mesh but are retained on a 42 μm mesh) are included (Schmid-Araya *et al.*, 2002a). Further, to detect many indirect food web effects (e.g., trophic cascades) requires experiments that run for at least twice the generation time of the longest-lived organism within the system (Yodzis, 1988), which is clearly impracticable for most situations. Consequently, some authors have argued in favor of assessing linkage strength via detailed surveys rather than attempting to conduct unrealistic experiments (e.g., de Ruiter *et al.*, 1995), and recent work has linked energy flux to interaction strength (Wootton, 1997). Although no truly complete community food web has been quantified to date, important progress has been made recently with semi quantitative measures, subsets of communities, and experimental systems (e.g., Paine, 1992; de Ruiter *et al.*, 1995; Raffaelli and Hall, 1996; Benke *et al.*, 2001; Emmerson and Raffaelli, 2004). Where attempts have been made at quantification, the shortcomings of connectance webs and the theoretical predictions derived from them have often been brought sharply into focus (McCann, 2000). The next logical—but logistically challenging—step is to produce detailed, fully-quantified, empirical food webs that are standardized sufficiently to allow the implicit connections between structural attributes and dynamics processes to be explored more fully, and for models to be parameterized from real data.

C. The Broadstone Stream Food Web

Broadstone Stream has had a long history of food web research (Hildrew *et al.*, 1985; Lancaster and Robertson, 1995; Woodward and Hildrew, 2001), culminating in one of the most completely described food webs for any system (Schmid-Araya *et al.*, 2002a). A major thrust of this research has been to increase taxonomic resolution and completeness by extending the lower size limit of the organisms included, to the meiofauna and beyond, and thence to test the effect on food web patterns. We collated all of the food web data collected from Broadstone to date to produce what we believe to be the most detailed connectance web yet described for any system, in order to examine body size constraints on web structure. However, with an emphasis on the soft-bodied meiofauna (e.g., rotifers, tardigrades, nematodes), overall replication, habitat coverage, and sampling extent are inevitably sacrificed in exchange for novel information on these small organisms. We are therefore restricted to examining static patterns in connectance webs because the dynamics of these small taxa are impossible to quantify empirically in the field.

Our primary objective in the present study was to quantify the Broadstone Stream food web. To do this, we made the strategic decision at the outset to exclude the “permanent meiofauna,” or taxa that spend their entire life cycle

within the meiofaunal size fraction of 42–500 μm (e.g., harpacticoids and rotifers), from the first attempt. Thus, we focused on quantifying the macrofaunal subweb, which—although omitting the permanent meiofauna—included representatives of the “temporary meiofauna” (i.e., macrofaunal taxa that spend only part of their entire life cycle within the meiofaunal size fraction, such as early instars of some of the smaller insect species). This focus enabled us to preserve samples (many soft-bodied permanent meiofauna can only be identified alive) and to substantially increase the extent and coverage of sampling. Therefore, the detection and assessment of energetically important links was improved, especially those of the larger, but less abundant, species near the top of the web.

We then used our data to construct a connectance web for each sampling occasion, thus addressing temporal variation in web structure. We were also able to construct yield-effort curves to examine seasonal and taxonomic influences on the estimation of food web statistics. Potentially important temporal patterns are often masked in other studies, because most webs are constructed from either a single sampling occasion or pooled over several occasions (but see Warren, 1989; Winemiller, 1990; Closs and Lake, 1994; Tavares-Cromar and Williams, 1996; Thompson and Townsend, 1999). Secondly, and most importantly, we sought to quantify the macroinvertebrate food web by calculating consumption rates of predators and relating their annual ingestion to the annual production of both predators and prey, thereby providing empirical estimates of the strength of feeding links. We then assessed the role of body size as a determinant of pattern (e.g., diet width) and process (e.g., ingestion rates, I/P) in the food web, in light of recent advances in theory that have implicated body size as a key driver in natural food webs (Warren, 1996; Williams and Martinez, 2000; Cohen *et al.*, 2003).

III. METHODS

A. Study Site

Broadstone Stream (51°05'N, 0°03'E; 120 m above sea level) is a headwater of the River Medway in southeast England (see Hildrew and Townsend, 1976 for a detailed site description). The acidity of the stream (pH, 4.7–6.6) excludes fish and other vertebrates are extremely rare, resulting in an invertebrate-dominated food web (Woodward and Hildrew, 2001). The most detailed web described to date contains 128 species, including the permanent meiofauna (species always passing a mesh of 500 μm but retained on 42 μm), although there are only about 25 common macroinvertebrate species (Schmid-Araya *et al.*, 2002a; Woodward and Hildrew, 2002b). Among the common predators, there are three large species (*Cordulegaster boltonii*

Donovan, *Sialis fuliginosa* Pict. and *Plectrocnemia conspersa* [Curtis]) and three small species (the larvae of the tanypod midges *Macropelopia nebulosa* [Meigen], *Trissopelopia longimana* [Staeger] and *Zavrelimyia barbatipes* [Kieffer]). Detritivorous stoneflies and chironomids dominate the macrofaunal prey assemblage in winter and summer, respectively. The hyporheic zone (i.e., the interstitial habitat between the surface and groundwater, inhabited by the hyporheos) is very restricted, due to subsurface anoxic conditions, and rarely exceeds 5 cm depth (Rundle, 1988). Allochthonous detritus, in the form of coarse particulate organic matter (mostly woody debris and leaf fragments of > 1 mm diameter), is by far the most important basal resource (Dobson and Hildrew, 1992).

B. Estimation of Abundance and Biomass of Trophic Elements

Thirty randomly-dispersed Surber sample units (25 × 25 cm quadrant; mesh aperture 330 μm) were taken on each of six sampling occasions (May/June, August, October, December 1996, February and April 1997) to a depth of 5 cm. Samples were preserved immediately in 5% formalin. Because poor taxonomic resolution can confound comparisons among webs and grouping taxa is less meaningful in quantitative webs (Martinez, 1991; Hall and Raffaelli, 1993), we described all taxa to species where possible. The few species that could not be distinguished with certainty in benthic samples or predator guts were grouped to the next taxonomic level (usually genus). These groups were the oligochaete worms, nonpredatory tipulids, *Dicranota* sp., *Pedicia* sp., *Bezzia* sp., *Pisidium* sp., *Simulium* sp., *Helodidae* sp., and terrestrial invertebrates. Very rare taxa (i.e., <0.01% of mean annual standing stock) were excluded from the webs. Most species were univoltine and present only as larvae, so populations were not continually reproducing and recruitment was largely restricted to the summer. Generation times for the dominant taxa are given in Appendix 1. To estimate invertebrate biomass, linear body dimensions were measured and converted to dry mass using regression equations (listed in Woodward and Hildrew, 2002b).

The benthic density of coarse particulate organic matter (CPOM) was calculated as the oven-dried (60 °C) mass per sample unit, with leaves, woody debris, and fruiting bodies being weighed separately. Because length-weight regressions were not available for the terrestrial invertebrates, this basal resource was omitted from the biomass webs. However, most of the terrestrial prey found in predator guts consisted of oribatid litter mites or collembola which, because of their small size and rarity, probably accounted for relatively little energy flux within the web. Iron-bacteria (*Leptothrix* sp.) form ephemeral flocs, which carpet the bed during low flow, particularly in summer (Hildrew *et al.*, 1985). Diatoms are sparse in Broadstone Stream,

and macroalgae are absent (Ledger, 1997); the heavily shaded channel, low pH, and presence of iron bacteria flocs prevent the formation of significant algal assemblage. The contributions of algae and iron bacteria to the web were not quantified, but were assumed to be small in comparison with detritus.

C. Construction of the Food Webs: Connectance Webs

We constructed a summary connectance web that included all links and species recorded over the six sampling occasions, excluding the permanent meiofauna. Connectance webs were also constructed for each sampling occasion, and are presented here as matrices (after Cohen *et al.*, 1993a). Yield-effort curves were constructed for taxa and links on each sampling occasion. To assess potential underestimation of species and links, we fitted rectangular hyperbolae to these data: $y = B_{\max} \cdot x/K + x$, where y is the number of taxa or links observed, x is the number of sample units processed (quadrats for species, guts for links), B_{\max} is the asymptote for the number of taxa or links and K is the number of sample units needed to reach half B_{\max} . Best-fit curves were generated using the GraphPad Prism Version 3.0 software package, and R^2 values were computed from the sum of the squares of the distances of the points from the best-fit curve determined by nonlinear regression (GraphPad Software Inc., 2000). Best-fit curves were derived iteratively, by varying the values of the variables to minimize the sum-of-squares.

We calculated several food web statistics for the connectance webs. Maximum chain length was the number of trophic elements (i.e., species or other taxonomic units) in the longest food chain from a basal resource to a top predator; where there were feeding loops, each cycle was counted once. Directed connectance was calculated as $C = L/S^2$ (Martinez, 1991), where L is the number of realized trophic links observed and S is the number of trophic elements in the web. We used this measure because it is less susceptible to variations in web size than other estimates of connectance (Martinez *et al.*, 1999). Complexity was calculated as $SC = S(L/S [S - 1]/2)$ (after Polis, 1991). The mean number of links per species, d , was calculated as L/S . We excluded basal resources from calculations of all web statistics (except chain length) because detritus could not be classified to species. Suctorial predators were omitted from the calculation of web statistics because their feeding links could not be described (after Closs and Lake, 1994).

We also constructed a highly resolved summary food web (including the permanent meiofauna) that included every link and species recorded in Broadstone Stream since sampling began in the early 1970s (webs were collated from the current study; Hildrew *et al.*, 1985; Lancaster and Robertson, 1995; Woodward and Hildrew, 2001; and Schmid-Araya *et al.*,

2002a). Because of the large number of samples used to construct this web, we assumed that asymptotes for the feeding links of the six most abundant predators had been reached (>1000 guts per species); these species were then used to examine relationships between predator body size and diet width. Basal resources were included in the calculation of food web statistics for this web to facilitate comparisons with earlier work.

D. Quantification of Feeding Links

The individual feeding links of the primary consumers (all detritivores with the exception of the very rare grazing mayfly, *Paraleptophlebia submarginata*) were not quantified. However, detritus is abundant throughout the year and not limiting as a food resource (Dobson and Hildrew, 1992). The predators used for gut contents analysis were *C. boltonii* ($n = 411$ guts), *S. fuliginosa* ($n = 450$ guts), *P. conspersa* ($n = 559$ guts), *M. nebulosa* ($n = 543$ guts), *T. longimana* ($n = 1039$ guts), *Z. barbatipes* ($n = 824$ guts) and three rarer species, the stonefly *Siphonoperla torrentium* (Pictet) ($n = 59$ guts) and the tipulids *Dicranota* sp. ($n = 102$ guts) and *Pedicia* sp. ($n = 24$ guts). Gut contents analysis was performed on individuals of all macroinvertebrate predators collected in the Surber samples on each occasion, except the two pentaneuriids (*T. longimana* and *Z. barbatipes*), which were randomly subsampled in August and October 1996 when they were extremely abundant. Subsampling reduced processing time but, nevertheless, over 400 pentaneuriid guts were analyzed in each of these two months.

The guts of the predators were dissected, mounted in euparal, and examined at $400\times$ magnification. Gut contents were identified from reference slides and the biomass of ingested prey was estimated from length-weight regressions from linear dimensions (listed in Woodward and Hildrew, 2002b). Because prey were generally consumed whole, or in large fragments, species could be identified relatively easily. Chironomid head capsule widths in the guts were reduced by 17%, to correct for flattening during mounting (after Hildrew and Townsend, 1982).

We wanted to use the gut contents data to estimate the *per capita* consumption rates (i.e., the number of prey per predator per day) in the food web links. Two problems were encountered: (1) the time during which consumed prey remain identifiable depends on temperature; and (2) the numbers observed in individual guts are highly variable and include many zeros. To deal with these problems, we used an approach based on that of Speirs *et al.* (2000). Let X be the mean number of prey per predator gut, and let τ be the characteristic residence time of an item of prey in the gut. If prey are ingested at rate I , then the rate of change of the numbers of recognizable

prey is $dX/dt = I - X/\tau$. Thus, if food consumption and digestion are in balance, we have $dX/dt = 0$ and so

$$I = \frac{X}{\tau}$$

The first requirement for estimating I is therefore obtaining an appropriate measure of X , the mean number of prey per predator gut. Since the observed number of prey is frequently zero and highly variable, it makes sense to view it as a Poisson variable with mean X . If r_i is the observed number of prey in the i th gut analyzed, then this has likelihood (i.e., the probability of the observation assuming a mean X) of

$$l_i = \frac{X^{r_i} e^{-X}}{r_i!}$$

Thus, the likelihood ℓ of the whole data set of n guts is

$$\ell = \prod_{i=1}^n \frac{X^{r_i} e^{-X}}{r_i!}$$

which yields a negative log-likelihood L of

$$L = \sum_{i=1}^n [\ln(r_i!) - r_i \ln X + X]$$

Now, this has derivative with respect to X of

$$\frac{dL}{dX} = \sum_{i=1}^n \left(\frac{r_i}{X} - 1 \right)$$

and this will be minimized when $dL/dX = 0$. Thus the maximum likelihood estimator of X is obtained by

$$X = \frac{\sum_{i=1}^n r_i}{n}$$

The second requirement for obtaining I is the gut residence time τ , which is known to be temperature dependent in a nonlinear fashion (Hildrew and Townsend, 1982). We assume the form

$$\tau = \tau_0 e^{-T/T_0}$$

where τ_0 and T_0 are constants, and T is the ambient temperature in $^{\circ}\text{C}$ during the period when the sample was taken. Thus, in calculating the ingestion rates for the seasonal webs, we used the mean stream temperature for the month under consideration. Annual *per capita* ingestion rates were then obtained by taking the mean of the seasonal values.

In order to determine τ_0 and T_0 , we note that the Q_{10} for this process is, by definition, the ratio of the rates (*i.e.*, $1/\tau$) 10°C apart. Thus,

$$Q_{10} = \frac{\tau_0 e^{-T/T_0}}{\tau_0 e^{-(T+10)/T_0}}$$

and hence,

$$Q_{10} = e^{10/T_0}$$

Thus, if we know the Q_{10} and the gut residence time τ at a reference temperature, we can determine both T_0 and τ_0 . In their study of fourth and fifth instar *Plectrocnemia conspersa*, Townsend and Hildrew (1977) report a Q_{10} of 2.3, which implies a value of $T_0 = 12^\circ\text{C}$. They also found that the prey-recognition “half-life” at 13°C was 9.8 hours for stoneflies and 7.3 hours for chironomids. Since the half-life is $\tau \ln(2)$, we get values of τ_0 of 41.7 hours for stoneflies and 31.1 hours for chironomids. A few prey species were neither chironomids nor stoneflies, and for these we used the values for either the former or the latter depending on how similar they were in morphology. For example, *Sialis* larvae in the guts of predators were of similar size and degree of sclerotisation to stoneflies, while Ceratopogonidae (*Bezzia* sp.) were considered equivalent to chironomids. An additional problem was that recognition time in the gut is inversely related to predator biomass, and increases with prey biomass Hildrew and Townsend (1982). However, since the mean biomass of individual prey in a predator’s gut also increases with predator biomass with a slope close to unity (Woodward and Hildrew, 2002b), we follow Speirs *et al.* (2000) in assuming that recognition time for ingested prey was constant across predator size classes.

