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THE IMPORTANCE OF TEMPORAL RESOLUTION IN FOOD WEB ANALYSIS: EVIDENCE FROM A DETRITUS-BASED STREAM¹

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Abstract. A series of time-specific food webs for the macroinvertebrate riffle community of Duffin Creek, Ontario was constructed using dietary information obtained from the analysis of gut contents. Trophic links were quantified using a dietary index of relative importance. Precision of the analysis was maintained at a high level by: (1) identifying dietary items as accurately as possible via direct gut analysis; (2) identifying web members to the species level, thus avoiding the taxonomic aggregation and lumping of size classes common in food web analyses; and (3) ensuring temporal resolution of the web by determining ontogenic variation in the diets of dominant members of the community.

The Duffin Creek webs are heavily detritus-based with a large proportion of top-to-basal, and intermediate-to-basal links. Top-to-basal links, proportions of top and intermediate species, and lower connectance (0.180–0.219) varied temporally. Trophic connectance ranged from 0.090 to 0.109, consistent with values expected for a web consisting largely of specialist feeders. Weak links made up the largest proportion of total links in the webs, whereas very strong links made up the smallest proportion. Omnivory was more common than indicated in other webs and can be attributed to ontogenic diet switching.

Comparison of the statistics for a summary web with those generated for the time-specific webs indicated that the total number of links per web, total number of species, number of top and intermediate species, and linkage density were much greater for the summary web. In view of these differences, the importance of temporal resolution when assessing food web structure and dynamics is emphasized. The possibility that some of the observed features in our web are common to other detritus-based webs is considered. Future studies of this calibre are justified.

Key words: aquatic macroinvertebrates; detritus-based; fresh water; life history omnivory; ontogenic diet switching; riffle community; temporal resolution; time-specific food webs.

INTRODUCTION

This study of food web structure is considered to be important to the understanding of ecosystem function (Pimm 1982). In the last decade, food webs have been approached from a theoretical aspect, with emphasis on food web structure and the constituent patterns (Pimm and Rice 1987, Schoener 1989). Food web theory indicates that complex web interactions are not random, but highly patterned and limited by simple biological processes, namely dynamic and energetic constraints, and the structural design of animals (Pimm 1982, Yodzis 1989). Pimm (1982) has identified 12 patterns of food web design, some of which may be non-independent. Analyses of previously published webs have revealed common features, even among webs from different habitats with widely varying species numbers (Sugihara et al. 1989). However, limitations in the collection of data used for these analyses and results from recent analyses (Winemiller 1990, Martinez 1991, Polis 1991, Paine 1992) have cast doubt on these putative common food web features and their validity (Pimm et al. 1991, Polis 1991).

Early food web studies often focused on a small subset of species from an entire community ("species-specific webs"; e.g., Hardy 1924, Paine 1966, Birke-land 1974, Hildrew et al. 1985). Although these studies provide important dietary information for specific members of an assemblage, they are of limited use in the assessment and/or development of food web theory at the community level. Since food webs are a community phenomenon, food web data sets should be community based. However, even community webs are plagued with inconsistencies, which include poor taxonomic resolution, inconsistent trophic accuracy (direct vs. implied trophic information), and poor quantification of links, all of which may bias the resulting food web statistics (Paine 1988, Lawton 1989, Sugihara et al. 1989, Hall and Raffaelli 1991, Martinez 1991, Pimm et al. 1991, Polis 1991). Recently, Cohen et al. (1993) proposed a list of recommendations to standardize food web analysis and make it more comparable with other studies. Their suggestions address many of the shortcomings of previous web studies and call for "more explicitness and more exhaustiveness."

Another important aspect of food web studies that has largely been ignored of late is temporal resolution. Perhaps the greatest impediment to understanding food

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web dynamics thus far has been the use of *static* “summary webs” (sensu Kitching 1987) to study the *dynamic* aspects of food webs. Although the analysis of summary webs is useful (see Kitching 1987), the spatial and temporal aspects of an otherwise dynamic system are obscured. Few studies have incorporated the spatial/temporal aspects of food webs (Kitching 1987, Warren 1989, Lockwood et al. 1990, Schoenly and Cohen 1991, Closs and Lake 1994). Incorporation of this temporal dimension is particularly important in clarifying size-, age-, and ontogenic-related changes in diet, and how these may affect food web structure and dynamics, as well as contributing to the compilation of good databases (Paine 1988, Lawton 1989, Polis 1991). This was recognized as early as 1924 when Hardy included diet switching in his North Sea herring study. Although dietary changes have been documented in other studies (e.g., Shapas and Hilsenhoff 1976, Short 1983, Chow-Fraser 1986), they have not been extensively incorporated into food web studies. It is not clear why temporal dietary changes have been overlooked, especially as their importance was acknowledged >70 yr ago; likely, the task of including different life cycle stages has proved intimidating.

Data on the trophic relations of aquatic macroinvertebrates in streams are extensive but, because most of these studies have focused on a limited number of species, few complete community food webs have been constructed for freshwater invertebrate communities. The aquatic insect riffle community is an ideal system for the study of food webs because it can be sampled relatively easily and efficiently and generation times are fast, allowing for a large amount of information to be obtained over a reasonable period of time.

This study presents detailed dietary information on an entire macroinvertebrate riffle community in a small river in east-central Canada in the form of a series of time-specific food webs. This temporal approach not only provides insight into the dynamics of food webs but also contributes to our understanding of community structure and function of a detritus-based stream ecosystem. Both pictorial representations and food web matrices are included since the former clearly summarize the trophic links visually while matrices facilitate the calculation of food web statistics. We have attempted to abide by the suggestions proposed by Cohen et al. (1993) so that our food web may be compared with others of similar scale, with similar ecological parameters, and with data collected in a similar fashion. In reporting our food web we clearly define the setting and scale by reporting environmental parameters (such as substrate type, riffle size, depth, current speed, water temperature, and surrounding vegetation). A rigorous sampling regime ensured complete representation of community members. Members of each web were identified to species and lumping of species was avoided wherever possible. We assessed trophic relations and diets through detailed gut analysis and treated different

size classes within a species as distinct web units in order to more realistically assess ontogenic diet switching. Trophic links were quantified using a dietary index of importance. Commonly applied food web statistics have been calculated and these are compared temporally and, where applicable, with those of previously published webs.

MATERIALS AND METHODS

The study site

The study was conducted on two riffles on the east branch of Duffin Creek, a third order stream in Durham County, Ontario (43°58' N, 79°05' W). The substrate in both riffles consisted of mixed sand and gravel with clay patches overlain with flat cobbles ≤ 20.0 cm in diameter (Williams 1982). The downstream riffle was 7.3×17.4 m. Throughout the sampling period, the mean depth was 22.9 cm (range: 16.3–34.3 cm) and the mean current speed was 0.54 m/s (range: 0.09–1.2 m/s). The upstream riffle was 6.3×10.1 m. The mean depth was 22.3 cm (range 17.0–31.0 cm) and the mean current speed was 0.55 m/s (range 0.12–1.4 m/s). Yearly minimum and maximum water temperatures were 0° and 21.1°C, respectively. Bankside vegetation consisted of eastern white cedar (*Thuja occidentalis* L.), eastern white pine (*Pinus strobus* L.) mixed with willow (*Salix* sp.), and largetooth aspen (*Populus gradidentata* Michx.).

Sampling and gut analysis

Samples were taken monthly for 14 mo from **October 1985 to November 1986**. Potential food resources were determined by sampling the water column, rock surfaces, and upper hyporheic zone, defined as the upper 10.0 cm of the substrate (Tavares and Williams 1990). On each occasion, five benthic samples were taken randomly from each riffle using a Mundie sampler of ≈ 0.06 m² area, fitted with a 53.0- μ m mesh net (Mundie 1971). The substrate within the sampler was disturbed to a depth of 6.0–8.0 cm. Large stones were wiped clean in the sampler and then removed. All animals clinging to the sides of the net were carefully rinsed to the bottom and the samples were immediately transferred to glass jars and preserved with full strength formalin to ensure good fixation of gut material.

In the laboratory, each benthic sample was rinsed with tap water in a 53.0- μ m net and drained to remove excess water. The samples were suspended in a saturated solution of CaCl₂ to separate organic and inorganic components. The supernatant was decanted through a 53.0- μ m net and the residue was resuspended four more times to ensure that all organic and inorganic material had been separated. The final fraction was rinsed in tap water, subsampled to one half using a compartmentalized air-driven subsampler, and stored in 70% ethanol.

The subsamples were subsequently hand-sorted us-

ing a stereomicroscope. Animals were identified to the species level (genus, if species identifications were not possible) and enumerated. Chironomidae were identified after mounting head capsules and decapitated bodies in Canada Balsam on a microscope slide. Pupae were identified after mounting in a drop of 70% ethanol or glycerol. Size classes were determined by randomly selecting ≤ 100 specimens of each taxon (if available) and measuring head capsule widths with an ocular micrometer.

Ten representatives of each taxon, from the monthly modal size class, were chosen at random and used for gut analysis. All animals were cleaned of any surface debris by rinsing in distilled water prior to dissection. Animals < 1.0 cm in length were placed in a small Petri dish with distilled water, decapitated, and squeezed along the length of the body until the gut was empty. Any body parts that may have fallen off during this process were removed. The gut contents were then dispersed by sonication in an E/MC ultrasonic cleaner for 30–60 s. Gut contents were then filtered onto 0.45- μ m gridded filters (cellulose acetate; Millipore Corporation, Bedford, Massachusetts). Animals > 1.0 cm in length were dissected under distilled water by slitting the body ventrally from the neck to the anus, removing the gut, and teasing out the gut contents. Pieces of the animal itself and/or gut wall were removed before filtering. The filters were cleared, mounted, and enumerated as described by Tavares and Williams (1990). Care was taken to identify chitinous parts in the gut to genus by comparing them with whole mounts made of the potential prey of the appropriate size classes. However, this often proved difficult when chitinous pieces were very small. In this case, and when chitinous pieces were clearly not associated with detritus, they were characterized as “chitin fragments.” Similarly, chironomid body parts were often identified in the guts, but it was difficult to discern the species to which they belonged. In this case, these pieces were classified as “chironomids.” Finally, any soft body parts of questionable origin were categorized as “soft body parts” and included in the intermediate species category.

The data collected from the gut analysis were used to compile a series of time-specific food webs, one for each sampling date for the Duffin Creek macroinvertebrate riffle community. Additionally, the following food web statistics were calculated: (1) the number of top, basal, and intermediate species, and associated links; (2) the predator–prey ratio; (3) connectance; and (4) connectivity.

Food web and analysis

Pictorial overview and index of relative importance.—Pictorial representations of the time-specific food webs for Duffin Creek were compiled using the data obtained from the gut analyses. Arrows point from consumer to resource and the thickness of the lines represents the relative importance of the resource in

the diet of the consumer (thickest lines indicate the most important resource). We have used the index of relative importance (IRI) of Pinkas et al. (1971) to quantify trophic links in terms of dietary importance:

$$\text{IRI} = (\%N + \%V) \times \%FO$$

where %N = the numerical percentage of a food type in the gut; %V = the volumetric percentage a food type occupies in the gut; and %FO = the percentage frequency of occurrence of a particular food type (i.e., the number of guts in which a particular food type appeared). The higher the IRI value, the more important the food item in the diet. Since the term “importance” can be ambiguous in this context, a definition is obligatory. In this study, the importance of a food type denotes the amount and bulk of the particular food item in the gut (Hyslop 1980). Although this type of compound index has been criticized (MacDonald and Green 1983) the IRI is useful for descriptive and comparative dietary studies. Combining %N, %V, and %FO (measures often used independently) reduces the inherent biases of each. This is especially important when the prey items ingested are of different sizes and represent many prey types (MacDonald and Green 1983). The IRI is thus a more representative measure of dietary importance than can be achieved by using numerical, volumetric, or frequency of occurrence measures alone (Hyslop 1980). Furthermore, it is important to note that our links are quantified via direct trophic analysis rather than by manipulation like those of Paine (1980, 1992).