The diet was characterized for all but two minor predator species: the larvae of *Platambus maculatus* (L.) (Dytiscidae) and *Bezzia* sp. (Ceratopogonidae) are suctorial predators, so the guts do not contain identifiable sclerotized material (cf. Closs and Lake, 1994). Because *P. maculatus* (species no. 7) was rare in Broadstone, it probably had little effect on prey populations. *Bezzia* sp. (species no. 11) was relatively abundant, but very small.

E. Construction of the Food Webs: Quantitative Webs

We constructed quantitative food webs, based on both density and biomass, on each of our six sampling occasions. Because reliable estimates of benthic density could not be obtained for very small individuals ($<10\ \mu\text{g}$) on each sampling occasion, they were excluded from the seasonal webs, although we were able to estimate the contributions of the temporary and permanent

meiofauna to the annual production-ingestion web (see below). Feeding links in the seasonal webs were expressed as *per capita* consumption 24 h^{-1} , as a percentage of the numbers or biomass of each prey population (i.e., if the abundance of *P. conspersa* was 50 m^{-2} and, on average, each *C. boltonii* ate one individual 24 h^{-1} , this link would be assigned a value of 2%). Links to the basal resources were not quantified.

We further estimated both annual secondary production (of prey and predators) and annual ingestion (by predators) to produce a quantified measure of biomass flux through the web over the entire year. Stead *et al.* (2005) recently measured secondary production of the meiofauna and macrofauna in a nearby acid stream (Lone Oak) that contains a very similar species complement to Broadstone. Both streams also have comparable macroinvertebrate faunal densities: mean annual standing biomass is 0.66 g m^{-2} and 0.83 g m^{-2} in Lone Oak and Broadstone, respectively. Although the meiofauna accounted for 52% of total production in Lone Oak, most of this was due to small instars of macrofaunal species in the temporary meiofauna (38% total production); the permanent meiofauna, such as rotifers and tardigrades, contributed relatively little (14%). Because we could not measure production across all size classes of the temporary meiofauna directly in Broadstone due to logistic constraints (we used a $330 \mu\text{m}$ mesh; Stead *et al.* used a $42 \mu\text{m}$ mesh), we estimated the “missing” biomass (and numbers of individuals) in this web by assuming that the ratio of the mean annual biomass (and numbers) of individuals $>10 \mu\text{g}$: $<10 \mu\text{g}$ was the same for identical macroinvertebrate taxa in the two streams. The data were split into these two body mass categories because all individuals of $\geq 10 \mu\text{g}$ were sufficiently large to be retained by the $330 \mu\text{m}$ mesh used in Broadstone. Similarly, the permanent meiofauna was assumed to account for the same proportion of total community production in both streams. We then multiplied the mean annual biomass of each taxon by its P/B ratio, as derived empirically in Lone Oak using the size-frequency method (Benke, 1993; Stead *et al.*, 2005), to estimate production in Broadstone.

Using P/B ratios measured in one system to predict production in another, comparable, system (e.g., Strayer and Likens, 1986) provides an alternative to the direct, but more labor-intensive, size-frequency method. We did employ the latter method, however, to directly measure the production of four of the larger Broadstone taxa for which we had reliable abundance data for all size classes. This enabled us to compare our calculated P/B ratios with those derived by Stead *et al.* (2005) in Lone Oak.

Gut contents data were used to estimate organic matter flux within the food web. Because some of the predators, particularly the smaller species, also fed on nonanimal prey, we estimated the contributions of these different food types to secondary production. We assumed that assimilation efficiency (AE, assimilation/ingestion) was 10% for coarse particulate organic matter

(CPOM, >1 mm diameter), 27% for fine particulate organic matter (FPOM, 50 μm – 1 mm diameter), 30% for algae, and 70% for animals (after Benke and Wallace, 1997). Annual ingestion of individual prey species by each predator was determined from both the predator's production and the percentage of the biomass in its diet represented by each prey species. Total ingestion by each predator was estimated, after Benke *et al.* (2001), as its production divided by the gross production efficiency (GPE), where $\text{GPE} = \text{AE} \times \text{net production efficiency (NPE, production/assimilation)}$. We assumed NPE to be 55%, after the studies of Smock and Roeding (1986) and Smith and Smock (1992); the latter study site was carried out in a headwater stream that contained similar predatory taxa to those in Broadstone, including *Cordulegaster* sp., and *Zavrelimyia* sp. GPE was estimated at 38.5% (i.e., $70 \times 55\%$, after Benke *et al.*, 2001) for the exclusively predatory taxa (*C. boltonii*, *S. fuliginosa*, *P. conspersa*, *P. maculatus* and *Bezzia* sp.), within the 33–39% range reported for invertebrate predators by Slansky and Scriber (1982). The predatory taxa that supplemented their diets with nonanimal food had GPE values ranging from as low as 7.0% for *Pedicia* (which ingested large quantities of CPOM) to 30.8% for *M. nebulosa* (which ingested mostly animal prey but also FPOM and, to a lesser extent, algae). Production and ingestion rates were calculated per unit area of stream bed per year ($\text{g dry mass m}^{-2} \text{y}^{-1}$), and the quotient of annual ingestion/production was used to provide a quantitative estimate of “interaction strength.”

IV. RESULTS

A. Summary Connectance Web (Including the Permanent Mei fauna)

This highly-resolved summary web, which includes all the food web data collected since the 1970s, contained 131 “species” and 842 links (Table 1). Addition of the permanent mei fauna to the equivalent macroinvertebrate-only summary web caused a slight decline in both complexity (13.11 to 12.93) and linkage density (6.45 to 6.42), a halving in connectance (0.104 to 0.049), but an increase in maximum chain length (12 to 15 species) (Table 1). This new summary web contained 17% more links than the web described by Schmid-Araya *et al.* (2002a), with 48 of the 121 additional links being from the invading top predator, *Cordulegaster boltonii*. Web size, however, increased by only 2.3%, following the inclusion of the mayfly *Paraleptophlebia submarginata* (Stephens), the amphipod *Niphargus aquilex* Schiödt and the isopod *Asellus meridianus* Racovitza, which were not recorded by Schmid-Araya *et al.* (2002a), probably because of the smaller sampling effort used in their study. Consequently, compared with Schmid-Araya *et al.*'s (2002a) highly resolved summary web, there was a

Table 1 Food web statistics for the Broadstone Stream food web at high and low (macrofauna only) resolution

	High resolution		Low resolution	
	Summary web	Schmid-Araya <i>et al.</i> (2002a)	Summary web (excludes permanent meiofauna)	Schmid-Araya <i>et al.</i> (2002a) (excludes permanent meiofauna)
No links (L)	842	721	400	319
Web size (S)	131	128	62	59
Directed connectance (C)	0.049	0.044	0.104	0.092
Links per species (d)	6.42	5.63	6.45	5.41
Complexity (SC')	12.93	11.35	13.11	11.00
Maximum chain length	15	12	12	9

The summary web represents data collated from all published sources in addition to the current study (see Methods); the summary web described by Schmid-Araya *et al.* (2002a) represents data collected over one year, 1996/97.

slight increase in connectance (0.044 to 0.049), but more marked increases in complexity (11.35 to 12.93) and linkage density (5.63 to 6.42).

The total number of links per predator was determined by simple logarithmic body-size relationships between predators and their prey (Fig. 1). For the six most intensively sampled predators, the \log_{10} total number of predatory links decreased with \log_{10} mean individual predator body size (μg) ($y = 1.78 - 0.049x$; $r^2 = 0.86$; $F = 24.52$; $p = 0.008$). The opposite was true, however, when the permanent meiofauna were excluded ($y = 1.48 + 0.035x$; $r^2 = 0.93$; $F = 55.85$; $p = 0.002$), suggesting the existence of both upper and lower size refugia for prey. Thus, more of the species in the web were vulnerable to the small-bodied tanypod *Z. barbatipes* than to the large-bodied dragonfly, *C. boltonii* (i.e., there is a lower size refugium from the dragonfly), whereas more macroinvertebrate prey are vulnerable to *C. boltonii* than to *Z. barbatipes* (i.e., there is an upper size refugium from the tanypod).

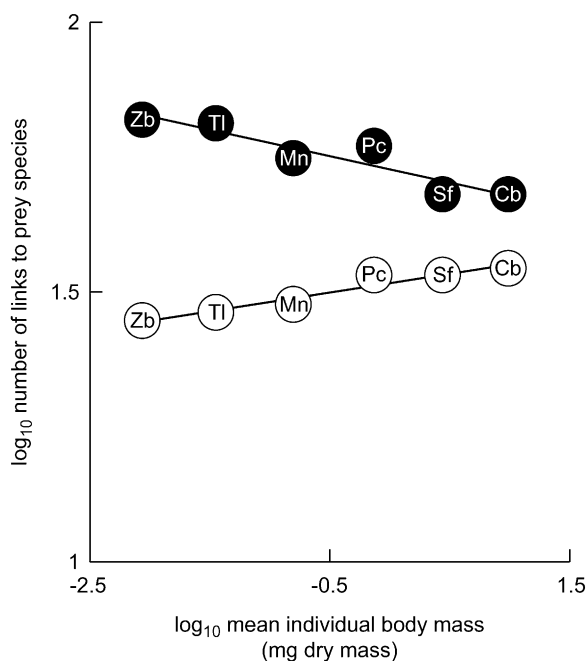


Figure 1 Relationships between predator body-mass and the number of feeding links to the macrofauna and permanent meiofauna within the highly-resolved summary food web for Broadstone Stream. The solid circles represent all links, including the permanent meiofauna; the open circles represent links to macrofaunal prey only. Predator codes: Cb, *Cordulegaster boltonii*; Sf, *Sialis fuliginosa*; Pc, *Plectrocnemia conspersa*; Mn, *Macropelopia nebulosa*; Tl, *Trissopelopia longimana*; Zb, *Zavrelimyia barbatipes*.

B. Seasonal Connectance Webs (Excluding the Permanent Meiofauna)

Although most members of the macroinvertebrate summary web (Fig. 2) were recorded on every sampling occasion, the number of links varied seasonally, being greatest in summer and declining progressively until the following spring (Table 2). Yield-effort curves suggested that sampling effort was sufficient to detect virtually every species, but not the total number of links, on each sampling date (Fig. 3). Rectangular hyperbolae described the curves for species and the links of the six dominant predators well, with high R^2 values (Table 3; mean $R^2 = 0.92$). For most predator species, the asymptote for the total number of links was not reached within individual sampling occasions, even when more than 200 guts were analyzed. Consequently, links from the rarest predators (*Pedicia* sp., *Dicranota* sp. and *Siphonoperla torrentium*) were those most severely underestimated. For the six most common predators, the asymptotic number of links increased with predator size (e.g., B_{\max} equalled 27 and 9 for *C. boltonii* and *Z. barbatipes*, respectively), whereas the number of guts required to estimate 50% of B_{\max} , called K , generally decreased with increasing predator size (trophic status) (e.g., K equalled 33 and 70 for *C. boltonii* and *Z. barbatipes*, respectively) (Table 3). Although predator size and abundance (sample size for guts) were inversely related and abundance varied seasonally (see also Woodward and Hildrew, 2002b), on average 63% of the predicted number of feeding links were recorded on each sampling occasion because of the compensatory effect of the inverse relationship between K and body size.

Web complexity, connectance, and links per species were greatest during summer, when abundance was highest and generations overlapped (Table 2). All these measures declined progressively until the following spring as the web became "simpler," and were always lower than in the summary web (e.g., each statistic in April was less than half the corresponding value in the summary web). Food chains included up to eight species (excluding loops) and were longest in summer and autumn. Mutual predation and cannibalism occurred among the dominant predators, especially during autumn, when the predator body size distribution was broadest. Omnivorous links were common: for example, in an eight-species food chain that linked *Cordulegaster boltonii* to the basal resources (terrestrial invertebrates), each species was preyed on directly by *C. boltonii*, including conspecifics. Further, the tany-pods, particularly *Macropelopia nebulosa*, derived a portion of their diet from algae, especially during summer when this resource was most abundant, and FPOM was also frequently ingested, particularly by the smaller instars. Because FPOM was abundant throughout the year, the increased consumption of detritus in winter (e.g., 25% and 42% of *T. longimana* guts contained FPOM in August and February, respectively; $\chi^2 = 7.35$, $P < 0.01$) suggested

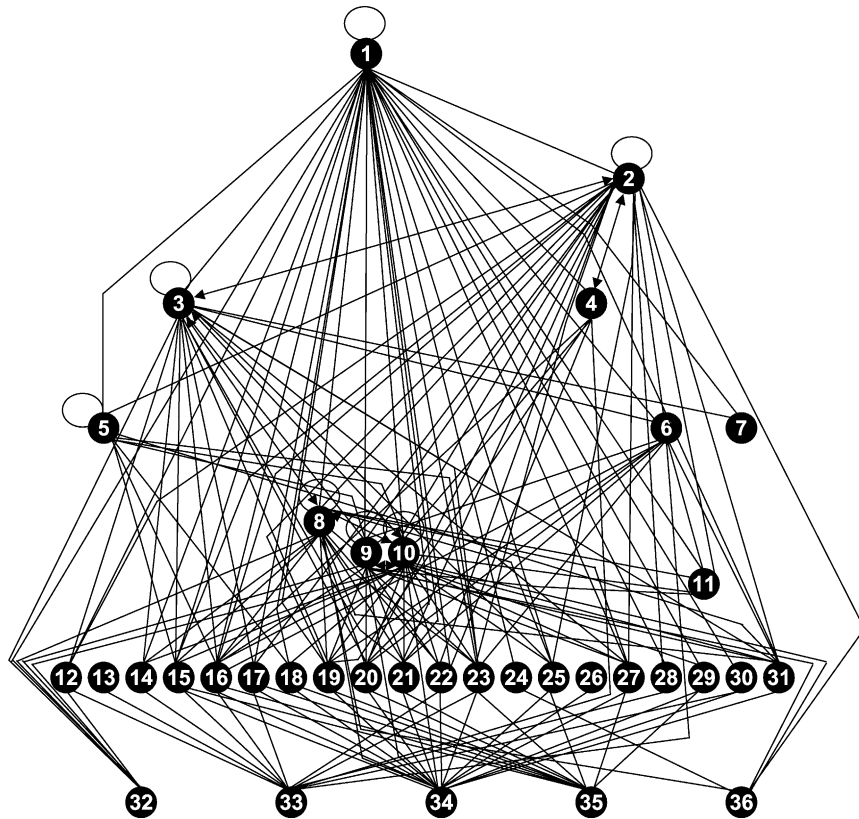


Figure 2 Summary connectance food web for the macrofaunal assemblage of Broadstone Stream (1996–1997). Double-headed arrows depict mutual predation, circular arrows cannibalism. Key to species: 1. *Cordulegaster boltonii* (Donovan); 2. *Sialis fuliginosa* Pict; 3. *Plectrocnemia conspersa* (Curtis); 4. *Pedicia* sp.; 5. *Siphonoperla torrentium* (Pictet); 6. *Dicranota* sp.; 7. *Platambus maculatus* (Pictet); 8. *Macropelopia nebulosa* (Meigen); 9. *Zavrelimyia barbatipes* (Kieffer); 10. *Trissopelopia longimana* (Staeger); 11. *Bezzia* sp.; 12. *Potamophylax cingulatus* (Stephens); 13. *Adicella reducta* (McLachlan); 14. Tipulidae (non-predatory); 15. *Nemurella pictetii* Klapalek; 16. *Leuctra nigra* (Olivier); 17. *Leuctra hippopus* Kempny; 18. *Corynoneura lobata* Edwards; 19. *Prodiamesa olivacea* (Meigen); 20. *Heterotrissocladius marcidus* (Walker); 21. *Micropsectra bidentata* (Goetghebuer); 22. *Brillia modesta* (Meigen); 23. *Polypedilum albicorne* grp.; 24. *Paraleptophlebia submarginata* (Stephens); 25. oligochaetes; 26. *Pisidium* sp.; 27. *Simulium* sp.; 28. Helodidae sp.; 29. *Niphargus aquilex* Schiödte; 30. *Asellus meridianus* Racovitza; 31. cyclopoids; 32. Terrestrial invertebrates; 33. CPOM; 34. FPOM; 35. Iron bacteria; 36. Algae.