Four levels of trophic interactions were recognized: (1) very strong, where IRI values were $> 10\,000$; (2) strong, where IRI values ranged from 2000 to 10000; (3) moderate, where IRI values ranged from 500 to 2000; and (4) weak, where IRI values ranged from 1 to 500.

Food web matrix.—Food web (predation) matrices (Cohen et al. 1990) were constructed for each sampling period. Species integrity was conserved by not lumping taxa into “trophic species.” Furthermore, different size classes were treated as individual species so as not to obscure differences in diets due to ontogenic diet switching.

“Species” composition and link proportions.—Top, intermediate, and basal species were determined using the definitions of Briand and Cohen (1984). Top species are fed upon by nothing else in the web, intermediate species eat other species and are themselves eaten, and basal species “feed” on nothing in the web. Classification of web species as top, intermediate, and basal has become standard in many food web studies. Not only does this classification convey topological information (web shape) but also general functional information such as the general trophic roles assumed by the web members. Furthermore, if one examines a web temporally, information on the changing trophic roles can be assessed. The number and proportion of top-to-basal links, intermediate-to-top links, intermediate-to-

intermediate links, and intermediate-to-basal links (Pimm et al. 1991) were determined for each food web. Relative strengths of the different links and their distribution were examined also. The total number of links in each web was determined from the appropriate food web matrix.

Predator-prey ratio.—The predator-prey ratio is the ratio of the number of kinds of predators to the number of kinds of prey. The predator-prey ratio was calculated after Jefferies and Lawton (1985) as:

$$\frac{\text{number of predator species}}{\text{number of prey species}},$$

where the prey species are detritivores, herbivores, and fungivores and the predator species are those eating other invertebrates.

Connectance and connectivity.—Connectance is a measure of system complexity (Pimm 1982) or, simply put, the degree to which the species in the web interact. Two connectance values were calculated for comparison with those found in the literature: lower connectance and trophic connectance. Because we had trophic data taken from direct gut observation, trophic connectance was an appropriate measure. Trophic connectance (Warren 1989) is simply the number of links in the web divided by the possible number of interspecific interactions:

$$C_T = L/S(S - 1).$$

Lower connectance represents the actual number of interspecific interactions divided by the possible number of interspecific interactions (Pimm 1982) and is defined as:

$$C_L = L/2/S(S - 1),$$

where L is the total number of links in the web (from the food web matrix) and S is the total number of species. This definition does not take into account potential competitive interactions. It is equivalent to the connectance values defined by Rejmanek and Stary (1979), Yodzis (1980), and Briand (1983). Martinez (1991) refers to lower connectance as "interactive connectance." We chose not to use upper connectance, which is often used in studies that have examined competitive interactions between species as, from our data set, we could not prove the potential for competition among the Duffin Creek species.

Linkage density was calculated as the measure of connectivity. It is simply the total number of links in the web divided by the total number of species (Pimm et al. 1991).

RESULTS

The similarity of substrate composition, current speed, temperature, potential food, and the species assemblage and composition in both riffles in Duffin Creek (Williams 1982) allowed us to group the dietary results from each riffle for each sampling period. This

dietary information was used to construct time-specific food webs for the duration of the study. A summary food web was also constructed and accompanying food web statistics were calculated for comparison with the time-specific webs.

Potential food

In Duffin Creek, detritus was the most abundant potential food type in the water column and on the rock surfaces. It was the second most abundant potential food type in the upper hyporheic zone. Micro-inorganic particles (MIP), primarily sand grains, are classified as a potential food type because they have a micro-flora and -fauna associated with them and thus, may have some nutritional value in addition to aiding mechanical breakdown of food in the gut. Micro-inorganic particles were the second most abundant potential food type in the water column. On the rock surfaces, the number of MIP was lower but they were very abundant in the upper hyporheic zone. Diatoms were most abundant on the rock surfaces, with some seasonal variability. In the water column, they were present in small but constant proportions. Diatoms were uncommon in the upper hyporheic zone. Other potential food sources such as fungal hyphae and spores, vascular plant material, other algae (unicellular and filamentous), and chitin fragments were rare in the samples (for a detailed account of the potential food sources in Duffin Creek see Tavares and Williams 1990). The potential food in the strata of Duffin Creek are summarized in Fig. 1.

Species analysis

The assemblage of macroinvertebrates depicted in the Duffin Creek food webs represents 91% of all the taxa sorted from the benthic samples. Three chironomids, *Microtendipes ?pedellus*, *Micropsectra* sp., and an unidentified orthoclad were not included in the food web as they were too scarce to provide sound gut analyses. Copepods were not found in the benthic samples nor in any of the guts, although they do occur in depositional areas (pools) of the stream.

The conventional three categories of basal, intermediate, and top species were used to classify web members. Basal "species" included decomposing organic material and its associated microorganisms which we defined as detritus, micro-inorganic material and associated microorganisms (MIP), and vascular plant material. Three general categories: diatoms, "other algae," and fungal material (hyphae and spores) were also designated basal "species." Detritus was the most heavily exploited of all the basal "species" and micro-inorganic particles were also common in all gut contents. Vascular plant material was scarcely found in the guts and was ranked low by the IRI. Diatoms, although present in substantial amounts on the rock surfaces, were not heavily exploited. Diatoms ranked low in terms of overall importance with a few exceptions (Appendix II). Of the total of 154 diatom links in the food

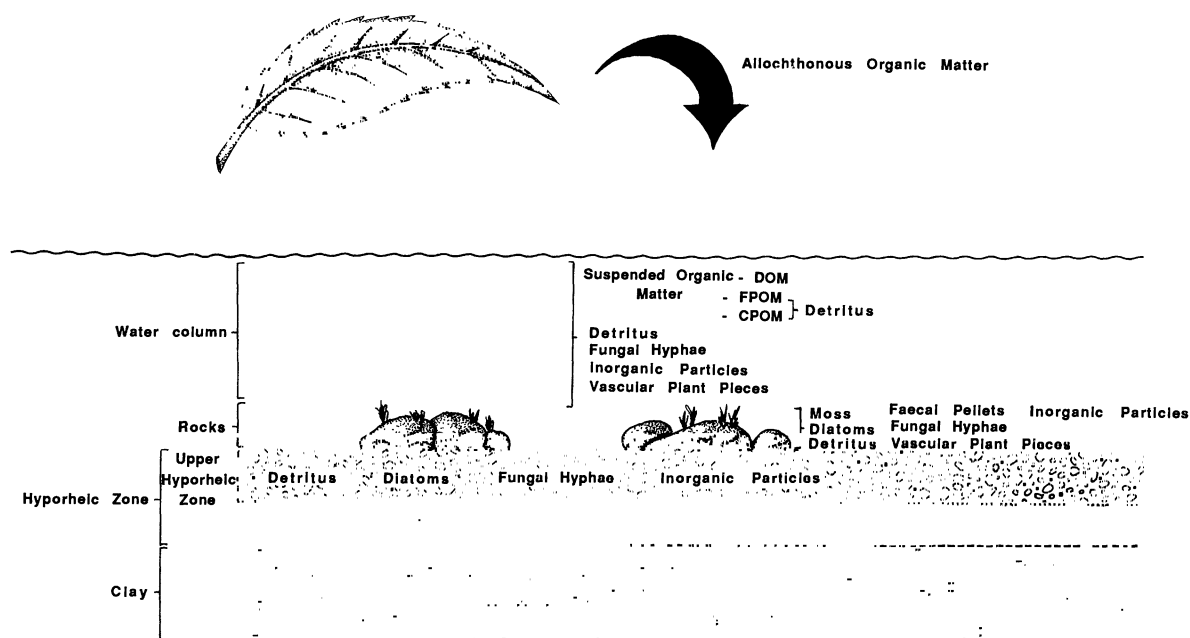


FIG. 1. Summary of the potential food sources in the strata of Duffin Creek. DOM, dissolved organic matter; FPOM, fine particulate organic matter; CPOM, coarse particulate organic matter.

webs, 5% were strong trophic interactions (as classified by IRI), 10% were moderate, and 85% were weak. This predominance of weak diatom–consumer trophic interactions was one reason we grouped all diatoms ingested into one category. Two other reasons for retaining one category for diatoms are, firstly, a substantial number of diatoms were fragmented (almost exclusively restricted to caddisfly guts), thus identification to the genus level was difficult and irresolute; secondly, even when a variety of diatoms was ingested, one species typically predominated (Fig. 2). Other algae (a combined category of rarely encountered unicellular and filamentous algae) also ranked low by the IRI as they made up a very small part of the diet. Fungal material was found in the guts more frequently than indicated in other studies (see Koslucher and Minshall 1973, Gray and Ward 1979) but it was not as heavily exploited as detritus or MIP. IRI values for all food types and species examined are given in Appendix I. Because this is an invertebrate community web and fishes were not included, it is important to realize that the top species, in this case, refers to the top invertebrate species. The trophic significance of fishes and how they may contribute to the structure of this food web is difficult to assess. Fishes were never collected in our samples, but suckers and dace are encountered with moderate frequency in other areas of Duffin Creek. Generally, top invertebrate species consisted of the stoneflies, caddisflies, elmids beetles, and the mayfly *Paraleptophlebia adoptiva*. In February 1986, April 1986, and August 1986, the chironomids were included as top species as there were no large stoneflies or caddisflies consuming them. Although most mayflies

switched between top and intermediate species, *P. adoptiva* was never found in the guts of other web members.

The total number of species in the webs ranged from 31 to 39 throughout the sampling period. Top and intermediate species proportions varied temporally throughout the sampling period but the proportion of basal species varied little (0.15–0.19), although the number of basal species (six) remained constant. This small range in the proportion of basal species was seen also in dung food webs (0.02–0.03; Valiela 1974) and the pond webs studied by Warren (1989; 0.04–0.08 in open ponds and 0.03–0.05 in margins of ponds). Proportions of basal species in the carrion webs studied by McKinnerney (1977, 1978) had a greater range (0.04–0.25 and 0.05–0.33), as did those in treeholes at various sites (Kitching 1987). In Duffin Creek, the proportion of top species varied from as low as 0.36 in October 1986 to as high as 0.77 in April and 0.78 in February and August of 1986. Generally, proportions were quite constant in October 1985, December 1985, and June 1986. Top, intermediate, and basal species proportions from the summary web indicated that top species were most numerous. Other webs, from a variety of aquatic and terrestrial systems (e.g., Cohen et al. 1990) have, generally, more intermediate species than top species and few basal species. This, however, may be an artefact of poor resolution of basal species. When one looks at the proportions of top, intermediate, and basal species in Duffin Creek, with reference to one another over time, it is evident that although basal species proportions remain quite constant (0.15–0.19), top and intermediate species vary considerably. For

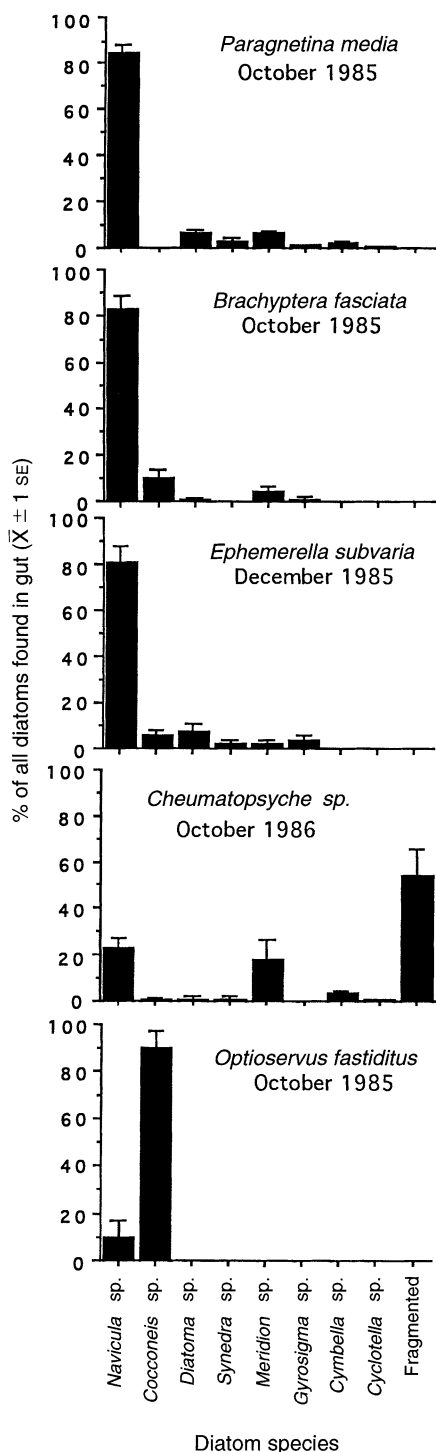


FIG. 2. Percentages of diatoms found in the guts of various insects in Duffin Creek. Note that only diatom links classified as "moderate" or "strong" were used for this comparison.

example, in October 1986 and June 1986 intermediate species proportions were slightly higher (0.43) than top species proportions (0.41). In October 1986, this difference was more pronounced (0.46 and 0.36, respectively). On the other hand, in February 1986, April 1986, and August 1986, top species proportions (0.78, 0.77, and 0.78, respectively) far exceed intermediate species proportions (0.03 for each of the three months). Table 1 summarizes commonly calculated food web statistics, such as species and link proportions, predator-prey ratios, connectance, and connectivity, as calculated for Duffin Creek.

Linkage analysis

The total number of links in the time-specific webs ranged from 101 to 146 links; there were more links (193) in the summary web. The proportion of linkages resulting from the observed trophic analysis were as follows: intermediate-to-top links (I-T), 0.05–0.07; basal-to-top links (B-T), 0.43–0.95; intermediate-to-intermediate links (I-I), 0–0.03; and basal-to-intermediate links (B-I) 0–0.47. The large number of basal-to-top and basal-to-intermediate links, coupled with the consistently large IRI values for detritus, indicate a large degree of detritus-dependence in this community. Values for link proportions in the summary web were comparable for I-I links; within, but closer to the upper range for the B-I links; closer to the lower range for the B-T links; and greater for the I-T links. Link proportions were not reported for the webs documented by Valiela (1974), McKinnerney (1977, 1978), and Kitching (1987). Link proportions calculated by Warren (1989) were done so from his summary web. When compared with link proportions from Duffin Creek's summary and time-specific webs, large differences are evident. Intermediate-to-intermediate links were far greater in Warren's web and I-T links were also substantially higher; however T-B and I-B links were lower in Warren's web than in Duffin Creek (Table 2).

The percentage of links of different strengths varied little temporally. Weak links made up the highest proportion of links in the webs (42–52%); very strong and moderate links followed (20.5–25% and 17–25%, respectively) whereas strong links made up only 5–13% of total links (Fig. 3). Very strong links represented detrital links, whereas strong and moderate links represented MIP and in some cases, other invertebrates. Weak links were associated with fungal material, diatoms, vascular plant material, and chitin fragments. These link distributions suggest that although detritus was the primary food source eaten, a wide variety of supplementary foods was being ingested.

Predator-prey ratio

The predator-prey ratio (Jefferies and Lawton 1985) ranged from 0.00 to 0.07 for the temporal webs. Zero values correspond to instances when no invertebrate predators were present. The predator-prey ratio for the

TABLE 1. Food web statistics as calculated for the Duffin Creek food webs in alternate months. Values in parentheses are proportions.

Statistic	Sampling date							Summary web
	October 1985	December 1985	February 1986	April 1986	June 1986	August 1986	October 1986	
Total number of links per web	146	110	107	102	120	101	104	193
Species proportions								
Total number of species	39	35	32	31	37	32	33	42
Top species (no.)	16 (0.41)	15 (0.43)	25 (0.78)	24 (0.77)	15 (0.41)	25 (0.78)	12 (0.36)	21
Intermediate species (no.)	17 (0.43)	14 (0.40)	1 (0.03)	1 (0.03)	16 (0.43)	1 (0.03)	15 (0.46)	15
Basal species (no.)	6 (0.15)	6 (0.17)	6 (0.19)	6 (0.19)	6 (0.16)	6 (0.19)	6 (0.18)	9
Predator-prey ratio	0.07	0.04	0	0	0.04	0	0.04	0.21
Link proportions								
Top-basal links	63 (0.43)	55 (0.50)	102 (0.95)	97 (0.95)	56 (0.47)	96 (0.95)	47 (0.45)	85
Intermediate-top links	11 (0.07)	7 (0.06)	5 (0.05)	5 (0.05)	8 (0.06)	5 (0.05)	8 (0.08)	25
Intermediate-intermediate links	4 (0.03)	0	0	0	1 (0.01)	0	0	5
Intermediate-basal links	68 (0.47)	48 (0.44)	0	0	55 (0.46)	0	49 (0.47)	78
Connectance								
Lower connectance	0.197	0.185	0.215	0.219	0.180	0.204	0.197	0.195
Trophic connectance	0.099	0.092	0.108	0.109	0.090	0.102	0.098	0.097
Connectivity								
Linkage density (L/S)	3.74	3.14	3.34	3.29	3.24	3.16	3.15	4.29

summary web was 0.21. These ratios are much lower than those obtained by Cohen (1977), Jefferies and Lawton (1985), Warren (1989), and Polis (1991).

Connectance and connectivity

Unlike species proportions and link proportions, connectance was one of the food web statistics that remained quite constant over time. Two values of connectance were calculated for Duffin Creek: lower and

trophic connectance. The lower connectance of our webs ranged from 0.180 to 0.219. Trophic connectance ranged from 0.090 to 0.109. Small variations in connectance were observed also in Warren's (1989) study at both his open site and the margin (except for one value). Lower connectance also showed great variability, overall, in Kitching's (1987) study of phytoelmata. However, in the latter study, the connectance was less variable within sites, over time, although it

TABLE 2. Food web statistics as calculated for the Duffin Creek food webs and compared with literature values of other time-specific webs.

Statistic	Source of data					
	Duffin Creek	Open pond*	Margins of pond*	Dung†	Carrion‡	Treeholes§
Total number of links per web	101–146	29–110	75–194	86–211	2–39	4–16
Total number of species	31–39	15–23	19–32	29–43	3–20	5–15
Species proportions						
Top species	0.36–0.78	0.17–0.38	0.19–0.26	0.37–0.45	0.67–0.92	0.10–0.76
Intermediate species	0.03–0.46	0.54–0.79	0.70–0.77	0.52–0.61	0–0.22	0.12–0.60
Basal species	0.15–0.19	0.04–0.08	0.03–0.05	0.02–0.03	0.05–0.33	0.29–0.43
Predator/prey ratio	0.00–0.07	0.38–0.60	0.60–1.00	1.79–2.78	0.08–0.50	0.78–0.82
Link proportions						
Top-basal links	0.43–0.95	0.01	<0.01
Intermediate-top links	0.05–0.08	0.29	0.20
Intermediate-intermediate links	0–0.03	0.51	0.69
Intermediate-basal links	0–0.47	0.18	0.09
Connectance						
Lower connectance	0.180–0.219	0.15–0.77
Trophic connectance	0.090–0.109	0.212–0.268	0.167–0.265
Connectivity						
Linkage density (L/S)	3.14–3.74

* Warren 1989.

† Valiela 1974.

‡ McKinnerney 1978.

§ Kitching 1987.

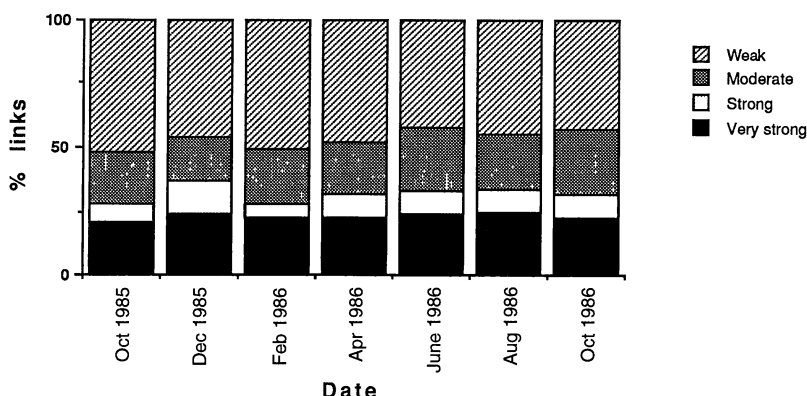


FIG. 3. Proportions of weak, moderate, strong, and very strong links in the time-specific food webs of Duffin Creek.

was still greater than observed in Duffin Creek. Both values of connectance, calculated from the summary web, fell in the middle of the ranges calculated for the time-specific webs.

The linkage densities of the Duffin Creek food webs ranged from 3.14 to 3.74. The highest linkage densities occurred in October 1985, February 1986, and April 1986.

Omnivory

Omnivory is defined as feeding on more than one trophic level. Omnivory was quite common in Duffin Creek, especially life history omnivory (also referred to as metaphoetesis in Cohen et al. 1993), defined as feeding at different trophic levels as an animal matures (Pimm and Rice 1987). The latter was observed in several of the top species: the stonefly nymphs, *Agnatina capitata* (Pictet) and *Paragnetina media* (Walker), and the caddisfly larvae *Rhyacophila fuscata* (Walker) and *Hydropsyche sparna* Ross (Figs. 4a–g).

Small *A. capitata* nymphs (head capsule width [HCW] < 2.00 mm), for example, primarily ingested detritus that was ranked highest by the IRI. Larger individuals (2.0–3.0 mm HCW) primarily ate *Baetis tricaudatus* Dodds and *Ephemerella subvaria* McDunnough nymphs, as well as chironomids and some trichopterans. Diatoms and MIP were ingested also, but in smaller quantities. Gut contents of *A. capitata* from Duffin Creek (HCW > 3.0 mm) contained up to 70% chitin (D. D. Williams and M. Yip, unpublished data). Large individuals of *Paragnetina media* have been reported as being predaceous (Tarter and Krumholz 1971, Shapas and Hilsenhoff 1976, Johnson 1981), any vegetable matter in the gut being attributed to the guts of the prey (Minckley 1963). However, small individuals in Duffin Creek (2.0 mm HCW) chiefly ate detritus; up to 94% of the gut volume of very small nymphs (0.2–0.3 mm HCW) and up to 79% of the guts of nymphs in the 1.0–2.0 mm HCW range comprised detritus. Although some chitin was found in the guts of small individuals, these were small fragments likely ingested along with the detritus. As the nymphs grew, more

recognizable chitinous pieces appeared in the guts, particularly legs of *B. tricaudatus*, legs and gills of *E. subvaria*, and larval chironomid antennae. Entire prey animals were not found in any of the guts of the smaller stoneflies examined. However, larger individuals from Duffin Creek were clearly mainly carnivorous and were capable of ingesting entire prey (D. D. Williams, unpublished data). Among the Trichoptera, *R. fuscata* exhibited diet switching. Small larvae (0.2–0.6 mm HCW) primarily ate detritus, MIP, and diatoms, plus some fragmented chitin. More animal material, as well as soft tissue (due to excavation of prey; Martin and Mackay 1982) was found in the largest larvae. Guts of *H. sparna* contained soft body parts and pieces of larval chironomid head capsules, including those of *Cricotopus* sp. and *Eukeifferiella brehmi* Thienemann. Larger larvae contained abdominal segments, legs, and gills belonging to *E. subvaria* and *B. tricaudatus*.