Table 2 Food web matrices for Broadstone Stream (1996–1997)

	Summary web	May	August	October	December	February	April
	1 2 3 4 5 6 8 9 10	1 2 3 4 5 6 8 9 10	1 2 3 4 5 6 8 9 10	1 2 3 5 6 8 9 10	1 2 3 4 5 6 8 9 10	1 2 3 4 5 6 8 9 10	1 2 3 4 5 6 8 9 10
1	1 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0
2	1 1 1 1 0 0 1 0 0	0 1 1 0 0 0 0 0 0	1 1 1 1 0 0 0 0 0	1 1 0 0 0 1 0 0	1 1 0 0 0 0 0 0 0	1 1 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0
3	1 1 1 0 0 0 1 0 1	1 1 1 0 0 0 0 0 0	1 1 0 0 0 0 0 0 1	1 1 1 0 0 0 0 0	1 1 1 0 0 0 0 0 0	1 1 1 0 0 0 0 0 0	1 0 1 0 0 0 0 0 0
4	1 1 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0		1 1 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0
5	1 1 0 0 1 0 0 0 0	1 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0	1 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0
6	1 1 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0	1 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0
8	1 1 1 0 0 0 1 0 1	1 0 0 0 0 0 0 0 0	1 1 1 0 0 0 0 0 0	1 1 1 0 0 1 0 1	0 1 0 0 0 0 1 0 1	0 0 0 0 0 0 1 0 0	1 0 0 0 0 0 0 0 1
9	1 1 1 0 1 1 1 1 1	1 1 1 0 0 1 1 1 1	1 1 1 0 0 0 1 0 1	1 1 0 0 0 1 0 1	1 1 0 0 0 0 1 0 1	1 0 1 0 1 1 1 1 1	1 1 0 0 0 0 0 0 1
10	1 1 1 1 1 0 1 1 1	1 1 0 0 1 0 1 0 1	1 1 1 1 0 0 1 0 1	1 1 1 1 0 1 1 1	1 0 0 0 1 0 1 1 1	1 0 0 0 0 0 1 0 1	1 0 1 0 1 0 1 0 1
12	1 1 1 0 0 0 1 0 0	1 0 1 0 0 0 0 0 0	1 0 1 0 0 0 0 0 0	1 1 1 0 0 0 0 0	0 1 1 0 0 0 0 0 0	1 1 1 0 0 0 0 0 0	1 0 1 0 0 0 0 0 0
13	0 0 0 0 0 0 0 0 0				0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	
14	1 0 1 0 0 0 1 0 1	1 0 0 0 0 0 1 0 0	0 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0	1 0 1 0 0 0 1 0 1	1 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
15	1 1 1 0 1 0 1 1 1	1 1 1 0 0 0 0 1 1	1 1 1 0 0 0 1 1 1	1 1 1 0 0 1 0 1	1 1 1 1 1 0 0 0 1	1 1 1 0 1 0 1 0 1	1 1 1 0 1 0 0 0 0
16	1 1 1 1 1 1 1 1 1	1 1 1 0 0 0 1 1 1	1 1 1 0 0 1 1 1 1	1 1 1 0 0 1 1 1	1 1 1 0 1 1 0 0 1	1 1 1 1 1 0 1 1 0	1 1 1 1 0 0 0 0 0
17	1 1 1 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	1 1 1 0 0 0 0 0	1 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
18	1 0 0 0 1 0 0 0 1		1 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1	0 0 0 0 1 0 0 0 0	
19	1 1 1 1 0 1 1 1 1	0 0 1 0 0 0 0 0 0	1 1 0 0 0 0 1 0 1	1 1 0 0 0 1 0 0	0 1 0 0 0 0 1 1 1	1 1 0 1 0 1 1 0 0	0 1 0 0 0 0 0 0 0
20	1 1 1 0 0 1 1 1 1	1 0 1 0 0 0 1 1 1	1 1 1 0 0 1 1 1 1	1 1 1 0 0 1 1 1	0 1 1 0 0 0 1 1 1	1 1 1 0 0 1 1 0 0	1 1 1 0 0 1 0 1 1
21	1 1 1 0 0 1 1 1 1	0 1 0 0 0 0 1 1 1	1 1 1 0 0 1 1 1 1	1 1 1 0 0 1 0 1	0 0 1 0 0 0 0 1 1	1 1 0 0 0 1 0 0 1	0 0 0 0 0 0 1 0 1
22	1 1 1 1 0 0 1 1 1	1 0 0 0 0 0 1 1 1	1 1 0 1 0 0 1 1 1	1 1 1 0 0 0 0 1	1 1 0 0 0 0 1 0 0	1 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0
23	1 1 1 0 1 1 1 1 1	1 1 1 0 1 1 1 1 1	1 1 0 0 0 0 1 1 1	1 0 0 0 0 1 0 1	1 0 0 0 1 0 0 0 1	0 1 1 0 0 1 1 1 1	1 1 1 1 1 0 0 1 1
24	1 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0		1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	
25	1 1 1 0 0 0 1 0 1	0 0 0 0 0 0 0 0 0	1 1 0 0 0 0 1 0 1	1 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
26	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
27	1 1 1 0 0 0 1 1 1	0 0 1 0 0 0 0 0 0	1 1 1 0 0 0 1 0 1	0 0 0 0 0 0 0 0	1 0 1 0 0 0 0 1 1	1 0 0 0 0 0 1 0 0	0 0 0 0 0 0 0 0 0
28	1 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0		1 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0
29	1 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1		0 0 0 0 0 0 0 0 0		0 0 0 0 0 0 0 0 0
30	1 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0			0 0 0 0 0 0 0 0 0		0 0 0 0 0 0 0 0 0
31	1 1 1 0 1 1 1 1 1	0 0 1 0 0 0 1 1 1	1 1 1 0 0 0 1 1 1	1 1 1 0 0 1 1 1	1 1 1 0 1 0 1 1 1	1 0 1 0 0 0 0 0 1	1 1 1 0 0 0 1 0 1
Links per species (<i>d</i>)	4.52	2.33	3.35	3.00	2.59	2.33	1.88
Directed connectance	0.16	0.09	0.13	0.13	0.09	0.09	0.07
Complexity (<i>SC'</i>)	9.36	4.84	6.96	6.26	5.36	4.85	3.92
Max chain length	8	7	8	8	8	7	6

Columns represent predators, rows represent prey. 1/0 represents presence/absence of a feeding link.

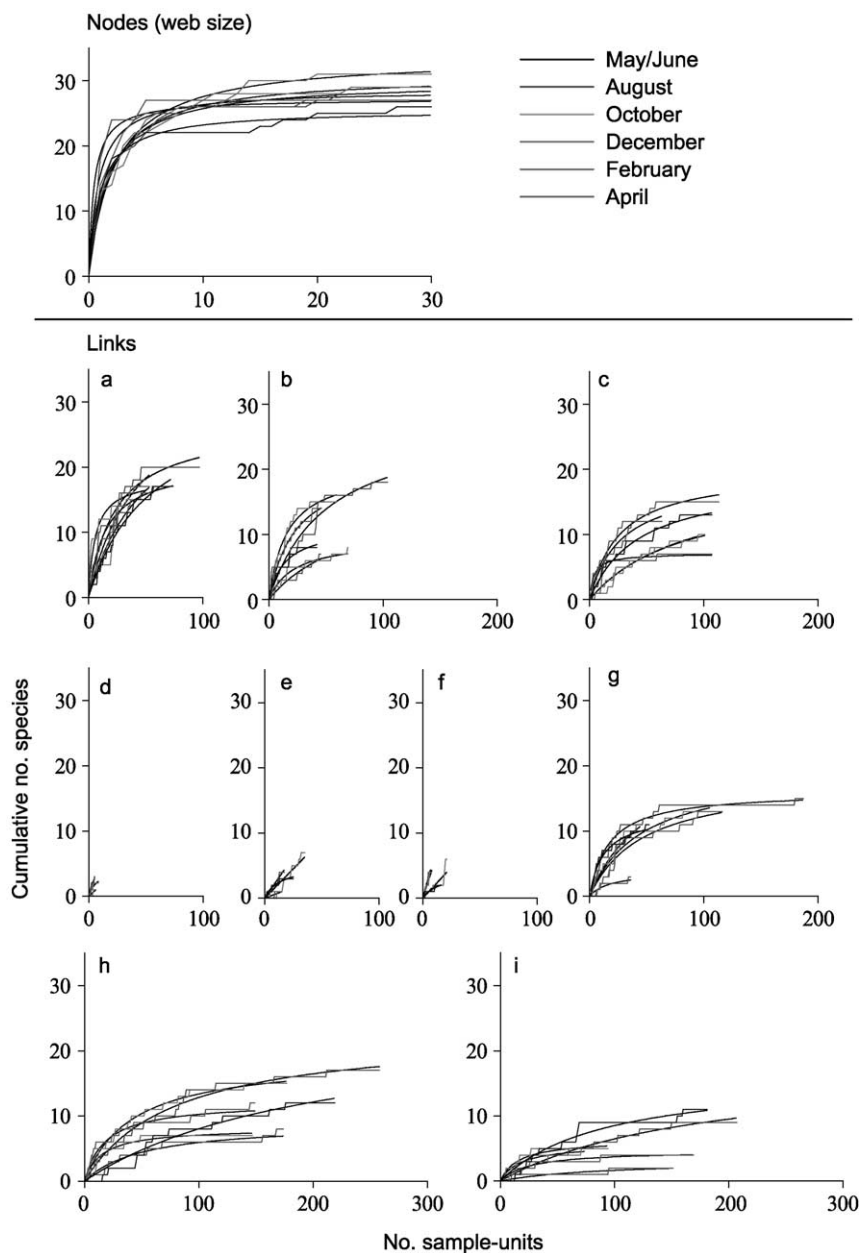


Figure 3 Yield-effort curves for the cumulative number of species included in the web as nodes (top panel) and as feeding links from prey to predators recorded within Broadstone Stream during 1996–97. Predators: a, *C. boltonii*; b, *S. fuliginosa*; c, *P. conspersa*; d, *Pedicia* sp.; e, *Dicranota* sp.; f, *S. torrentium*; g, *M. nebulosa*; h, *T. longimana*; i, *Z.*

Table 3 Predicted asymptotes (B_{\max}) for the number of prey species consumed per predator species, and the number (K) of samples (benthic quadrats for species; guts for links) required to detect 50% of the predicted asymptote for the total number of feeding links

	<i>C.</i> <i>Species^b</i>	<i>S.</i> <i>boltonii</i>	<i>P.</i> <i>fuliginosa</i>	<i>M.</i> <i>consersa</i>	<i>T.</i> <i>nebulosa</i>	<i>Z.</i> <i>longimana</i>	<i>barbatipes</i>
B_{\max}							
May	25.53	31.98	11.19	18.61	12.73	24.86	16.37
Aug	27.20	26.58	27.87	18.28	16.08	22.94	17.91
Oct	28.54	34.55 ^a	21.34	19.75	18.08	12.11	4.68
Dec	33.75 ^a	33.53 ^a	20.4	18.08	23.61	18.88	5.64
Feb	30.89	18.34	9.32	18.76	19.55	8.14	6.30
Apr	29.9	20.6	16.41	7.07	3.72	8.95	3.14
Mean	29.30	27.60	17.75	16.76	15.63	15.98	9.01
K							
May	1.01	55.2	13.68	42.39	12.25	209.6	92.28
Aug	0.45	23.15	50.37	27.04	16.81	78.65	176.3
Oct	0.85	44.57	23.66	25.7	47.09	18.25	25.79
Dec	2.26	52.3	15.88	83.95	53.49	41.17	17.55
Feb	1.81	5.909	21.97	88.3	46.25	15.2	16.08
Apr	1.64	15.09	73.9	3.73	17.6	51.11	89.38
Mean	1.34	32.70	33.24	45.19	32.25	69.00	69.56
Mean R^2	0.98	0.94	0.94	0.94	0.92	0.95	0.84

^a B_{\max} values for links that exceed the total number of invertebrate taxa included in the summary web (very rare species were excluded from the web; see Methods).

^bSpecies ranked from left to right in order of decreasing body size.

that in summer, when small prey were most abundant, the tanypods became actively more predatory and less detritivorous.

There were clear trivariate relationships between body size, abundance, and web structure (after Cohen *et al.*, 2003), with most of the consumption flowing from smaller, more abundant prey to larger, rarer predators (i.e., energy moves upwards and to the left in Fig. 4a). Averaging across all the links in the web, predators were about one order of magnitude larger, by mass, than their prey (8–13 times larger, when cyclopoids were excluded or included in the web, respectively). These “rules” were broken in a few instances where predators fed on prey that were (on average) larger than themselves (Fig. 4b), but these links were rare and reflected seasonal and ontogenetic shifts in the relative body sizes of predators and prey, as described below.

barbatipes. Sample-unit (x-axis) for feeding links = 1 gut; for nodes = 1 Surber sample (25 cm × 25 cm quadrant). The black curves are models fitted to the data for each month and are rectangular hyperbolae (see text and Table 2).