Ontogenic diet switching also was examined in the secondary food sources of the detritivorous species. While primary food sources, such as detritus and MIP, ranked high in importance throughout the life cycle of the detritivores, secondary food sources, such as diatoms and fungal material increased in importance in the diets of larger individuals (Appendix 1). For example, diatoms and/or fungal material ranked higher in dietary importance in larvae of *Antocha* sp. (Tipulidae) >3.0 mm in length than in smaller individuals. This trend was observed also in riffle beetle larvae, mayfly nymphs, and some of the chironomid larvae (especially *Cricotopus* sp., *Parametriocnemus* sp., and *Rheotanytarsus* sp.; Appendix 1). Ontogenic diet switching did not appear to be linked to seasonal changes in resource abundance.

DISCUSSION

A few studies have attempted to address temporal resolution in food webs. For example, Warren's (1989) consideration of spatial and temporal variation in the food web structure of a freshwater pond emphasized the dynamic nature of food webs. Kitching's (1987) study of phytotelmata, McKinnerney's (1978) studies

of treeholes, and Valiela's (1974) study of dung arthropod communities all took into account the temporal nature of food webs. Most recently, Closs and Lake (1994) have focused on the spatial and temporal resolution of an intermittent stream. More studies of this type, from a variety of habitats, are needed.

Species and link proportions

In Duffin Creek, web size exhibited little variability (total number of species per web ranging from 31 to 39) compared with the webs of Closs and Lake (1994) where the mean number of species ranged from 24 to 53, and those of Warren (1989) where the number of species ranged from 12 to 23 in the open webs and 19 to 32 in the margin webs. The large variations in the latter webs may be a factor of habitat type. The observed variation in the total number of species in the Duffin Creek webs is expected since several of the web members exhibited fast life cycles. Three species were bivoltine: *Rheotanytarsus* sp., *Baetis tricaudatus*, and *Dolophilodes distinctus* (Walker). Apart from *Paragnetina media*, *Promoresia elegans* LeConte, and *Optioservus fastiditus* (LeConte), which were semi-voltine, the rest of the species were univoltine (Tavares-Cromar 1990). The absence of several species due to life history effects accounted for changes in the total number of species in February, April, August, and October 1986. For example, *D. distinctus* was absent in February as it usually overwinters in the egg stage at this time. In April 1986, *Paracapnia angulata* Hanson nymphs emerged and *H. morosa* and *Cheumatopsyche* sp. began pupation (Rutherford and MacKay 1986). In August, *B. fasciata* was in a summer nymphal diapause; nymphs were not collected as they were buried deep in the substrate (Harper and Hynes 1970). *Agnetina capitata* oviposits in July and August; therefore, many are likely in the egg stage at this time, explaining the absence of nymphs in these samples. Large numbers of empty guts also may account for variability in web species numbers (individuals with empty guts cannot be used in gut analysis and are thus not included in the webs). Life history stage typically affects the amount of food in the gut. For example, small, newly hatched individuals are often encountered with empty guts (perhaps they have not yet begun to feed) as are very large individuals that cease feeding prior to pupation (Gillott 1980)—for example, many large, prepupal *R. fuscus* larvae were found with empty guts in April 1986. The total number of links per web followed the same pattern as the total number of species per web, probably for the same reasons.

Species proportions in Duffin Creek showed considerable variation and were very different from those observed in a variety of aquatic and terrestrial webs that were not resolved temporally (Cohen et al. 1990). The latter webs had, generally, more intermediate species than top species, and few basal species. In Duffin Creek, little variability in the proportion of basal spe-

cies is consistent with the fact that detritus and other basal food resources in Duffin Creek were not limiting and showed little seasonal variation (Tavares and Williams 1990). The dependence on detritus by a large proportion of web members is typical of other stream systems of this type (Jones 1948, Jones 1950, Chapman and Demory 1963, Koslucher and Minshall 1973, Warren 1989, Closs and Lake 1994). Detritus-dependence suggests that many of these trophic interactions are weak and therefore the system is donor-controlled (DeAngelis 1975, Pimm 1982). The size of the detritus pool further influences food web stability. Since Duffin Creek has such a large detritus pool, it should, according to DeAngelis (1975), be quite resilient.

Unlike basal species proportions, intermediate and top species showed much greater variations throughout the year, which may have been associated with life history strategy effects and life history omnivory. Top species proportions were lowest when invertebrate predators like *P. media*, *A. capitata*, and *R. fuscus* were present and feeding on mayflies and chironomids. When these predators were small (February, April, and August 1986) and no longer occupied the top species position, the number of top species increased. This was a consequence of previous intermediate species being reclassified as top species because they were no longer being preyed upon by the stoneflies or caddisfly.

Link proportions followed the same trends as the species proportions. Top-to-basal links were highest in February, April, and August. There were few I-I links and I-T links but I-B links were high except in February, April, and August. Links involving basal species were always numerous because of the great degree of detritus-dependence in the stream.

The high number of top-to-basal and intermediate-to-basal links is not unexpected in a web with such a high degree of detritus-dependence. Many web members were detritivores or otherwise supplemented their diets with detritus; however, the link proportions in Duffin Creek were quite different from those reported in the literature. Duffin Creek had a greater proportion of basal-to-intermediate and basal-to-top links, and a smaller proportion of intermediate-to-intermediate links and intermediate-to-top links, than webs examined by Cohen and Briand (1990). Top species in our web were not solely carnivorous but also exploited the detritus reserve. The many intermediate species were herbivorous; therefore, the high dependence on basal species (and thus the more T-B and I-B links) is not surprising and not likely to be an artefact of excluding fishes. The large proportion of top species seems to be a common feature of lotic webs (Schoener 1989). Schoener et al. (1991) report that many insects occupy top predator positions in webs. A large fraction of detritivores is also common in aquatic systems (Schoener 1989).

Food web trophic links can be quantified by observation or by manipulation (linkage strength; Menge and

Sutherland 1987). Paine (1980) first introduced the concept of linkage strength, which focuses on the functional role occupied by species in a food web. More recently, he reported a method for estimating per capita interaction strengths that takes into account biologically important and statistically significant influences. Based on this, predictions can be made as to the effect that a single species may have on the structure of an assemblage (Paine 1992). Duffin Creek link strengths are based on direct trophic observation rather than on manipulation.

The distribution of link strengths in Duffin Creek is consistent with a detritus-based food web. The high percentage of weak and moderate links suggests that, although detritus is the primary food source, a variety of supplementary foods are eaten also. It can be argued that these may be eaten in association with detritus, but this was not evident from the gut analysis as these supplementary foods (with the exception of fungal hyphae and some diatoms) were not found associated with the detritus. The association of MIP with links that were moderate or strong suggests that these may be important in the diet whether for mechanical breakdown of food or by virtue of their associated micro-flora and -fauna. Perhaps many of the supplementary food sources provide trace nutrients required for growth and development.

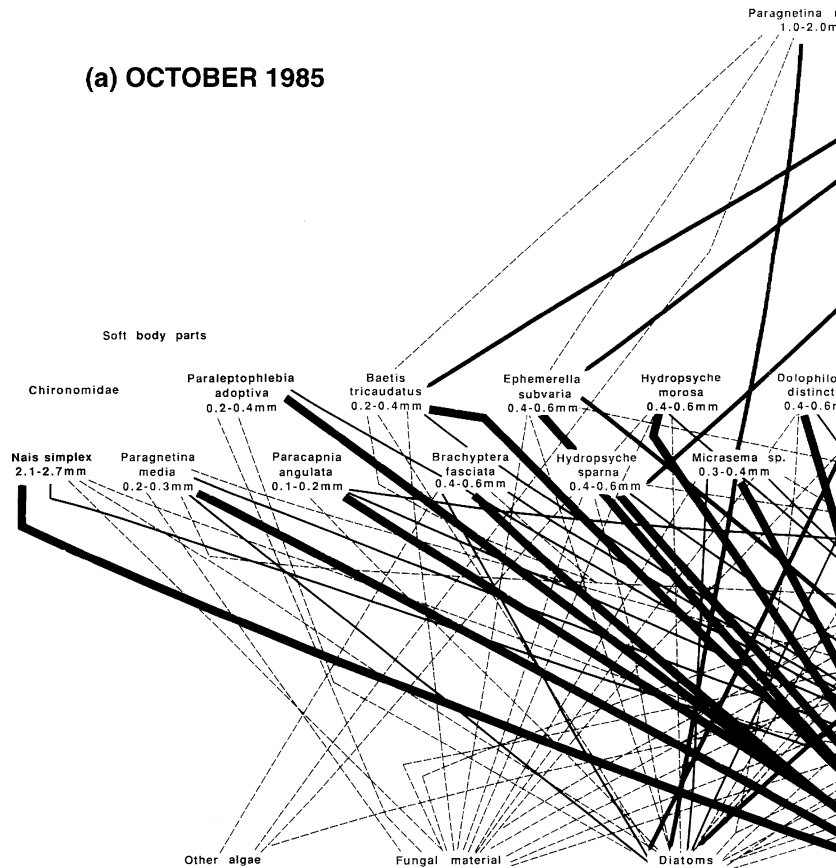
Examination of Duffin Creek's temporal food web statistics relates information not only about food web structure and dynamics but also about community structure and how temporal aspects and the biology of the web members may affect structure. The latter aspect of food web research tends to be obscured when summary web statistics exclusively are examined. There is no doubt that some ecological systems may be more affected by temporal processes than others and that food webs from certain ecological systems will be more variable. For example, a system in which generation times are fast, where diet switching is common, and where some members are present at certain times of year but not at others, will show a greater amount of variation than a system in which generation times are long, little dietary switching occurs, and the same members are always present at the same time. In the former case, a summary web would obscure many important dynamic relationships and present inaccurate information. Even in systems where a portion of the web members are long-lived, their food resources may be subject to seasonal variation—this imparts a dynamic aspect to the food web. Furthermore, there may be instances where long-lived web members are dietary generalists at certain times of year but dietary specialists at other times. One can easily see, in such a case, how the number of links would change, how species proportions may change but, especially, how link proportions would change and how these relate to the biology of the web species.

Connectance and connectivity

Because there are several measures of connectance that can be calculated, each generating values of different magnitude, caution must be exercised when comparing connectance values. Considering the number of connectance values that are available, it is difficult to assess which should be used. The most frequently cited tend to be the easiest to calculate but they may not necessarily be the most representative of a particular web. Simply put, connectance is the degree to which the species in the web interact, but there are many types of interactions to consider (e.g., trophic, defensive, and competitive). Both measures of connectance that we calculated generated low values. Low connectance values in Duffin Creek could be due to the fact that many web members were specialists, eating primarily one food type supplemented with a few other food items available to them; also, there were few carnivorous species. In addition, although few web members fed exclusively on one food item, none fed on the whole gamut present in the environment. (It is important to note that a previous analysis of the Duffin Creek community designated community members [e.g., Elmidae] as generalists; this was largely due to a shortcoming of the niche breadth index used at the time [Tavares and Williams 1990].) Since connectance is simply the degree to which species in a web interact, whether web members are generalists or specialists should be one factor which dictates how connected a web is. Our detritus-based web seems to be made up of many specialist feeders, eating large amounts of detritus. Duffin Creek carnivores typically took a small variety of species. The Duffin Creek food web matrices showed that the average number of food types eaten ranges from 4.04 to 4.86 (range: minimum 2–3; maximum 5–8) for the time-specific webs compared with 5.33 food types for the summary web (range: 3–9). Warren's (1989) matrix showed an average of 11.15 species being eaten by each consumer and a maximum of 32 food types taken by one consumer alone. This may be due to the fact that he included links from the literature, as well as links inferred from similar species, together with links established via direct observation. Thus, he may have overestimated the number of prey types eaten per species, which may have inflated his connectance values.

Connectivity would be expected to vary depending on the number of species and number of links in the web. This indeed was the case in Duffin Creek, as the summary web statistics for connectivity were quite different from those obtained from the time-specific webs. Linkage density was high in the summary web largely because both the total number of links per web and the total number of species were greater. Linkage density in Duffin Creek (3.14–3.74 and 4.29 for the time-specific and summary webs, respectively) was comparable

(a) OCTOBER 1985



(c) FEBRUARY 1986

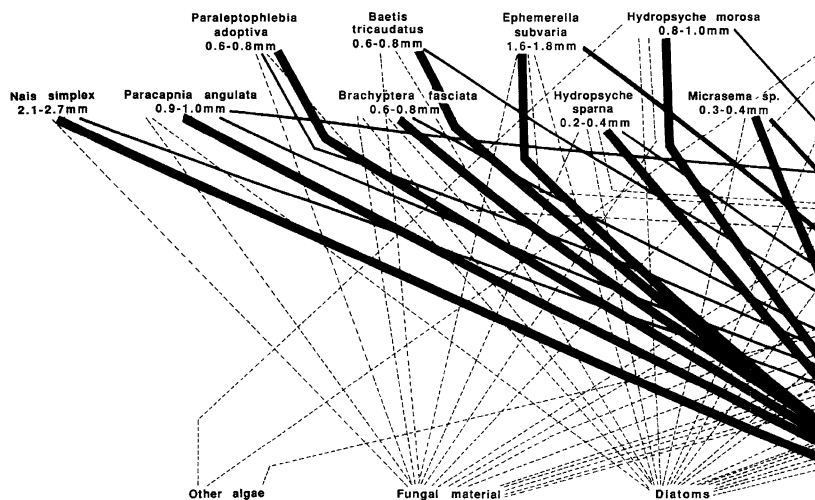
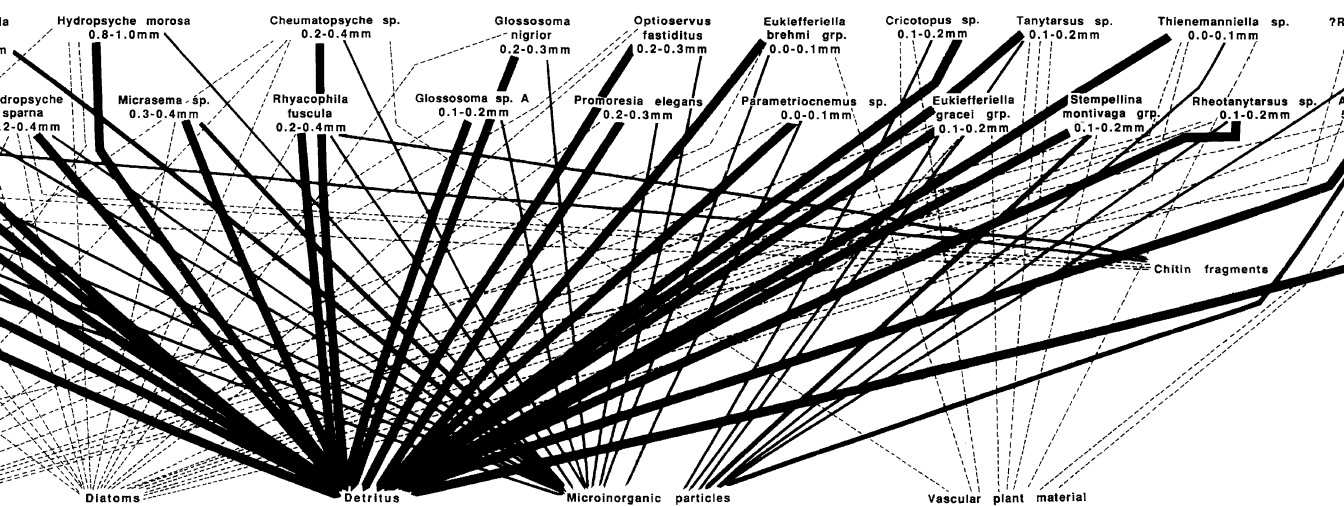
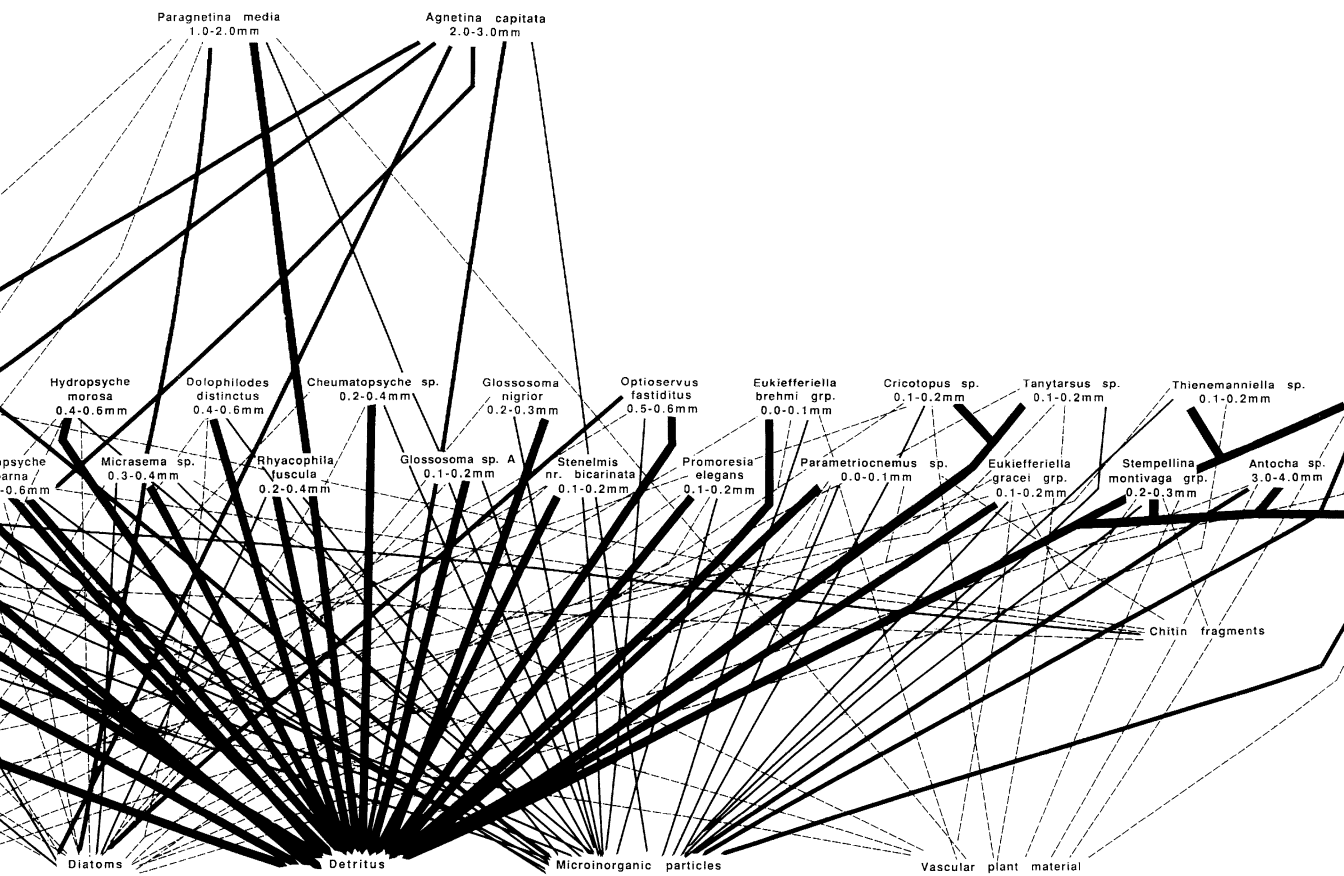
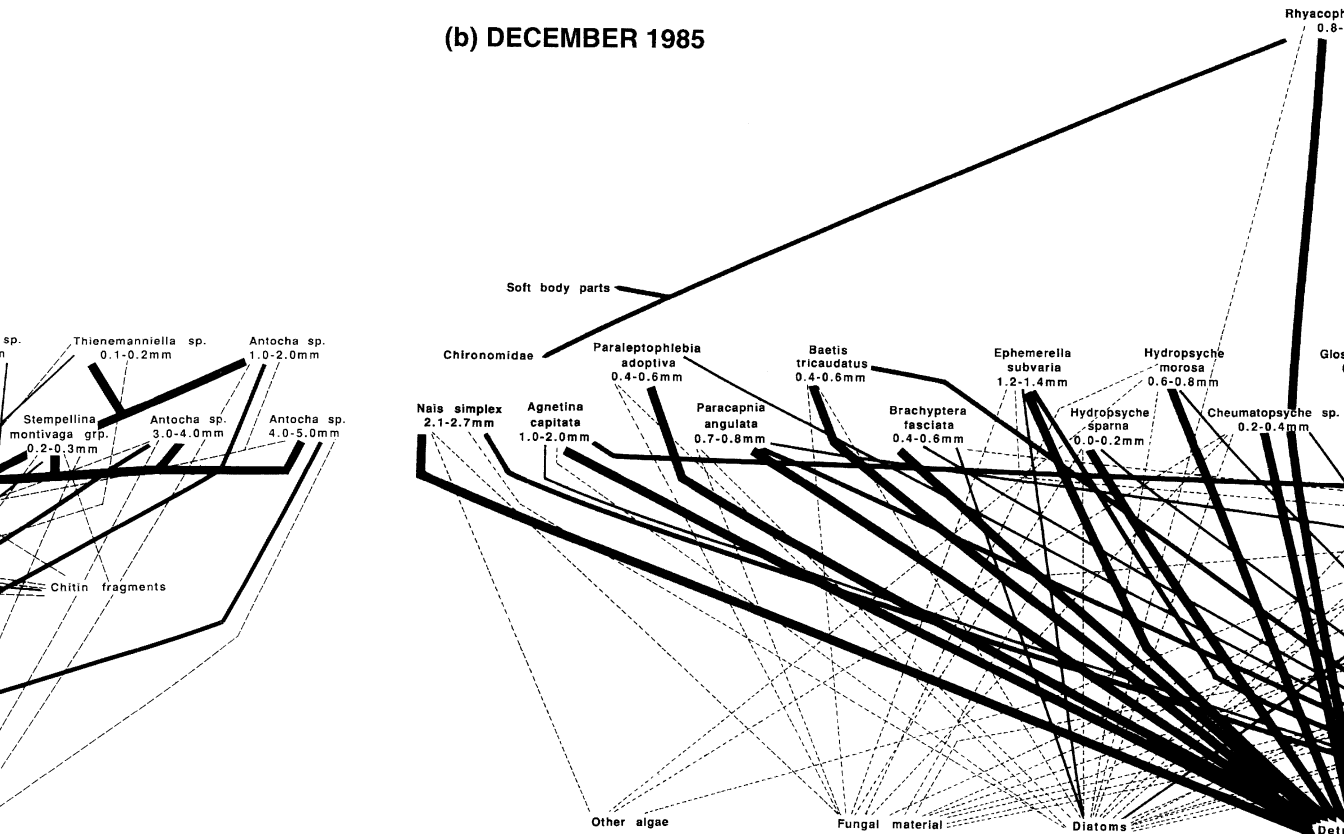