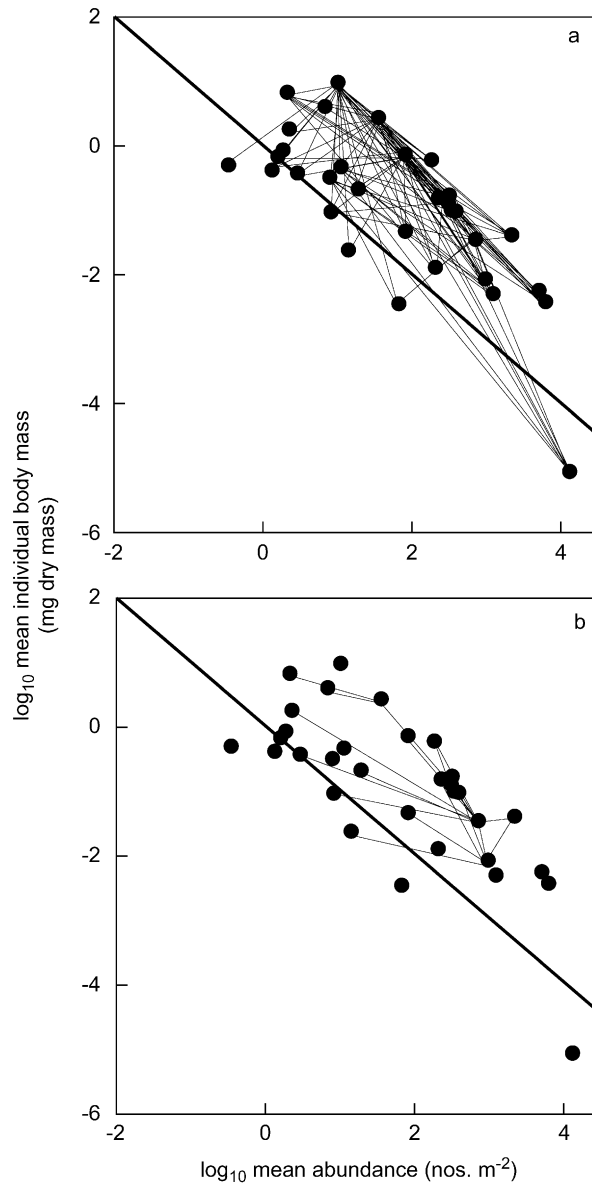


Figure 4 Summary food web for Broadstone stream, plotted on axes of mean abundance (x -axis) and mean body-mass (y -axis), after Cohen *et al.* (2003). Links that represent consumption where the predator is larger than its prey are shown in the top panel (a), whereas links that represent the opposite are shown in the lower panel (b). The dashed line, with a slope of -1 , represents a biomass ratio that is equivalent between a consumer and resource: links with slopes that are more negative than -1 represent instances where a consumer has a greater biomass abundance than its prey (assuming the consumer is above and to the left of its prey in this plane, as in the top panel).

C. Quantitative Webs

There were strong seasonal shifts in invertebrate abundance. Peak recruitment after summer oviposition was followed by a progressive decline until spring for most taxa (Fig. 5). Among the basal resources, terrestrial detritus was extremely abundant, with little difference among months beyond a slight peak in February (which also corresponded with a slight winter peak in invertebrate abundance) (Fig. 5). Terrestrial invertebrates were most abundant during autumn, presumably due to inputs via leaf-fall, but were always rare relative to the aquatic fauna. Iron bacteria were present throughout the year, but only formed dense flocs in the summer. Algae were not visible in the stream to the naked eye, but ingestion of diatoms by the tanypods revealed that a limited algal biofilm persisted throughout the year. These seasonal changes in the availability of consumers and resources were reflected in the marked temporal changes in the magnitude and distribution of ingestion rates of prey by predators. Large numbers, especially of the smaller temporary meiofauna, were consumed in the summer, both *per capita* and per unit area (Table 4), although most links accounted for a relatively small proportion of total consumption (Fig. 6).

The presence/absence and strength of individual links varied seasonally as prey species entered or exited the different size ranges that could be handled by the respective potential predators (Figs. 7 and 8). For example, the *Macropelopia nebulosa* population ate equivalent to 14% (0.05% *per capita*) of the *Nemurella pictetii* population per 24 hours in August, but this link was not detected in April, when these prey were mostly too large to be handled by the predator (Fig. 7). Further, because of the negative relationship between mean abundance and body size (Fig. 4), often the numerical webs were effectively mirror-images of the biomass webs. The taxa and links that dominated the former, in terms of benthic abundance and ingestion rates, were usually relatively insignificant in the biomass webs, and *vice-versa*. The distribution of biomass among species within the webs, however, was less variable over time than in the numerical webs (Figs. 7 and 8), as individual growth mitigated the post-oviposition decline in numbers (Fig. 4). Within the predator guild, the large species dominated standing biomass throughout the year, whereas the smaller tanypods dominated numerically (Figs. 7 and 8). The relative importance of small and large predators varied seasonally, however, with the tanypods contributing considerably less to numbers or biomass per unit area other than in summer and autumn. Similar shifts occurred within the prey assemblage, with small species (chironomids) dominating in summer and large species (stoneflies) in winter (Figs. 7 and 8).

Although the tanypods ate a similar number of prey per unit area to the larger predators during summer and autumn (Table 4), they consumed considerably less biomass throughout the year because, being small

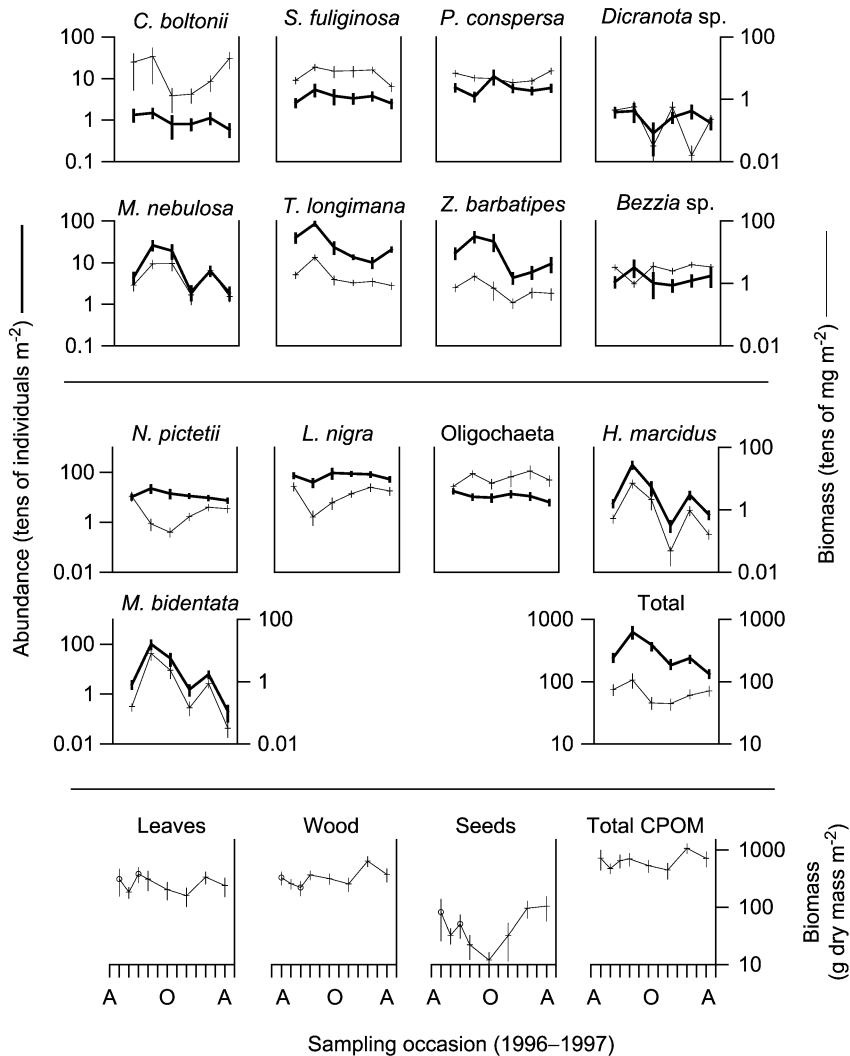


Figure 5 Seasonal changes in the mean (± 1 SE) abundance and biomass of the major macrofaunal consumers and basal resources in Broadstone Stream (1996–1997). Top panels represent predators, middle panels primary consumers, and lower panels represent the dominant basal resource, detritus (open circles represent additional sampling dates that were not used to estimate invertebrate abundance).

themselves, they ate much smaller prey (Figs. 7 and 8). *Per capita* ingestion, ingestion/ m^2 , the number of feeding links, and web complexity all fell markedly between August and April (Tables 1 and 4), tracking the decline in invertebrate abundance and shifts in the size spectrum. However,

Table 4 Estimated daily ingestion of prey in Broadstone Stream, 1996–1997

Month	Predator	Ingestion per predator (nos. eaten <i>per capita</i> 24 h ⁻¹)	Ingestion per unit area (nos. eaten m ⁻² 24 h ⁻¹)
May	Cb	0.73	9.75
	Sf	0.80	20.94
	Pc	1.33	81.59
	Mn	0.86	37.90
	Tl	0.19	76.96
	Zb	0.45	76.89
	Total	5.09	312.33
Aug	Cb	9.52	141.71
	Sf	4.22	227.43
	Pc	1.09	40.23
	Mn	4.31	1136.11
	Tl	1.83	806.25
	Zb	0.61	262.94
	Total	25.98	2656.70
Oct	Cb	1.88	15.01
	Sf	1.06	40.74
	Pc	0.68	77.07
	Mn	1.20	234.80
	Tl	1.75	268.10
	Zb	0.60	58.58
	Total	8.44	706.57
Dec	Cb	0.67	5.39
	Sf	1.00	33.44
	Pc	0.20	12.14
	Mn	0.73	14.29
	Tl	0.71	66.07
	Zb	0.19	8.36
	Total	4.24	146.16
Feb	Cb	0.87	9.77
	Sf	0.67	25.29
	Pc	0.28	14.15
	Mn	0.40	26.00
	Tl	0.37	37.91
	Zb	0.16	9.83
	Total	5.03	140.32
Apr	Cb	2.46	14.59
	Sf	0.83	20.75
	Pc	0.62	36.84
	Mn	0.17	3.15
	Tl	0.36	36.22
	Zb	0.02	2.17
	Total	5.76	119.09

The six dominant predators are shown separately; monthly totals include all predators. Predator codes: Cb, *Cordulegaster boltonii*; Sf, *Sialis fuliginosa*; Pc, *Plectrocnemia conspersa*; Mn, *Macropelopia nebulosa*; Tl, *Trissopeloia longimana*; Zb, *Zavrelimyia barbatipes*.

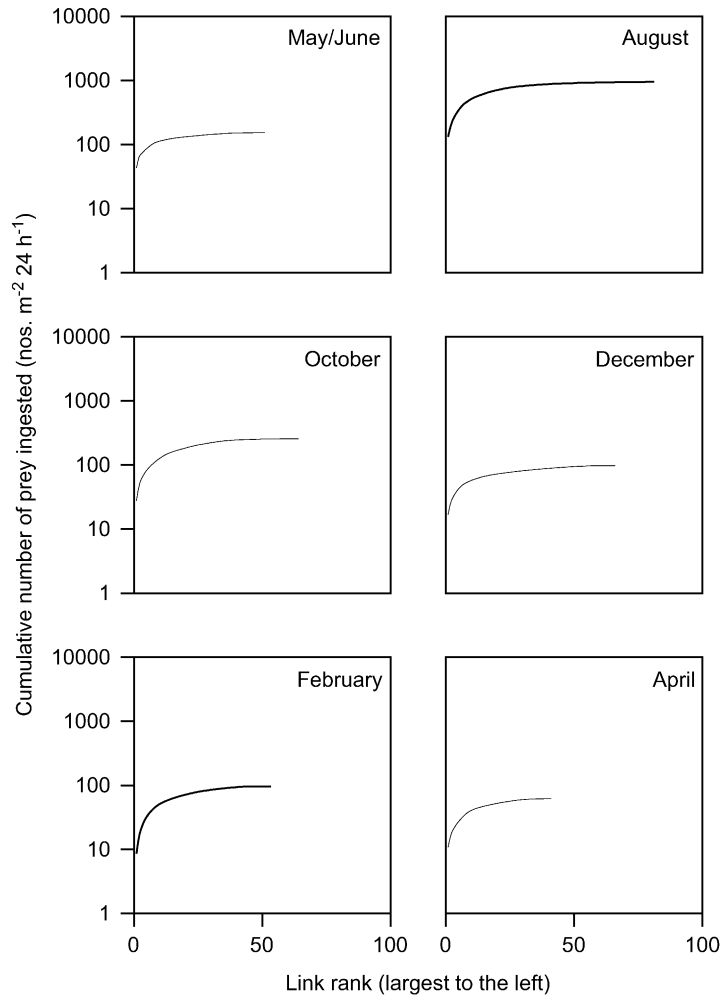


Figure 6 Structure of the Broadstone Stream food web: Feeding links. Links are ranked along the x -axis in order of decreasing magnitude (nos. individuals consumed $\text{m}^{-2} 24 \text{ h}^{-1}$).

although overall consumption declined progressively from summer until spring, when expressed as a percentage of the total numerical standing stock (equivalent to 16.1% of the total macrofaunal standing stock ingested $\text{m}^{-2} 24 \text{ h}^{-1}$ day in August, falling to 5.5% in April), the remaining links often increased in magnitude, so that the degree of skew within the web increased as complexity declined. Ingestion rates were skewed both among and within predator species and did not necessarily reflect prey density (i.e., the

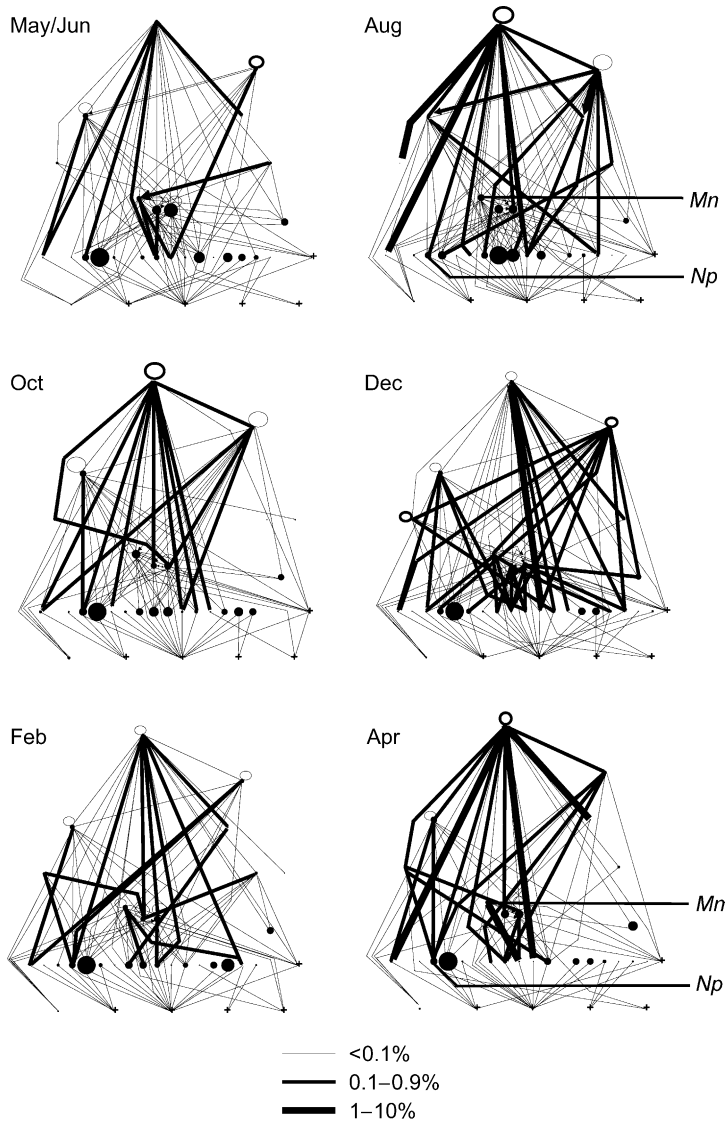


Figure 7 Quantified food webs representing numbers of macrofaunal prey (individuals $> 10 \mu\text{g}$) eaten *per capita* 24 h^{-1} (as a percent of numbers m^{-2}) during 1996–1997. The area of each circle is proportional to total numerical standing stock within sampling occasions (see Fig. 5 for absolute values). Links to basal resources and the meiofaunal cyclopoids were not quantified (see Fig. 2 for comparison with connectance web and identity of taxa).