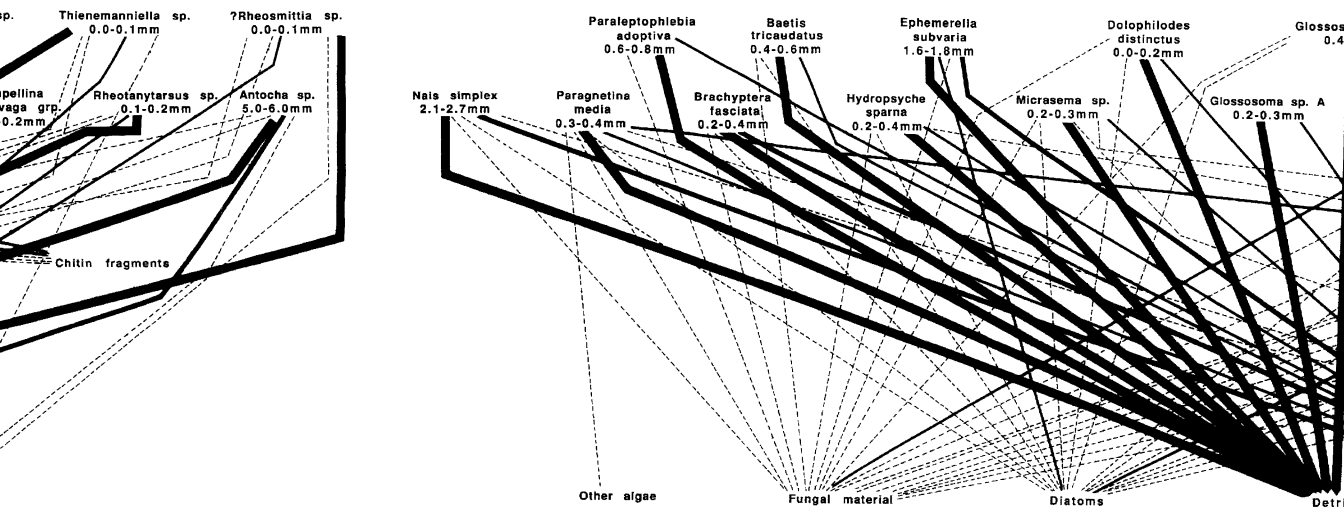
FIG. 4. Pictorial representations of macroinvertebrate riffle community food webs in Duffin Creek. (a)–(g), time specific food webs on different sampling dates; (h), summary food web. In all web diagrams, the arrows point from consumer to resource and the thickness of the lines represent the importance of the resource in the diet based on the IRI. The IRI values range from 0 to 20 000. Thickest lines represent greatest dietary importance (IRI > 10 000) and dashed lines represent least dietary importance (IRI < 500). Chitin and soft body parts of unknown or suspected origin were assigned to those respective categories. Chitinous fragments (i.e., head capsule, leg, and antennae fragments) of known chironomid origin but not identifiable to the genus or species level were assigned to the chironomid category. Numerical values are head capsule widths, except for *Antocha* sp. and *Nais simplex*; numerical values for these species represent body length.

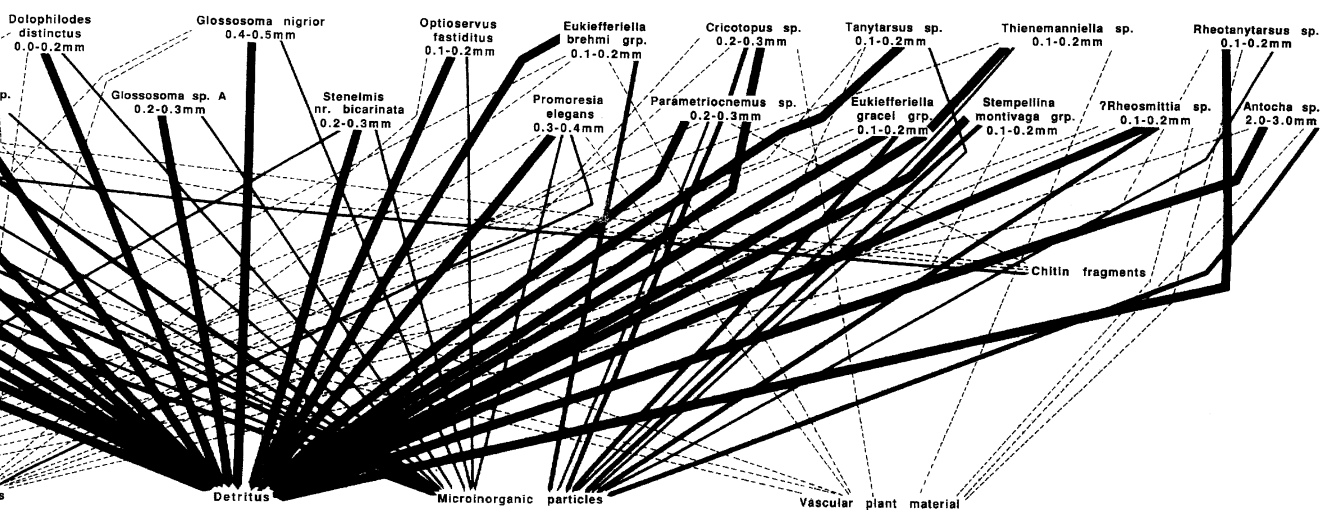
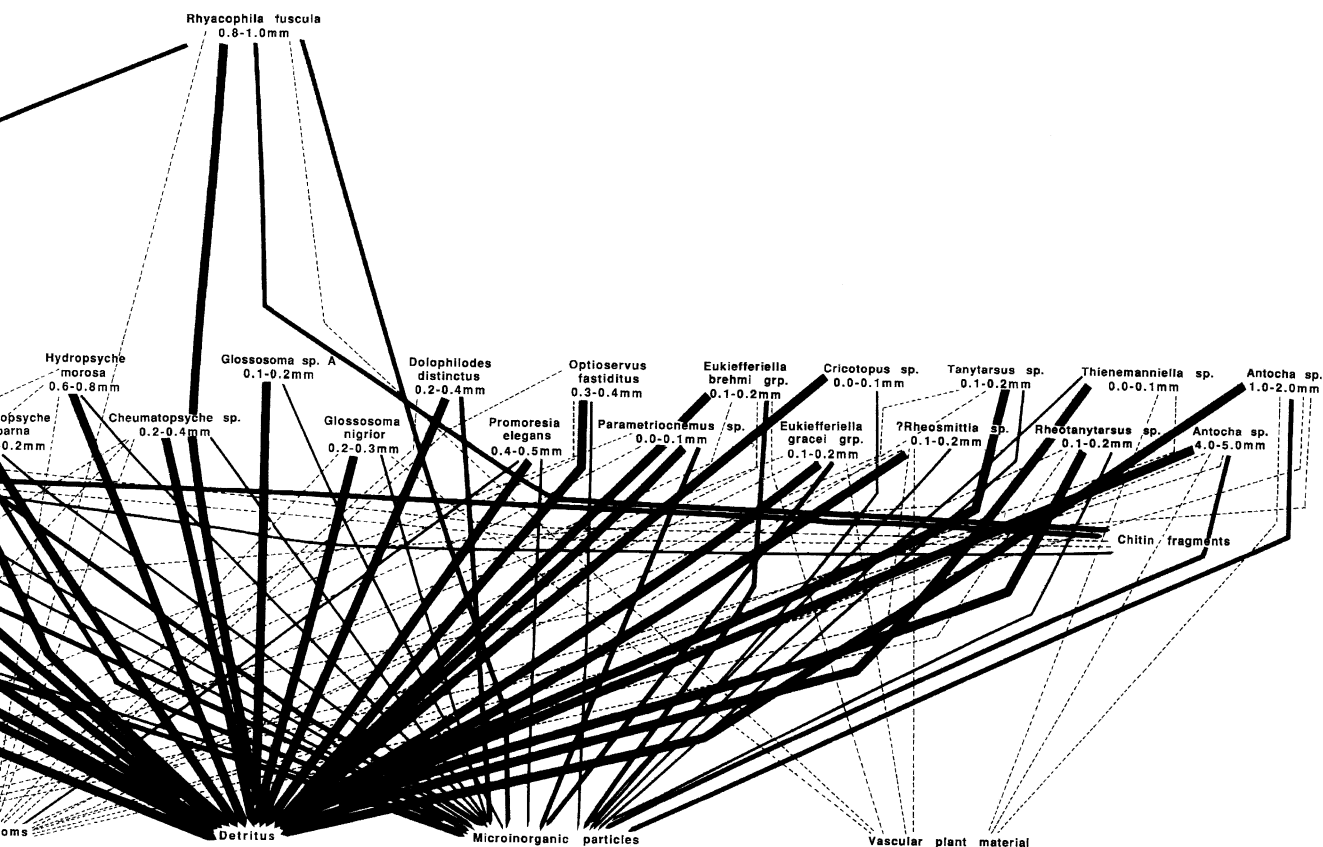


(b) DECEMBER 1985

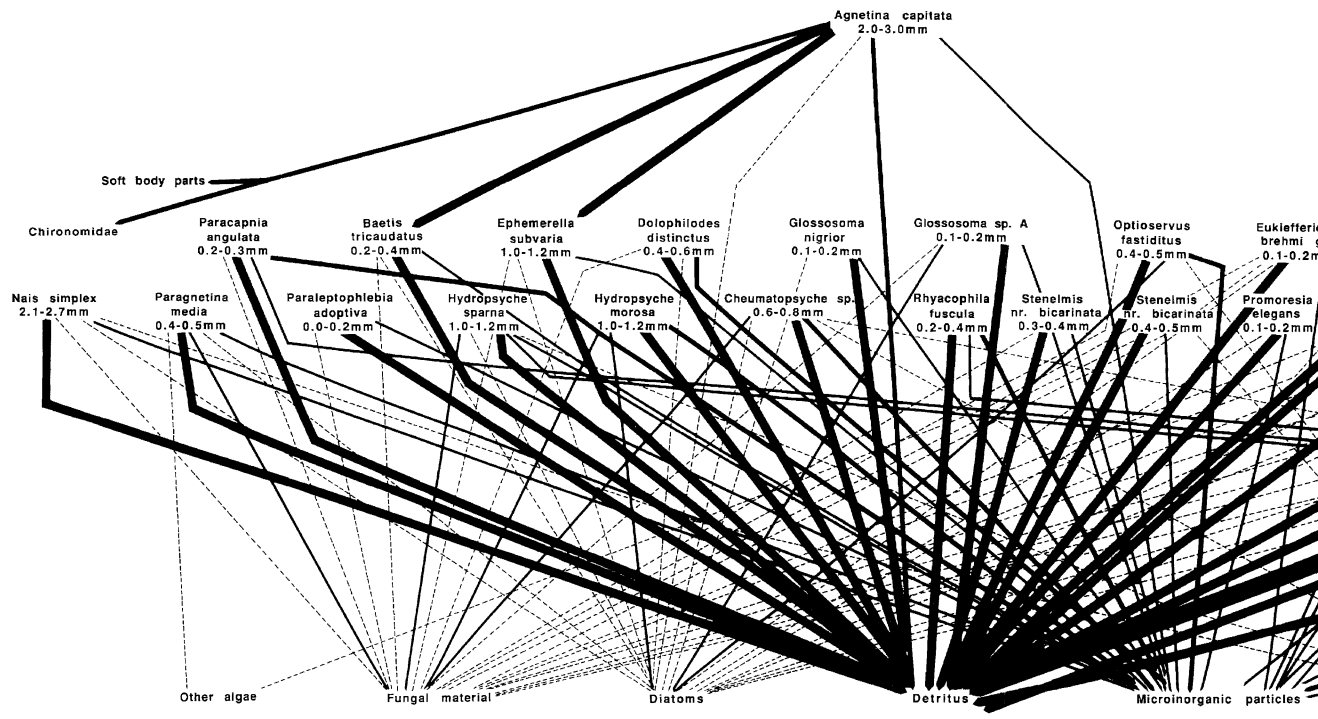


(d) APRIL 1986

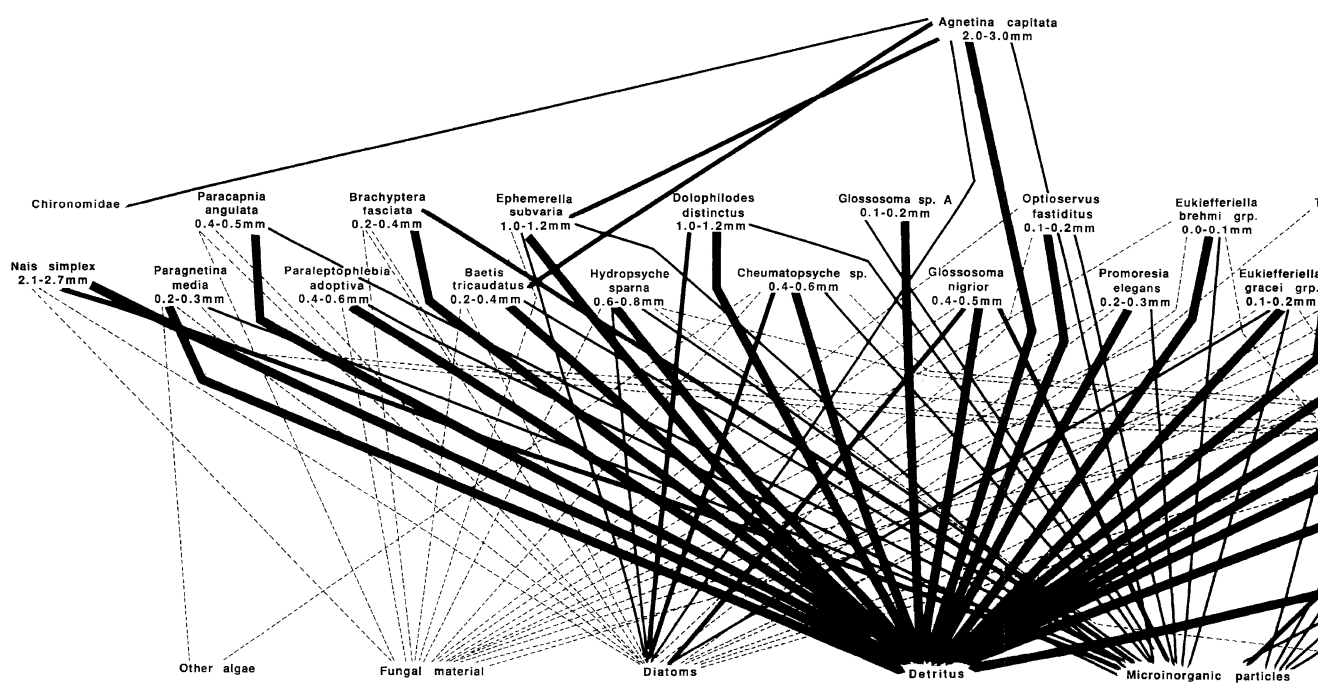




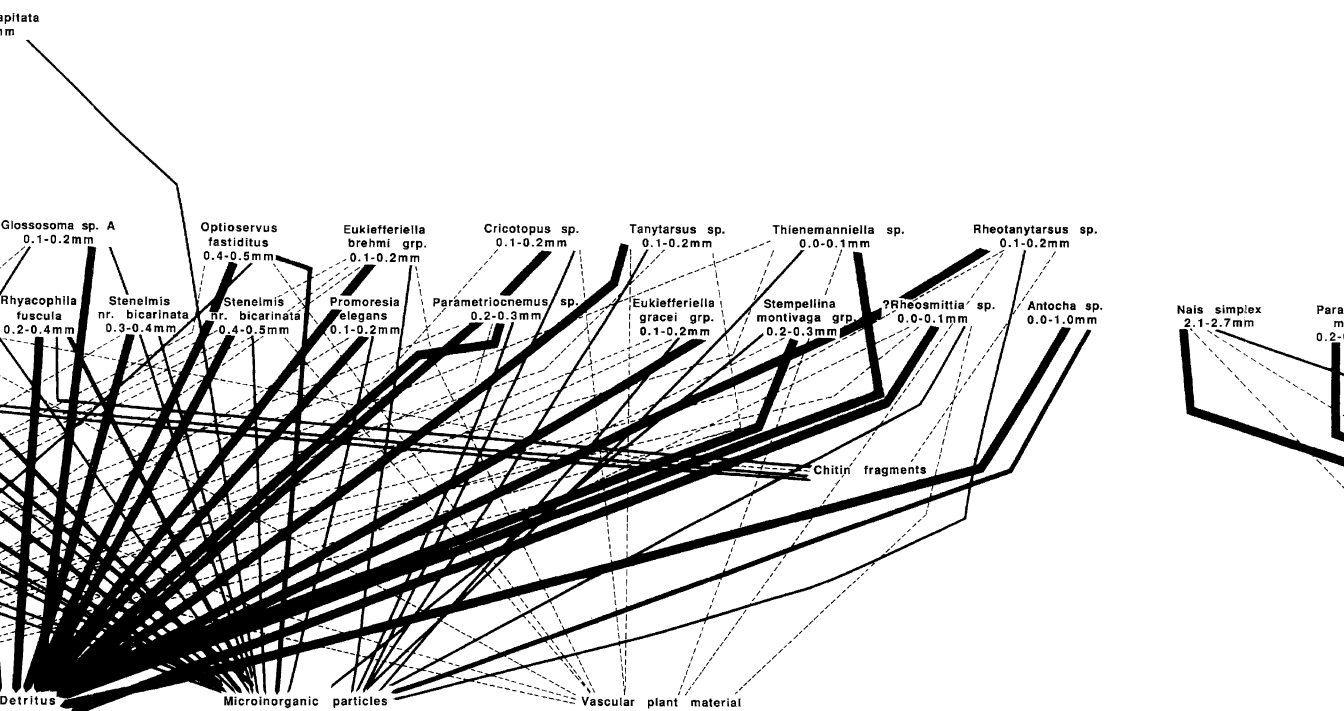
(e) JUNE 1986



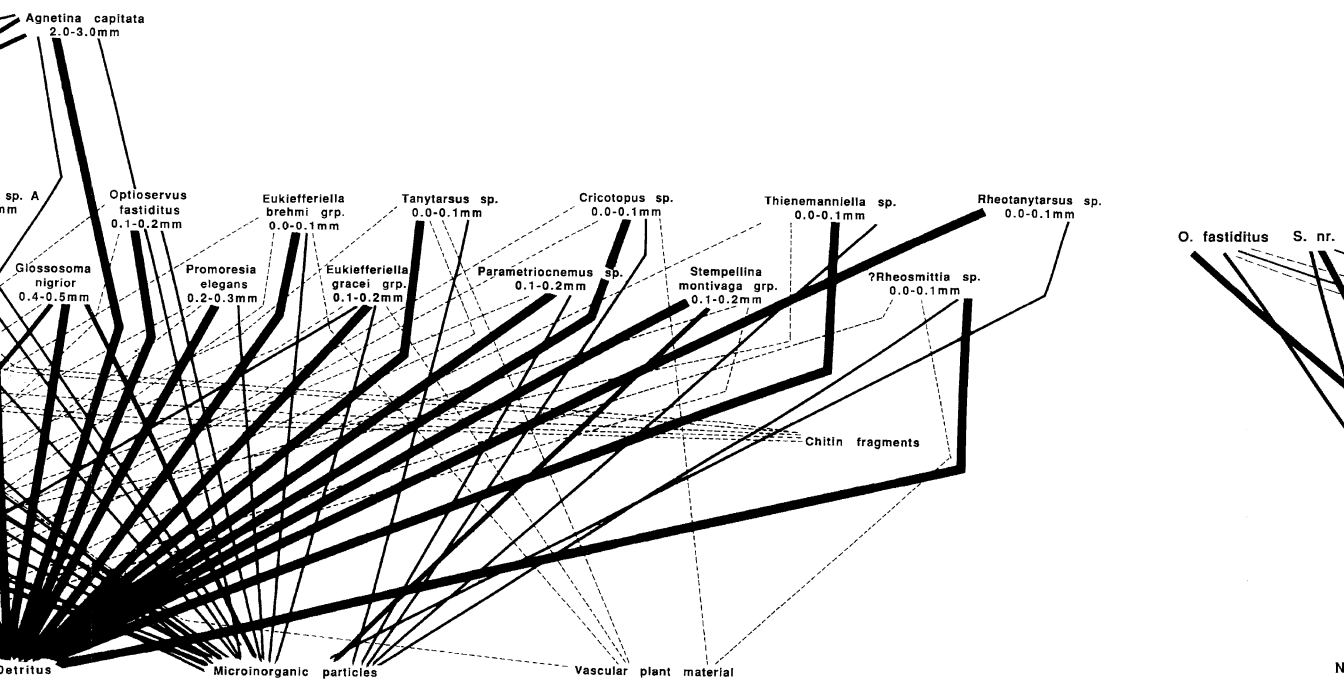
(g) OCTOBER 1986



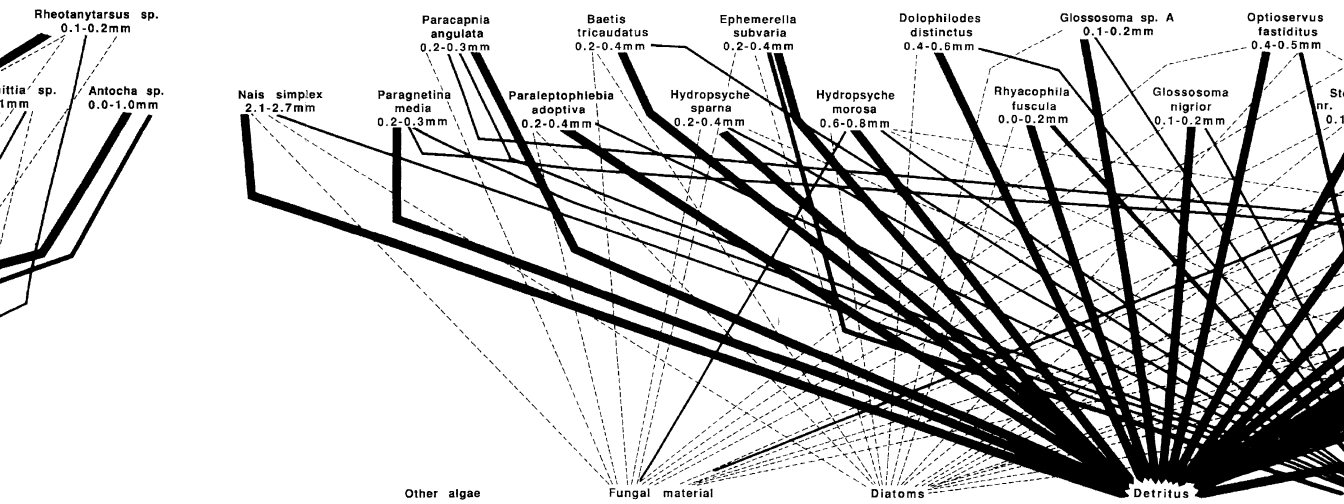
(f) AU



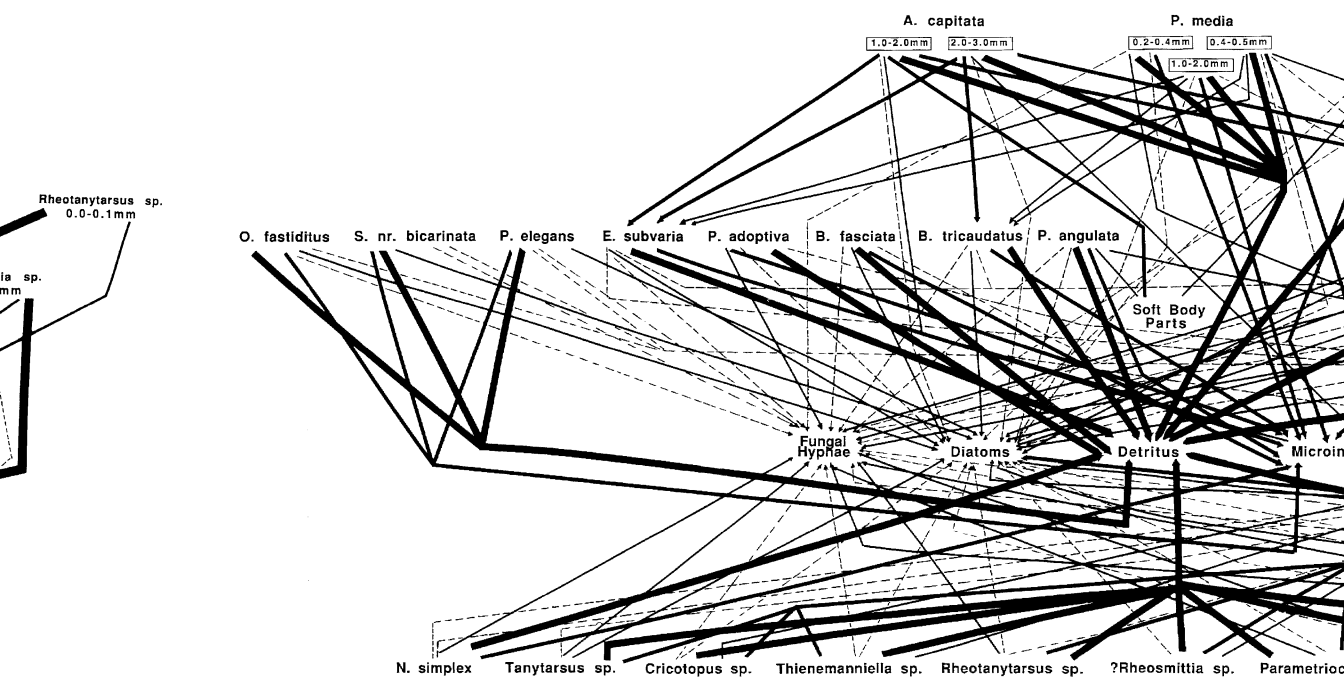
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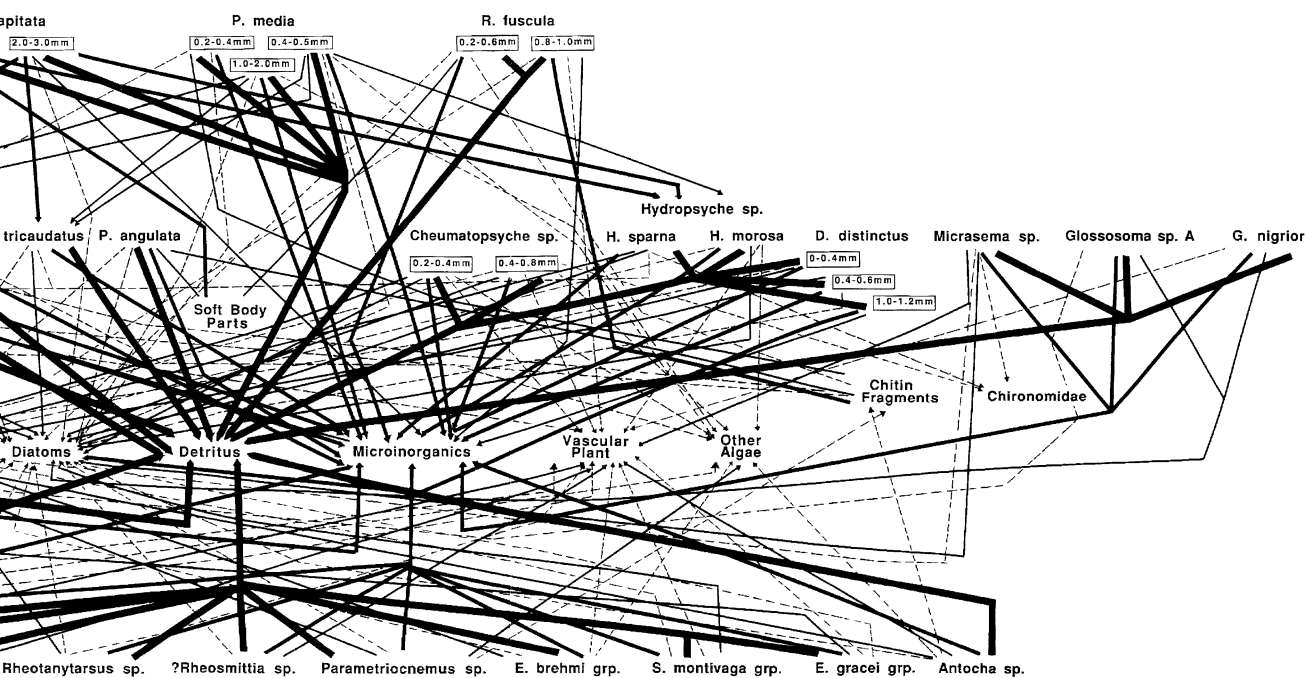
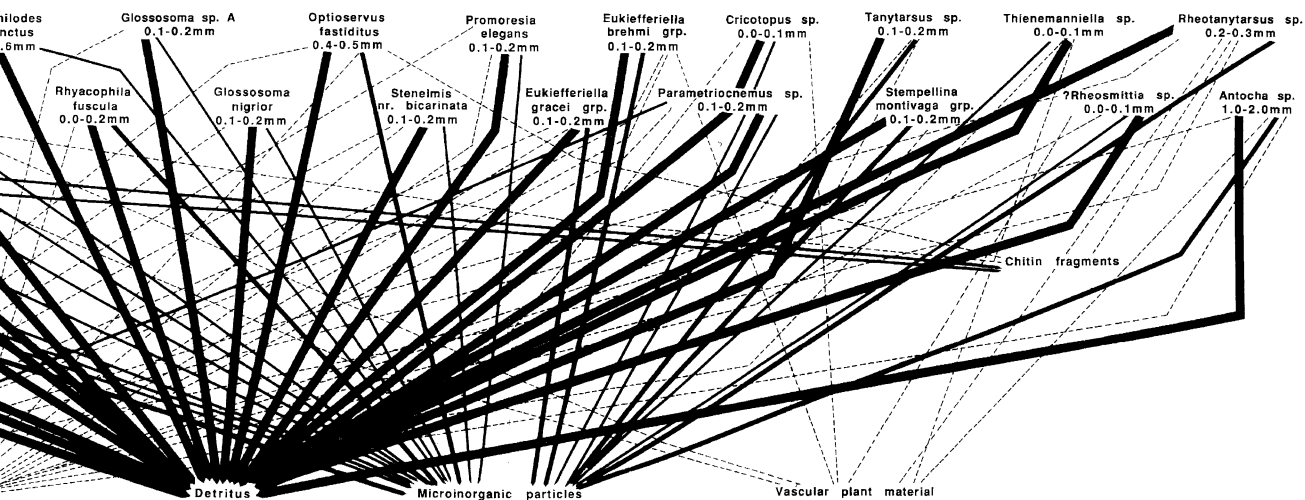


(f) AUGUST 1986



(h) SUMMARY WEB





to the mean value, 3.2 ± 0.8 , calculated by Schoenly et al. (1991) for aquatic insect webs.

Omnivory and life history omnivory

Life history omnivory (as opposed to conventional omnivory) is defined as "different life history stages of a species feeding in trophically different positions in the food web" (Pimm and Rice 1987); thus, each life stage must be treated as a distinct (although linked) entity, departing from the traditional concept of an omnivore. This affects links in the food web such that a strong detrital link early in the life cycle of a predatory stonefly, for example, becomes a moderate or weak link later in the life cycle when more animal material and less detritus is eaten. In webs modelled to incorporate life history omnivory, it has been found that life history omnivory reduced stability, but much less so than for conventional omnivory (Pimm and Rice 1987).

The question of why omnivory is now more often observed when, because of its destabilizing effects, it is predicted to be rare, is still unanswered. The incidence of omnivores in real webs ranges from none to many (Pimm and Lawton 1978). Pimm (1982) states that, in model webs, which are required to be stable, omnivores should be rare but, when they are present, they should feed on species in adjacent trophic levels rather than on those separated by more than one level. Insect-dominated systems may show more complex patterns of omnivory, as will systems that are best modelled by donor-controlled dynamics. Sprules and Bowerman (1988) challenge the validity of Pimm's models of omnivory and suggest that the equilibrium assumptions that he used would not apply to systems with seasonally variable resources and, possibly, to many other communities. Furthermore, the clumping of species and/or lack of species resolution