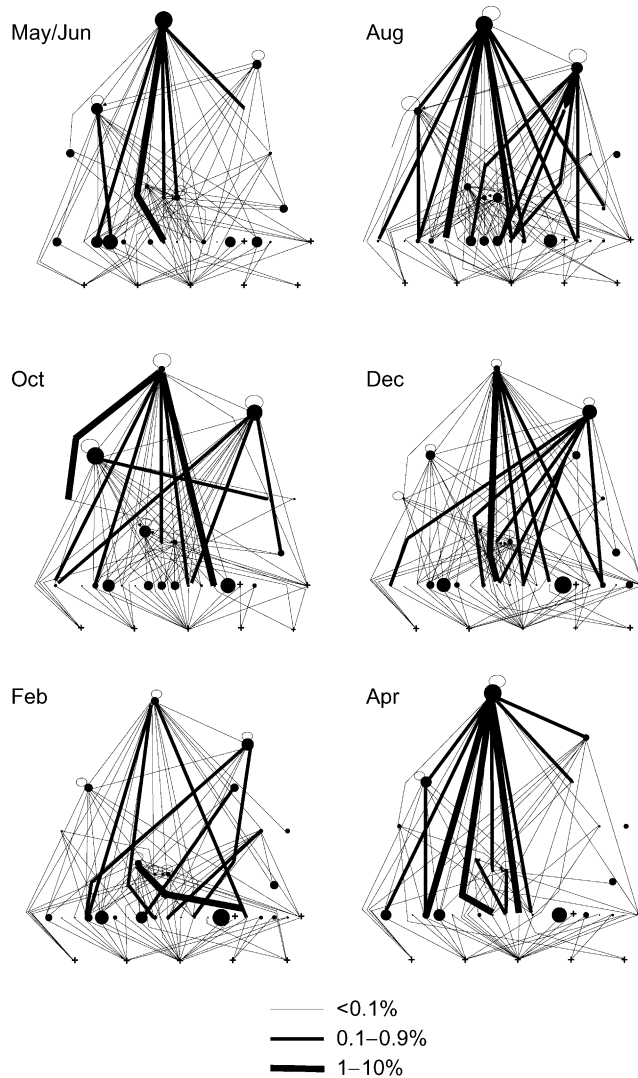


Figure 8 Quantified food webs representing biomass of macrofaunal prey (individuals $> 10 \mu\text{g}$) eaten *per capita* 24 h^{-1} (as a percent of biomass m^{-2}) during 1996–1997. The area of each circle is proportional to total standing biomass within sampling occasions (see Fig. 5 for absolute values). Basal resources are denoted nominally by '+'. Links to basal resources and the meiofaunal cyclopoids were not quantified (see Fig. 2 for comparison with connectance web and identity of taxa).

predators fed “selectively” on different portions of the size spectrum). In addition, there was a secondary effect of encounter rate increasing the predators’ relative consumption of prey. For example, *per capita* consumption of the highly mobile, epibenthic stonefly *N. pictetii* was far higher than for the slow-moving, interstitial species *L. nigra*, despite the numerical dominance of the latter within the web (Fig. 7).

D. Annual Production and Ingestion Web

Total annual production for the entire community, excluding the permanent meiofauna, was estimated at $4.58 \text{ g m}^{-2} \text{ y}^{-1}$. Of this total, 33% ($1.52 \text{ g m}^{-2} \text{ y}^{-1}$) was accounted for by the predator guild, although it should be kept in mind that many of these were omnivorous and often consumed the basal resources directly (Table 5). The three tanypod species accounted for equivalent to half the production (total, $0.42 \text{ g m}^{-2} \text{ y}^{-1}$) of the three dominant large species (total, $0.80 \text{ g m}^{-2} \text{ y}^{-1}$), despite being 15 times more abundant numerically. Production of the permanent meiofauna was estimated to account for an additional 14% (after Stead *et al.*, 2005), thus our estimate of total secondary production was $5.22 \text{ g m}^{-2} \text{ y}^{-1}$ (i.e., $4.58 + 0.64 \text{ g m}^{-2} \text{ y}^{-1}$). There was marked variation among species (in terms of their relative contributions to production) with the larger species, especially the predators and detritivorous stoneflies, being relatively productive per unit area despite having generally low P/B ratios (Table 5). Note that our estimated values of P/B for three large species were similar to those for the same taxa in Lone Oak calculated by Stead *et al.* (2005). Conversely, the detritivorous chironomids, with some of the highest P/B values (e.g., 10.12 for *Heterotrissocladius marcidus*), accounted for only 22% of total annual macrofaunal production despite their numerical dominance (41% and 70% of total and macrofaunal abundance, respectively), because of their low biomass per unit area. Similarly, the cyclopoids, with high P/B ratios (11.85) accounted for only 0.03% of production but 41% of total benthic density. The only species conventionally accepted as a “grazer,” the mayfly *P. submarginata*, contributed a negligible 0.08% to prey production, suggesting the dominance of detritus as the principal basal resource: detritivores accounted for >99% of primary consumer production. *Pisidium* sp. and *Simulium*, the only filter-feeding taxa, accounted for 5.6 and 0.6% of prey production, respectively, but the former were not eaten by any of the predators. Consequently, the vast majority of energy reached the higher trophic levels via detrital food chains and by the processing of CPOM by shredders (mostly stoneflies) or FPOM by deposit feeders (mostly chironomids). Detritus was unlikely to be a limiting resource at any time throughout the year; assuming an assimilation efficiency of 10% (after Benke and Wallace,

Table 5 Mean annual production (dry mass), biomass, abundance and P/B ratio estimates for Broadstone Stream during 1996–1997^b

Species	Production (g m ⁻² y ⁻¹)	Biomass (g m ⁻²)	Abundance (nos m ⁻²)	Body mass (mg)	P/B
<i>Oligochaeta</i>	0.782	0.112515	185	0.60807	6.95
<i>Leuctra nigra</i>	0.616	0.091976	2,208	0.04166	6.70
<i>Prodiamesa olivacea</i>	0.396	0.055252	320	0.17275	7.16
<i>Sialis fuliginosa</i> ^a	0.370	0.098786	36	2.75631	3.75 (3.72)
<i>Heterotrissocladius marcidus</i>	0.295	0.029145	5,104	0.00571	10.12
<i>Plectrocnemia conspersa</i> ^a	0.261	0.060629	82	0.73961	4.30 (5.80)
<i>Micropsectra bidentata</i>	0.241	0.023912	6,293	0.00380	10.07
<i>Nemurella pictetii</i>	0.239	0.034748	341	0.10188	6.87
<i>Bezzia</i> sp.	0.205	0.038367	393	0.09760	5.35
<i>Macropelopia nebulosa</i>	0.194	0.035855	228	0.15711	5.42
<i>Cordulegaster boltonii</i> ^a	0.173	0.099326	10	9.72509	1.74 (absent)
<i>Pisidium</i> sp.	0.172	0.040518	311	0.13034	4.24
<i>Trissopelopia longimana</i>	0.161	0.025646	722	0.03553	6.27
<i>Potamophylax cingulatus</i> ^a	0.137	0.027995	7	4.08489	4.89 (4.02)
<i>Zavrelimyia barbatipes</i>	0.060	0.008414	974	0.00863	7.14
<i>Polypedilum albicorne</i>	0.058	0.006317	1,242	0.00509	9.14
<i>Pedicia</i> sp.	0.049	0.014521	2	6.80678	3.38
<i>Dicranota</i> sp.	0.036	0.005356	11	0.47485	6.75
<i>Brillia modesta</i>	0.028	0.002718	208	0.01306	10.20
<i>Leuctra hippopus</i>	0.028	0.004135	19	0.21504	6.70
<i>Simulium</i> sp.	0.019	0.0039	82	0.04741	4.94
Helodidae	0.017	0.004155	2	1.82649	4.12
<i>Siphonoperla torrentium</i>	0.012	0.002584	8	0.32587	4.51
<i>Niphargus aquilex</i>	0.009	0.001114	3	0.38013	8.12
<i>Asellus meridianus</i>	0.008	0.001625	2	0.86680	5.00
Tipulidae	0.005	0.000784	8	0.09493	6.75
<i>Platambus maculatus</i>	0.004	0.0011	2	0.68738	3.97
<i>Diptera</i> spp.	0.004	0.000563	1	0.42209	6.75
<i>Paraleptophlebia submarginata</i>	0.002	0.000344	14	0.02433	6.92
<i>Corynoneura lobata</i>	0.002	0.000238	67	0.00354	7.09
Cyclopoids	0.001	0.000117	13,196	0.00001	11.85
<i>Adicella reducta</i>	0.001	0.000176	0.3	0.50769	4.02
Sum	4.58	0.832	32,082		

^alarger taxa without temporary meiofaunal stages for which P/B ratios were measured directly in Broadstone (values in parentheses are estimates for Lone Oak; see Methods). Taxa are ranked in order of descending production.

^bPermanent meiofauna excluded except for cyclopoids.

The summary quantified food web illustrates the skewed contributions to both annual production (species nodes) and ingestion (feeding links) within the web (Fig. 9): a few taxa accounted for the majority of secondary production and most links were weak ($I/P < 0.01$). The composition of predator diets was determined by the relative sizes of predators and prey. The three large

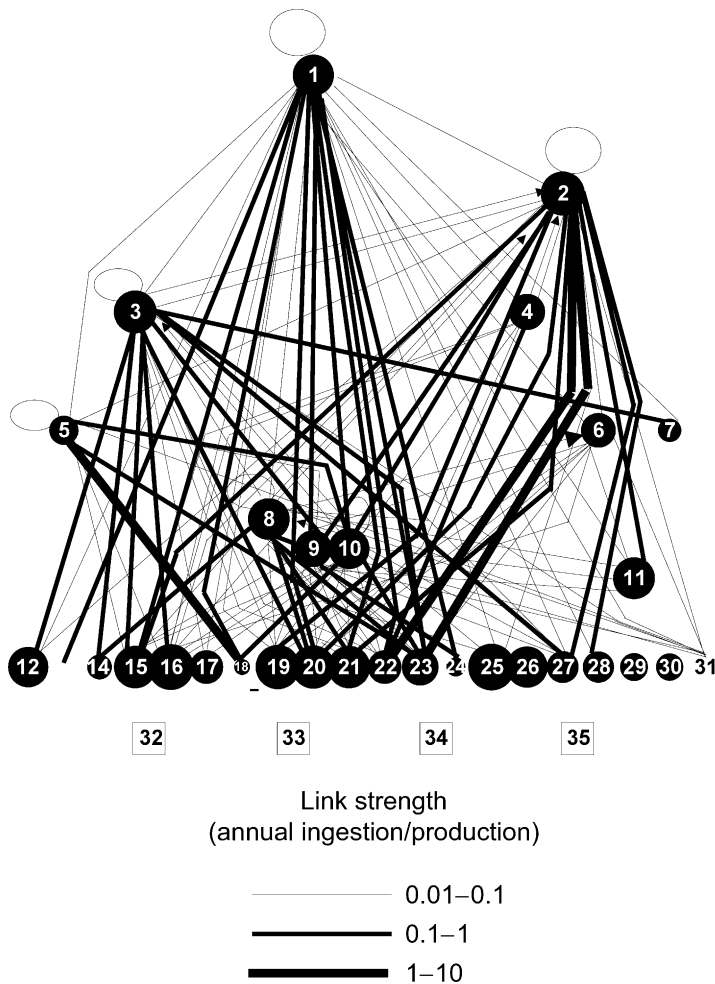


Figure 9 Summary quantified food web for Broadstone Stream, illustrating annual secondary production of predators and prey (proportional to circle area) with the strength of feeding links expressed as annual ingestion/annual production (I/P). Links to basal resources were not quantified.

predators preyed mostly on large prey (stoneflies, caddis, and other large predators: 40–65% of annual ingested prey biomass), whereas the smaller predators took mostly small prey (chironomids: 70–85% of annual ingested prey biomass). Although the overall distribution of the strength of individual feeding links (i.e., \log_{10} I/P) within the entire web was positively skewed, the position of individual predator species within this distribution reflected differences in body mass (trophic status) (Fig. 10): the smaller predators had fewer and weaker links to macrofaunal prey than the larger species, despite their numerical dominance. However, recall that they had many more links to the permanent meiofauna than did the larger predators (Fig. 1).

There were significant log-log correlations (all at $r > 0.5$ and $P < 0.005$) between mean annual abundance, mean and maximum body mass, total annual ingestion/production (I/P), P/B, and the frequency of ingestion (nos ingested m^{-2} and *per capita*), suggesting that the trivariate relationships seen in Figure 4 could be extended further to reveal multivariate relationships in quantified webs (Table 6). The strength of predation pressure (as I/P) exerted on prey species was negatively correlated with \log_{10} mean (and maximum) prey body mass and positively correlated with prey abundance. We calculated the total consumption of each prey species by summing total ingestion across all of its predators, to provide a single measure of “susceptibility” to predators for each species in the web (expressed as \log_{10} total I/P). Most of the production of the smaller taxa was consumed by the predators (Fig. 11). Thus, larger prey species had relatively strong “bottom-up” effects on predator production, but suffered weaker “top-down” effects, in terms of the proportion of their annual production that was eaten, when compared with smaller species. For some of the very small taxa, ingestion exceeded production, possibly due to sampling errors, an overestimation of mean water temperature, and/or external subsidies (e.g., drift). In terms of relating the strength of links (total I/P) to their frequency of occurrence (numbers ingested *per capita* 24 h^{-1}), there was a positive log-log correlation ($r = 0.65$; $p < 0.001$), as stronger links were those most frequently observed. This therefore suggested a relationship between the connectance and quantified webs, in that increasing sampling effort simply leads to a greater proportion of weak links being included in a web.

V. DISCUSSION

A. Connectance Webs

Schmid-Araya *et al.* (2002b) have recently documented a decline in connectance with increasing web size in a suite of well-characterized stream food webs. While we cannot rule out a possible role of sampling artefact, our data

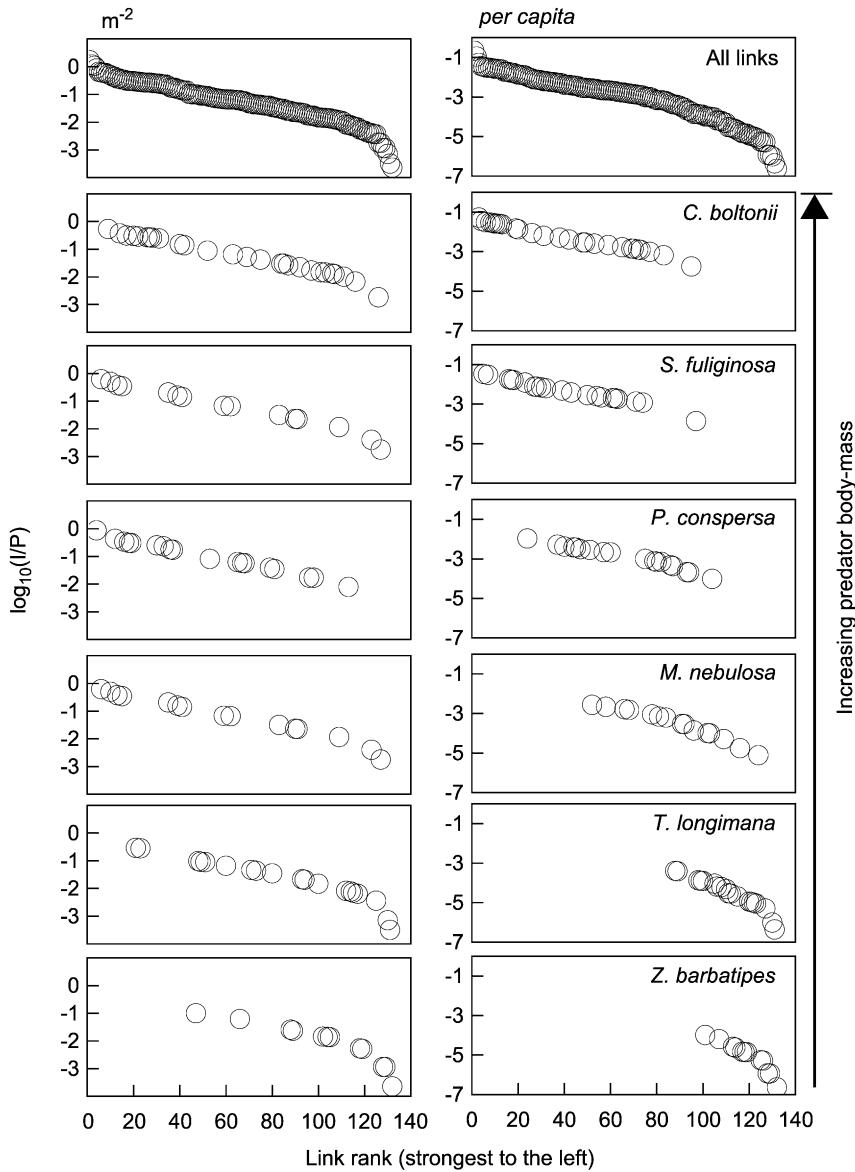


Figure 10 Distribution of interaction strength ($\log_{10} [I/P]$) within the entire food web (top two panels) expressed as m^{-2} (left) and *per capita* (right). Each point represents an individual link within the food web. The positions of the individual links from the six dominant predator species within the overall distribution are shown in the 12 lower panels (m^{-2} , left panels; *per capita*, right panels).

Table 6 Pearson Product Moment Correlations (r) for \log_{10} - \log_{10} relationships among biological and ecological traits and measures of interaction strength for the macroinvertebrate taxa in the quantified Broadstone Stream food web (Table 1)

	Nos m^{-2}	Mean body mass	Max body mass	P/B	I/P	I/P <i>per</i> <i>capita</i>	Nos. eaten m^{-2} 24 h^{-1}
Mean body mass	−0.74 −0.77						
Max body mass	−0.65 −0.69	0.88 0.88					
P/B	0.58 0.69	−0.80 −0.86	−0.78 −0.84				
I/P	0.59 0.67	−0.81 −0.88	−0.77 −0.83	0.59 0.81			
I/P <i>per capita</i>	0.52 0.60	−0.66 −0.81	0.67 −0.76	*0.37 0.69	0.89 0.90		
Nos. eaten m^{-2} 24 h^{-1}	0.94 0.95	−0.68 −0.68	−0.61 −0.61	0.67 0.70	0.61 0.68	**0.48 0.58	
Nos. eaten <i>per</i> <i>capita</i> 24 h^{-1}	0.92 0.93	−0.59 −0.59	−0.57 −0.58	0.50 0.59	0.65 0.64	0.63 0.61	0.93 0.95

Pisidium sp, which were not eaten by any predator species, were excluded. The italicized values show correlations where the two predominantly hyporheic taxa, oligochaetes and *N. aquilex*, were excluded. All correlations were significant at $P < 0.005$, except those denoted by *($P < 0.05$) or **($P < 0.01$).

provide clear evidence for a mechanism that could account for the pattern obtained. Body size constraints had strong effects on predator diet width and this created a degree of compartmentalization between the permanent meiofaunal and macrofaunal subwebs in Broadstone Stream. Because the larger predators could not perceive or handle very small prey and, conversely, very large prey were invulnerable to small predators, size-refugia existed at both extremes of the size spectrum. Thus, speciose food webs including very small species are inevitably less richly connected than webs containing macrofauna alone, as was found here (Table 3). Essentially, there are no direct links between species at the two extremes of the food web, as was proposed in the “size disparity” hypothesis of Hildrew (1992) and Schmid-Araya *et al.* (2002b). The permanent meiofauna are rarely included in freshwater food webs (but see Schmid-Araya *et al.*, 2002a,b), and yet may provide an important energy source for predatory invertebrates, particularly in their early life stages (Woodward and Hildrew, 2002a). The highly-resolved summary web for Broadstone Stream contained 261 predatory links between the macrofauna and the permanent meiofauna. Ultimately, although the

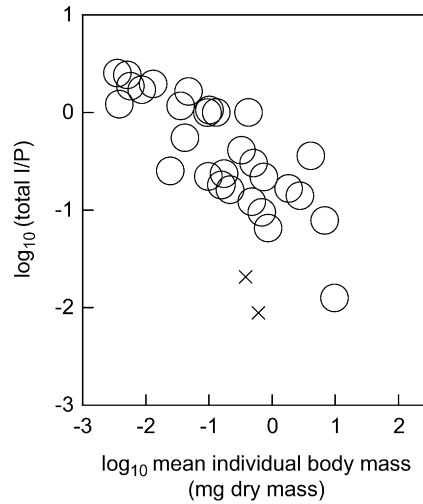


Figure 11 Prey body-size versus total interaction strength (total $\log_{10} [I/P]$). Each datapoint represents the sum of annual ingestion/predation for each species (i.e., the total consumption of that species by all predators within the web). Two taxa that are predominantly hyporheic, *Niphargus aquilex* and oligochaete worms, and which were excluded from the second set of correlations in Table 6 (values in *italics*), are denoted by crosses, rather than circles.

task is daunting, by incorporating the permanent meiofauna into quantified webs, we should gain a better understanding of the trophic importance of these little-known taxa in freshwaters.

Our results support the findings of the few other studies that have examined temporal variations in web structure, which have also demonstrated striking seasonality (e.g., Warren, 1989; Winemiller, 1990; Closs and Lake, 1994; Tavares-Cromar and Williams, 1996; Thompson and Townsend, 1999). This seasonality is, unfortunately, inevitably masked in the summary webs that dominate much of the food web literature (e.g., catalogues in Cohen, 1978; Pimm, 1982; and Williams and Martinez, 2000). Web complexity in Broadstone was greatest in summer, when the availability of specimens for gut contents analysis was highest, and this might suggest that some of the seasonal patterns in web structure reported here (and elsewhere) were simply artefacts of sampling effort. However, there were no clear seasonal biases in the degree of our underestimations of food web links: about 60% of the predicted total number of links for the six dominant predators were detected on each occasion. This lack of any obvious seasonal methodological bias might be because, unlike many other studies, our sampling effort was relatively high and scaled to benthic abundance,

rather than a fixed number of guts (Tavares-Cromar and Williams, 1996; Townsend *et al.*, 1998; Thompson and Townsend, 1999). The absence of taxonomic bias in the detection of links (at least among the dominant predators) reflected a compensatory effect between predator body size and food web links in that, although the larger predators were rarer than their smaller counterparts, fewer needed to be sampled to characterize the diet. The *total* number of links detected on each sampling occasion, however, would clearly have been higher if gut contents analysis had been more exhaustive, and was underestimated even in the summary web because of the rarity of some predators (i.e., *Pedicia*, *Dicranota* and *S. torrentium*). However, the projected number of samples required to describe every individual feeding link within the web on a single sampling occasion would impose excessive disturbance upon the system and, because of the positive correlation between the frequency of occurrence and linkage strength (as I/P), many of the very rare links would probably represent only very weak interactions (at least as measured by energy flow). This cannot always simply be assumed to be true, however, and this seems to be the first time that such a relationship has been demonstrated. Further, weak links may stabilize food webs, and can thus be dynamically important even if rare (McCann, 2000).

Seasonal variations in the Broadstone webs showed how the number of connections among species varied over time for a standard unit of effort (i.e., all species and links that were detected in 30 quadrats). As such, comparing connectance webs among sampling occasions provided insight into real patterns in the frequency of interactions per unit area, whereas comparisons with other, less exhaustively sampled, systems should be treated with caution because of autocorrelations between sampling artefacts and web size.

B. Trivariate Relationships, Ontogenetic Shifts, and Seasonally Quantified Webs

Trivariate relationships between body size, abundance, and web structure—similar to those reported recently by Cohen *et al.* (2003) in the Tuesday Lake food web—were apparent in the Broadstone Stream web, despite the latter having a more truncated size spectrum that spanned only six orders of magnitude in body mass, compared with twelve orders in Tuesday Lake (which contained fish). On average, prey were about ten times smaller than their predators in Broadstone, a generally smaller size disparity than in Tuesday Lake, where predators were often two or three orders of magnitude larger than their prey. However, the maximal size difference between predators and prey in both webs was about six orders of magnitude, suggesting an upper bound to the predator-prey size ratio. In both Broadstone Stream and Tuesday Lake, the vast majority of links represented the consumption of

smaller, more abundant prey by larger, rarer predators. These “rules” were broken in a few instances in both systems, with predators sometimes feeding on prey less abundant than themselves. However, there were very few instances where predators fed on prey that were (on average) larger than themselves (18% of observed links), and there was only one link in the Broadstone web where a predator fed on a prey species that was both larger *and* rarer than itself (<1% of observed links). These exceptions can be ascribed to seasonal shifts in the relative body sizes of predators and their prey (described below), revealing the importance of including both temporal and ontogenetic data when assessing food web structure (see also Woodward and Hildrew, 2002b).

After quantifying our seasonal connectance webs, it was clear that the webs were far simpler than implied by the presence-absence data: a few species and links accounted for most of the trophic interactions in the web, whether measured in terms of numbers or biomass of prey ingested. However, because of the negative correlation between body size and abundance, species and links that dominated numerically were often relatively unimportant in terms of biomass, and *vice versa*. The biomass webs represented snapshots of the major pathways of organic matter (energy) flow. Conversely, the abundance webs highlighted the major population dynamics: most individuals that were eaten were small and contributed relatively little to energy flux. Energy flow and population dynamics can be important in different ways in structuring communities (Power, 1990; Wootton, 1997; Hall *et al.*, 2000), and the construction of either biomass or abundance webs without the other would tend to obscure one or other of these processes.

In systems where prey availability is low, such as acid streams, generalist feeding is probably advantageous and this will inevitably result in highly interconnected food webs (Woodward and Hildrew, 2002a). Indeed, the predators in Broadstone were extreme trophic generalists that ate virtually any prey item smaller than themselves. However, this generalism was over-emphasized in the connectance web. *Quantitatively*, some prey were clearly overrepresented in predator diets compared with the benthos or the diets of other carnivores; this was largely due to seasonal and ontogenetic differences in size-related handling constraints, which generated differential susceptibility to predators among species and over time. For instance, within the predator guild, cannibalism and mutual predation were particularly prevalent only when generations overlapped, resulting in seasonal “*ontogenetic reversals*” (after Polis *et al.*, 1989) in trophic status that were driven by changes in the relative size of predators and prey (see also Woodward and Hildrew, 2002b). Such feeding loops, once thought to be rare (Pimm, 1982; Cohen and Newman, 1985), now appear to be common in nature, as suggested by the recent “niche models” of food web structure (Warren,

1996; Williams and Martinez, 2000). However, because these situations only arose at certain times of the year, and since only the smallest individuals—which are also those least likely to survive (Hildrew *et al.*, 2004)—were eaten, the effects of ontogenetic reversals were probably relatively weak on average when compared with “top-down” effects. The seasonal and ontogenetic changes in the size-spectrum of the web meant that although 18% of the links were from larger to smaller species, not surprisingly *none* of these individual links represented ingestion of a larger individual by a smaller individual.

During summer and autumn, the web was dominated by a profusion of small detritivorous chironomids that were consumed mostly by the small predators; by winter and spring, the web was dominated by large predators and prey (mostly stoneflies). Consequently, the number, magnitude, and distribution of ingestion rates varied seasonally, with complexity and consumption per unit area (Tables 1 and 4) peaking during summer and declining progressively over time, with many links being broken as prey outgrew their potential predators. Inevitably, the smaller predators were those most affected and the tanypods became increasingly detritivorous as prey availability declined (Smith and Smock, 1992), a trait that would also presumably reduce the risk of intraguild predation while foraging actively for increasingly scarce animal prey (Woodward and Hildrew, 2002b).

The seasonal decline in invertebrate abundance in Broadstone following the summer has been previously attributed to predation because ingestion rates are high and detritus is not limiting to the prey assemblage (Hildrew and Townsend, 1982; Dobson and Hildrew, 1992). Reduced ingestion rates in spring, when prey are rarer, might reflect an increase in the relative availability of physical refugia (Hildrew and Townsend, 1977; Townsend and Hildrew, 1979; Woodward and Hildrew, 2002d), which could potentially stabilize the food web by weakening links (e.g., McCann, 2000). Indeed, consumption rates of the Broadstone predators, which are limited by encounter rate, are markedly lower than their potential (Speirs *et al.*, 2000; Woodward and Hildrew, 2002c). During summer, prey abundance and mobility are both at their peak (Hildrew and Townsend, 1976; Winterbottom *et al.*, 1997) and small individuals dominate the size spectrum (Woodward and Hildrew, 2002b). This would, in theory, maximize both prey availability and predation, as is also suggested by the strong depletion of prey by predators in field experiments at this time of year (Woodward and Hildrew, 2002d). Occasional strong pulses of predation can also occur at other times, such as during spates, when predators and prey are concentrated in flow refugia (Lancaster, 1996). Thus, predator impacts can be highly variable, both seasonally and over much shorter temporal scales.

C. Food Web Topology and Interaction Strength

Recent food web models have shown that complexity (i.e., many species and/or high connectance, after May, 1972) can enhance web stability if most links are weak, leading ecologists to reassess the established paradigm that complex webs are unstable (May, 1972, 1973; Polis, 1998; McCann, 2000). Unfortunately, interaction strength (*sensu stricto*, May, 1973) is notoriously difficult to measure in real systems, although approximations may be made from empirical and experimental evidence to provide insight into the relative importance of different links (Berlow *et al.*, 2004).

So, accepting these limitations, can we say anything about interaction strengths in the Broadstone food web? There are several independent lines of evidence that lend support to our estimates of link strength (as I/P) from the quantified food web, which suggest that most interactions might be “weak,” particularly over intergenerational scales. For instance, at the base of the web, detritus is superabundant; also, links between this dominant basal resource and primary consumers are donor-controlled, suggesting an abundance of weak links, at least between these two trophic levels (Dobson and Hildrew, 1992). Although predatory links do not necessarily follow the same pattern, the Broadstone predators consumed prey biomass equivalent to 65% total benthic production (excluding *Pisidium* sp., which were not eaten), leaving a relatively large portion available for other losses (e.g., disease, drift, and the production of adults). These estimates of consumption are somewhat lower than reported elsewhere (e.g., >100% reported by Allen, 1951; 94% reported by Smith and Smock, 1992), but most other studies have ignored meiofaunal production (but see Stead *et al.*, 2005) and our estimate rises to 80% if the temporary and permanent meiofauna are excluded.

Our estimates of total secondary production, including the permanent meiofauna, in Broadstone (total, $5.22 \text{ g m}^{-2} \text{ y}^{-1}$; insects only, $3.61 \text{ gm}^{-2} \text{ y}^{-1}$) are very similar to those reported by Stead *et al.* (2005) from their study in the neighboring Lone Oak stream (total, $4.48 \text{ g m}^{-2} \text{ y}^{-1}$; insects only, $1.93 \text{ gm}^{-2} \text{ y}^{-1}$). Further, the predator guild accounted for almost exactly the same proportion of macrofaunal production in both streams (33% in Broadstone, 34% in Lone Oak). Total meiofaunal production, including macrofaunal species within the temporary meiofauna, however, accounted for 52% of the total in Lone Oak but only 19% in Broadstone, primarily because the small chironomids and oligochaetes that dominated the temporary meiofauna in Lone Oak were rarer in Broadstone. Clearly, meiofauna have the potential to contribute significantly to production in other systems, and the widespread omission of this portion of the community size-spectrum might account for some of the unexpectedly high estimates of consumption reported. Predator production in Broadstone was

1.53 g m⁻² y⁻¹, similar to the 1.73 g m⁻² y⁻¹ reported by Smith and Smock (1992), but lower than that in the Ogeechee River (14.35 g m⁻² y⁻¹), where water temperature was sufficiently high to permit multivoltinism (Benke and Wallace, 1997). In all of these systems, a few prey species supported the majority of predator production, suggesting the predators might have strong effects on only a small fraction of the community. Energy flux, however, does not necessarily equate with interaction strength, unless expressed as the proportion of prey production that is ingested. In Broadstone, our estimates of I/P suggested that only a few links were strong, and that 63% of them accounted for <10% of annual prey production.

In terms of the proportion of annual production that was ingested, the smaller, more 'r-selected' species, which had no access to upper size-refugia, suffered the strongest predation pressure in Broadstone, suggesting that we might be in a position to start identifying species traits (e.g., body size and its associated correlates) that determine the distribution of interaction strength. Some researchers, however, have argued that only experimental manipulations can provide true measures of interaction strength (e.g., Paine, 1992). Although it is logistically impossible to manipulate any more than a tiny proportion of the links within almost any natural food web, field enclosure/exclosure manipulations of the larger predators in Broadstone have also revealed that only a few prey species were strongly depleted, whereas most others were relatively unaffected (Lancaster *et al.*, 1991; Woodward and Hildrew, 2002d).

All of the lines of evidence cited above are based entirely on short-term (i.e., intragenerational) interactions among the benthic larvae. Many mathematical food web models are, however, constructed using intergenerational population dynamics (e.g., May, 1973; McCann *et al.*, 1998), which are extremely difficult, or even impossible, to measure and parameterize in most natural systems. Some researchers have addressed this by examining interactions among short-lived protists in microcosms under different food web configurations (e.g., Petchey, 2000) but, although they can provide undoubtedly valuable insight into the potential importance of interactions within small food web "modules," such studies can also lack realism because they consider artificial assemblages of species that interact in very simple and homogenous environments (usually glass bottles) with little or no physical refugia or environmental disturbance.

Broadstone Stream, however, is unusual in that we have empirical and experimental data that span a broad range of temporal and spatial scales and degrees of realism. These studies suggest that, although predation can be intense between recruitment periods (Hildrew and Townsend, 1982), it does not appear to destabilize individual prey populations at the intergenerational

scale (Speirs *et al.*, 2000). Indeed, long-term data suggest that the entire larval assemblage as a whole is extremely persistent with very little interannual variation, even over several decades, which are equivalent to tens of generations for most taxa (Woodward *et al.*, 2002). The constancy in the composition of the food web may be due to compensatory responses to predation, whereby alternative feeding paths are used at low prey densities (Speirs *et al.*, 2000). This could, in theory, weaken the strength of interactions, thereby increasing the stability of the food web (e.g., McCann, 2000). The system is also resilient to physical perturbations, with rapid recovery following large flood events (Lancaster and Hildrew, 1993). Further, most of the members of the food web are very fecund, and relatively few adults may be required to reset the next generation (Wilcock *et al.*, 2001).

A recent large-scale, intergenerational manipulation of one of the dominant large predators, *Sialis fuliginosa*, which is densely connected within the food web, revealed strongly stabilizing density-dependent mortality, which was ascribed to predation on the early life stages (Hildrew *et al.*, 2004). Following experimental reductions or increases in recruitment of >90% across 150 m stretches of the stream, the effects on population size were only transient, such that they persisted for no more than a few months and did not carry over to subsequent generations (Hildrew *et al.*, 2004). The dynamics of the adult and eggs of most aquatic insects are still poorly understood, but might provide the key to understanding how freshwater communities are able to persist over long time scales, even when competitive and predatory interactions among the aquatic larvae may seem intense (Woodward and Hildrew, 2002a). The predictable seasonality of Broadstone Stream might permit the vast majority of the secondary production of the small and supposedly more “vulnerable” prey to be eaten and yet still allow sufficient prey to survive each year to repopulate the benthos. The current mismatch between the temporal (and spatial) scales at which models are constructed and empirical data are collected has, to date, hindered the advancement of food web ecology in freshwaters and elsewhere, and more large-scale studies are urgently required (Woodward and Hildrew, 2002a).

D. Limitations and Future Directions

Inevitably, there exist numerous sources of potential error in the construction of quantified food webs. For instance, estimates of production and ingestion may be influenced by external subsidies of drifting and terrestrial prey, in addition to vertical colonization from the hyporheos. Fortunately, these confounding effects are likely to be relatively small in Broadstone

because the hyporheic zone is very shallow (usually <5 cm), drift is low due to the sluggish nature of the stream (Lancaster and Hildrew, 1993), and the rarity of terrestrial insects in predator guts suggested that they contributed little to energy flux. Similarly, the soft-bodied permanent meiofauna, although eaten by the predators (Schmid-Araya *et al.*, 2002a,b), were unlikely to contribute significantly to total energy flux because of their small size and low production per unit area. For instance, these taxa accounted for only 3% of total production in the neighbouring Lone Oak stream (cf. Stead *et al.*, 2005). Though energetically trivial, however, food web links to the meiofauna could play a strong structuring role by contributing to the early survival of larger predators.

Stable isotope analysis (SIA) offers a potential alternative method of measuring long-term assimilation (a_{ji} in the Jacobian matrix) directly, but it lacks the taxonomic precision of gut contents analysis. The quantitative contributions of iron bacteria and algae to the Broadstone web remain largely uncertain, but an earlier study showed that terrestrial detritus dominated the $\delta^{13}\text{C}$ signature of *L. nigra*, *N. pictetii*, *S. fuliginosa* and *P. conspersa* (Winterbourn *et al.*, 1986). Because these four taxa alone accounted for about 30% of the secondary production in Broadstone, and the only grazer we found was an extremely rare mayfly, any chemosynthetic production by iron bacteria flocs and any conventional primary production by the impoverished algal biofilms in the stream were likely to represent relatively trivial basal inputs. The vast majority (>99%) of the energy flux in the web must rest on the processing of CPOM by detritivores (mostly stoneflies) and FPOM consumption by deposit feeders (mostly chironomids and oligochaetes).

It has been suggested that the considerable effort required to increase the sample of well-described connectance webs might be better directed toward studying processes (e.g., energy flux, ingestion rates) rather than patterns (e.g., connectance) (Hall and Raffaelli, 1993; Benke and Wallace, 1997; Woodward and Hildrew, 2002a). Although the quantified and semi-quantified webs that have been published in the last decade (e.g., de Ruiter *et al.* 1995; Raffaelli and Hall, 1996) have often emphasized the limitations of qualitative webs, important advances have been made recently in the study of the topological properties of food webs (e.g., Warren, 1996; Williams and Martinez, 2000; Cohen *et al.*, 2003). Food web architecture and dynamics are clearly linked, as we can see in the Broadstone web and in other systems (e.g., Emmerson and Raffaelli, 2004), and the dynamic and static approaches are therefore likely to complement one another, rather than necessarily serving to provide contrasting viewpoints.

The current hindrance to the development of the field is, undoubtedly, however, the shortage of detailed quantified webs that allow us to explore the potential relationships between dynamics and structure. As more, and

better quantified, food webs emerge, the search for such generalities (or the lack of them) will become easier. A major challenge for food web ecologists is to produce webs that are standardized sufficiently to allow meaningful comparisons across systems. Producing yield-effort curves, quantifying webs for numbers or biomass consumed per unit area (or volume) per unit time, and expressing ingestion relative to production, for instance, will facilitate such comparisons, which are imperative if we are to parameterize and validate models with real, empirical data (Cohen *et al.*, 1993a; McCann 2000).

Despite this current lack of standardization, however, some surprisingly robust similarities appear to be emerging from some of the better-described webs, especially in relation to the potential structuring role of body size (e.g., Cohen *et al.*, 1993b; Warren, 1996; Martinez and Williams, 2000). Of particular relevance in the light of results from the current study are some of the trivariate relationships between body size, abundance and web topology reported by Cohen *et al.* (2003) for the Tuesday Lake food web, which also hold true for Broadstone Stream. These suggest that food web structure might be bound by a set of rules, potentially relating to energetic constraints. Perhaps equally as intriguing is the suggestion that, at least in Broadstone Stream, there are clear *multivariate* relationships between suites of species traits, food web topology, and interaction strength, derived from body size and its correlates (e.g., P/B ratio, abundance, diet width). These relationships now need to be investigated in a range of different systems if we are to assess their generality.

ACKNOWLEDGMENTS

Financial support for this research project was provided by a Natural Environment Research Council Studentship Grant awarded to G. Woodward while studying at Queen Mary University of London. We would like to thank the Conservators of the Ashdown Forest, the numerous people who helped with fieldwork, Jenny Schmid-Araya for providing additional meiofaunal data, and Tracey Stead for providing data on secondary production in Lone Oak Stream. We also wish to thank Joel Cohen and Dan Reuman for their insightful and helpful comments, which greatly improved the manuscript.

Appendix 1 Generation times for the dominant Broadstone Stream taxa

Order	Taxon	Equivalent Broadstone taxon	Generation time (days)		Mean flight period (days)	Data source
			min	max		
Odonata	<i>Cordulegaster boltonii</i>	<i>C. boltonii</i>	1,095	1,418	42	Woodward, 1999
Megaloptera	<i>Sialis fuliginosa</i>	<i>S. fuliginosa</i>	730*	730	28 [†]	*Speirs <i>et al.</i> , 2000
Trichoptera	<i>Plectrocnemia conspersa</i>	<i>Plectrocnemia conspersa</i>	365*	365*	24.5 [†]	*Speirs <i>et al.</i> , 2000; [†] Hildrew, pers. comm.
Trichoptera	<i>Potamophylax cingulatus</i>	<i>P. cingulatus</i> ; <i>Adicella reducta</i>	365	365	24.5	Waters, 1977
Plecoptera	Plecoptera	<i>Siphonoperla torrentium</i> , <i>Nemurella pictetii</i>	365*	365*	31.5 [†]	*Hynes, 1977; [†] Petersen, pers. comm.
Plecoptera	<i>Leuctra hippopus</i>	<i>Leuctra hippopus</i>	365*	365*	31.5 [†]	*Zwick, pers. comm.; [†] Petersen, pers. comm.
Plecoptera	<i>Leuctra nigra</i>	<i>Leuctra nigra</i>	365*	547.5*	31.5 [†]	*Zwick, pers. comm.; [†] Petersen, pers. comm.
Ephemeroptera	<i>Paraleptophlebia</i> spp.	<i>Paraleptophlebia submarginata</i>	365	365	24.5	Humpesch, pers. comm.
Diptera	<i>Zavrelymia melanura</i>	<i>Zavrelymia barbatipes</i>	365	365	<7	Morgan, 1980
Diptera	Tanypodinae	<i>Trissopelopia longimana</i> ; <i>Macropelopia nebulosa</i>	365	365	<7	Schmid, pers. comm.
Diptera	<i>Chironomus anthracinus</i>	<i>Procladius olivaceae</i>	730	730	<7	Waters, 1977
Diptera	<i>Micropsectra</i>	<i>M. bidentata</i>	365	365	<7	Schmid, pers. comm.
Diptera	<i>Stempellinella</i>	<i>Brillia modesta</i>	365	365	<7	Schmid, pers. comm.
Diptera	<i>Heterotrissocladius marcidus</i>	<i>H. marcidus</i>	365	365	<7	Morgan, 1980
Diptera	<i>Polypedilum</i> spp.	<i>P. albicorne</i> grp.	182.5	365	<7	Schmid, pers. comm.
Simuliidae	Simuliidae	<i>Simulium</i> spp.	121.7	365	—	Waters, 1977
Amphipoda	<i>Gammarus lacustris</i>	<i>Niphargus aquilex</i>	182.5	182.5	—	Morgan, 1980
Isopoda	<i>Asellus aquaticus</i>	<i>A. meridianus</i>	730	730	—	Waters, 1977
Oligochaeta	Enchytraeidae	Oligochaeta	365	365	—	Bird, 1982
Mollusca	<i>Pisidium crassum</i>	<i>Pisidium</i> spp.	547.5	547.5	—	Morgan, 1980

REFERENCES

- Allen, K.R. (1951) The Horokiwi Stream: A study of a trout population. *New Zealand Marine Dep. Fish. Bull.* **10–10a**, 1–231.
- Benke, A.C. (1993) Concepts and patterns of invertebrate production in running waters. *Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen.* **25**, 15–38.
- Benke, A.C. and Wallace, J.B. (1997) Trophic basis of production among riverine caddisflies: Implications for food web analysis. *Ecology* **78**, 1132–1145.
- Benke, A.C., Wallace, J.B., Harrison, J.W. and Koebel, J.W. (2001) Food web quantification using secondary production analysis: Predaceous invertebrates of the sang habitat in a subtropical river. *Freshwater Biol.* **46**, 329–346.
- Berlow, E.L., Neutel, A.M., Cohen, J.E., de Ruiter, P., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Jones, J.I., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M. and Petchey, O. (2004). Interaction strengths in food webs: Issues and opportunities. *J. Anim. Ecol.* **73**, 585–598.
- Bird, G.J. (1982) Distribution, life cycle and population dynamics of the aquatic enchytraeid *Propappus volki* (Oligochaeta) in an English chalkstream. *Holarctic Ecol.* **5**, 67–75.
- Closs, G.P. and Lake, P.S. (1994) Spatial and temporal variation in the structure of an intermittent stream food-web. *Ecol. Monogr.* **64**, 1–21.
- Cohen, J.E. (1978) Food webs and niche space. Monographs in Population Biology. No. 11. Princeton University Press.
- Cohen, J.E. and Newman, C.M. (1985) A stochastic theory of community food webs. I. Models and aggregated data. *Proc. Royal Soc. London B* **224**, 421–448.
- Cohen, J.E. (1989) Food webs and community structure. In: *Perspectives in Ecological Theory* (Ed. by J. Roughgarden, R.M. May and S. Levin), pp. 181–202. Princeton University Press, Princeton, NJ.
- Cohen, J.E., Jonsson, T. and Carpenter, S.R. (2003) Ecological community description using food web, species abundance, and body-size. *Proc. Natl. Acad. Sci. USA* **100**, 1781–1786.
- Cohen, J.E., Pimm, S.L., Yodzis, P. and Saldaña, J. (1993b) Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.* **62**, 67–78.
- Cohen, J.E., Beaver, R.A., Cousins, S.H., DeAngelis, D.A., Goldwasser, L., Heong, K.L., Holt, R.D., Kohn, A.J., Lawton, J.H., Martinez, N., O'Malley, R., Page, L.M., Patten, B.C., Pimm, S.L., Polis, G.A., Rejmánek, M., Schoener, T.W., Schoenly, K., Sprules, W.G., Teal, J.M., Ulanowicz, R.E., Warren, P.H., Wilbur, H.M. and Yodzis, P. (1993a) Improving food webs. *Ecology* **74**, 252–258.
- de Ruiter, P.C., Neutel, A.M. and Moore, J.C. (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* **269**, 1257–1260.
- Dobson, M. and Hildrew, A.G. (1992) A test of resource limitation among shredding detritivores in low order streams in southern England. *J. Anim. Ecol.* **61**, 69–77.
- Elton, C. S. (1927) *Animal ecology*. Sedgwick and Jackson, London.
- Elser, J.J. and Urabe, J. (1999) The stoichiometry of consumer-driven nutrient recycling: Theory, observations and consequences. *Ecology* **80**, 735–751.
- Emmerson, M.C. and Raffaelli, D.G. (2004) Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* **73**, 399–409.
- Goldwasser, L. and Roughgarden, J. (1997) Sampling effects and the estimation of food web properties. *Ecology* **78**, 41–54.

- GraphPad Software Inc. (2000) *GraphPad Prism Version 3.0*. GraphPad Software Inc., 5755 Oberlin Drive #110, San Diego, CA 92121, USA.
- Hall, R.O., Wallace, J.B. and Eggert, S.L. (2000) Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* **81**, 3445–3463.
- Hall, S.J. and Raffaelli, D. (1993) Food webs: Theory and reality. *Adv. Ecol. Res.* **24**, 187–239.
- Hildrew, A.G. (1992) Food webs and species interactions. In: *The Rivers Handbook* (Ed. by P. Calow and G.E. Petts), pp. 309–330. Blackwell Sciences, Oxford.
- Hildrew, A.G. and Townsend, C.R. (1976) The distribution of two predators and their prey in an iron-rich stream. *J. Anim. Ecol.* **45**, 41–57.
- Hildrew, A.G. and Townsend, C.R. (1977) The influence of substrate on the functional response of *Plectrocnemia conspersa* (Curtis) larvae (Trichoptera: Polycentropodidae). *Oecologia* **31**, 21–26.
- Hildrew, A.G. and Townsend, C.R. (1982) Predators and prey in a patchy environment: A freshwater study. *J. Anim. Ecol.* **51**, 797–815.
- Hildrew, A.G., Townsend, C.R. and Hasham, A. (1985) The predatory Chironomidae of an iron-rich stream: Feeding ecology and food web structure. *Ecol. Entomol.* **10**, 403–413.
- Hildrew, A.G., Woodward, G. Winterbottom, J.H. Orton, S. (2004) Strong density-dependence in a predatory insect: Larger scale experiments in a stream. *J. Anim. Ecol.* **73**, 448–458.
- Hynes, H.B.N. (1977) A key to the adults and nymphs of the British Stoneflies (Plecoptera). Titus Wilson & Son, Kendal, UK.
- Lancaster, J. (1996) Scaling the effects of predation and disturbance in a patchy environment. *Oecologia* **107**, 321–331.
- Lancaster, J. and Hildrew, A.G. (1993) Flow refugia and the microdistribution of lotic macroinvertebrates. *J. N. Am. Benthol. Soc.* **12**, 385–393.
- Lancaster, J. and Robertson, A.L. (1995) Microcrustacean prey and macroinvertebrate predators in a stream food web. *Freshwater Biol.* **34**, 123–134.
- Lancaster, J., Hildrew, A.G. and Townsend, C.R. (1991) Invertebrate predation on patchy and mobile prey in streams. *J. Anim. Ecol.* **60**, 625–641.
- Ledger, M.E. (1997) *Grazing of biofilm by invertebrates in streams of contrasting pH*. PhD Thesis. Queen Mary and Westfield College, University of London.
- MacArthur, R. H. (1955) Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–536.
- Martinez, N.D. (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web *Ecol. Monogr.* **61**, 367–392.
- Martinez, N.D., Hawkins, B.A., Dawah, H.A. and Feifarek, B.P. (1999) Effects of sampling effort on characterization of food-web structure. *Ecology* **80**, 1044–1055.
- May, R.M. (1972) Will a large complex system be stable? *Nature* **238**, 413–414.
- May, R.M. (1973) *Stability and Complexity in Model Ecosystems*. (Princeton University Press).
- McCann, K.S. (2000) The diversity-stability debate. *Nature* **405**, 228–233.
- McCann, K., Hastings, A. and Huxel, G.R. (1998) Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.
- Morgan, N.C. (1980) Secondary production. In: *The Functioning of Freshwater Ecosystems* (Ed. by E. D. LeCren and Lowe-McConnell), Cambridge University Press, Cambridge, U.K.
- Paine, R.T. (1988) On food webs: Road maps of interactions or the grist for theoretical development? *Ecology* **69**, 1648–1654.

- Paine, R.T. (1992) Food web analysis through field measurements of per capita interaction strength. *Nature* **355**, 73–75.
- Petchey, O.L. (2000) Prey diversity, prey composition, and predator population stability in experimental microcosms. *J. Anim. Ecol.* **69**, 874–882.
- Pimm, S. L. (1980) Properties of food webs. *Ecology* **61**, 219–225.
- Pimm, S.L. (1982) *Food webs*. Chapman and Hall, New York.
- Polis, G.A. (1991) Complex trophic interactions in deserts: An empirical critique of food web theory. *Am. Nat.* **138**, 123–155.
- Polis, G.A. (1994) Food webs, trophic cascades and community structure. *Austral. J. Ecol.* **19**, 121–136.
- Polis, G.A. (1998) Stability is woven by complex webs. *Nature* **395**, 744–745.
- Polis, G.A., Myers, C.A. and Holt, R.D. (1989) The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Ann. Rev. Ecol. Systemat.* **20**, 297–330.
- Power, M.E. (1990) Effects of fish in river food webs. *Science* **250**, 811–814.
- Raffaelli, D. and Hall, S.J. (1996) Assessing the relative importance of trophic links in food webs. In: *Food Webs: Integration of Patterns and Dynamics* (Ed. by G.A. Polis and K.O. Winemiller), pp. 185–199. Chapman and Hall, New York.
- Rundle, S.D. (1988) *The micro-arthropods of some southern English streams*. PhD thesis. Queen Mary and Westfield College, (University of London).
- Schmid, P. E., Tokeshi, M. and Schmid-Araya, J. M. (2000) Relationship between population density and body size in stream communities. *Science* **289**, 1557–1560.
- Schmid-Araya, J.M., Hildrew, A.G., Robertson, A., Schmid, P.E. and Winterbottom, J.H. (2002a) The importance of meiofauna in food webs: Evidence from an acid stream. *Ecology* **83**, 1271–1285.
- Schmid-Araya, J.M., Schmid, P.E., Robertson, A., Winterbottom, J.H., Gjerlv, C. and Hildrew, A.G. (2002b) Connectance in stream food webs. *J. Anim. Ecol.* **71**, 1062.
- Slansky, F. and Scriber, J.M. (1982) Selected bibliography and summary of quantitative food utilization by immature insects. *Bull. Entomol. Soc. Am.* **28**, 43–55.
- Smith, L.C. and Smock, L.A. (1992) Ecology of invertebrate predators in a Coastal Plain stream. *Freshwater Biol.* **28**, 319–329.
- Smock, L.A. and Roeding, C.E. (1986) The trophic basis of production of the macroinvertebrate community of a southeastern USA blackwater stream. *Holarctic Ecol.* **9**, 165–174.
- Speirs, D.C., Gurney, W.S.C., Winterbottom, J.H. and Hildrew, A.G. (2000) Long-term demographic balance in the Broadstone Stream insect community. *J. Anim. Ecol.* **69**, 45–58.
- Stead, T.K., Schmid-Araya, J.M. and Hildrew, A.G. (in press) Meiofauna and the secondary production of a stream metafoam community. *Limnol. Oceanogr.* **50**, 398–403.
- Strayer, D. and Likens, G.E. (1986) An energy budget for the zoobenthos of Mirror Lake, New Hampshire. *Ecology* **67**, 303–313.
- Sugihara, G., Bersier, L. F. and Schoenly, K. (1997) Effects of taxonomic and trophic aggregation on food web properties. *Oecologia* **112**, 272–284.
- Tavares-Cromar, A.F. and Williams, D.D. (1996) The importance of temporal resolution in food web analysis – evidence from a detritus-based stream. *Ecol. Monogr.* **66**, 91–113.

- Thompson, R.M. and Townsend, C.R. (1999) The effect of seasonal variation on the community structure and food web attributes of two streams: Implications for food web science. *Oikos* **87**, 75–88.
- Tokeshi, M. (1999) *Species Coexistence: Ecological and Evolutionary Perspectives*. Blackwell Science.
- Townsend, C.R. and Hildrew, A.G. (1977) Predation strategy and resource utilization by *Plectrocnemia conspersa* (Curtis) (Trichoptera: Polycentropodidae). Proceedings of the 2nd International Symposium on Trichoptera, Junk, The Hague.
- Townsend, C.R. and Hildrew, A.G. (1979) Resource partitioning by two freshwater invertebrate predators with contrasting foraging strategies. *J. Ani. Ecol.* **48**, 909–920.
- Townsend, C.R., Thompson, R.M., McIntosh, A.R., Kilroy, C., Edwards, E. and Scarsbrook, M. (1998) Disturbance, resource supply, and food web architecture in streams. *Ecol. Lett.* **1**, 200–209.
- Warren, P.H. (1989) Spatial and temporal variation in the structure of a freshwater food web. *Oikos* **55**, 299–311.
- Warren, P.H. (1996) Structural constraints on food web assembly. In: *Aspects of the Genesis and Maintenance of Biological Diversity* (Ed. by M.E. Hochberg, J. Clobert and R. Barbault), pp. 142–161. Oxford University Press, Oxford, U.K.
- Warren, P.H. and Lawton, J.H. (1987) Invertebrate predator-prey body-size relationships: An explanation of upper triangularity in food webs and patterns in food web structure. *Oecologia* **74**, 231–235.
- Waters, T.F. (1977) Secondary production in inland waters. *Adv. Ecol. Res.* **10**, 91–164.
- Wilcock, H.R., Hildrew, A.G. and Nichols, R.A. (2001) Genetic differentiation of a European caddisfly: Past and present gene flow among fragmented larval habitats. *Mol. Ecol.* **10**, 1821–1834.
- Williams, R.J. and Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature* **404**, 180–183.
- Winemiller, K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* **60**, 331–367.
- Winterbottom, J.H., Orton, S.E. and Hildrew, A.G. (1997) Field experiments on the mobility of benthic invertebrates in a southern English stream. *Freshwater Biol.* **38**, 37–47.
- Winterbourn, M.J., Rounick, J.S. and Hildrew, A.G. (1986) Patterns of carbon resource utilization by benthic invertebrates in two British river systems. *Archiv für Hydrobiologie* **107**, 349–361.
- Woodward, G. and Hildrew, A.G. (2001) Invasion of a stream food web by a new top predator. *J. Ani. Ecol.* **70**, 273–288.
- Woodward, G. and Hildrew, A.G. (2002a) Food web structure in riverine landscapes. *Freshwater Biol.* **47**, 777–798.
- Woodward, G. and Hildrew, A.G. (2002b) Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Ani. Ecol.* **71**, 1063–1074.
- Woodward, G. and Hildrew, A.G. (2002c) Differential vulnerability of prey to an invading top predator: Integrating field surveys and laboratory experiments. *Ecol. Entomol.* **27**, 732–744.
- Woodward, G. and Hildrew, A.G. (2002d) The impact of a sit-and-wait predator: Separating consumption and prey emigration. *Oikos* **99**, 409–418.
- Woodward, G., Jones, J.I. and Hildrew, A.G. (2002) Community persistence in Broadstone Stream (U.K.) over three decades. *Freshwater Biol.* **47**, 1419–1435.

- Woodward, G., Thompson, R., Townsend, C.R. and Hildrew, A.G. (in press) Pattern and process in food webs: Evidence from running waters. Chapter 16. In *Aquatic Food Webs: An Ecosystem Approach*. (Ed. by A. Belgrano, U. Scharler, J. Dunne and B. Ulanowicz). Cambridge University Press.
- Wootton, J.T. (1997) Estimates and tests of *per capita* interaction strength: Diet abundance and impact of intertidally foraging birds. *Ecol. Monogr.* **67**, 45–64.
- Wootton, J. T., Parker, M. S. and Power, M. E. (1996) The effect of disturbance on river food webs. *Science* **273**, 1558–1561.
- Yodzis, P. (1988) The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* **69**, 508–515.
- Yodzis, P. (1998) Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *J. Ani. Ecol.* **67**, 635–658.