in previous studies may mask omnivorous interactions (Walter 1987, Sprules and Bowerman 1988). The lack of omnivores in webs reported so far may be due also to ignorance of ontogenic diet changes, poorly studied juvenile stages (Polis 1991), and the lack of direct dietary information (Pimm et al. 1991). The importance of temporal food web analyses becomes clear when omnivory, especially life history omnivory, is prevalent in a community.

A number of recent studies (including ours) have shown omnivory to be common in food webs (Hildrew et al. 1985, Chow-Fraser and Wong 1986, Walter 1987, Sprules and Bowerman 1988), and this appears to be especially so in systems dominated by insects, an observation that applies equally to forest floor and soil feeders (Polis 1991) as it does to benthic species. However, omnivory is not restricted to invertebrate webs as, for example, coyotes eat a variety of foods: from deer, hare, small mammals and insects to apples, leaves, grasses, and seeds (Bowyer et al. 1983, Moore and Millar 1986). Moreover, there are differences in the diets of juvenile and adult coyotes such that juveniles

feed lower in the web than adults (Todd 1985). Differences in adult and juvenile diets have also been observed in Ring-necked ducks and linked to changing nutritional requirements during development (Hohman 1985, McAuley and Longcore 1988). In addition, changing adult diets have been documented during the breeding season. Again, this has been attributed to increased nutrient and energy requirements at this time (Hohman 1985). Although it has been suggested that omnivory is rare because, for behavioral, morphological, and physiological reasons, it is difficult to feed on more than one trophic level (Yodzis 1984), evidence disputes this. In fact, it would seem that, in the context of the nutritional requirements of many organisms and the ultimate goal of achieving maximum fitness, omnivory is inevitable. Variability of resources, abiotic factors, and the presence of predators are a few factors that can prevent an organism from reaching its nutritional optimum. To compensate, organisms can modify not only physiological and metabolic processes but also feeding and other behaviors. Modifications in feeding behavior include changes in the quantity and type of food eaten and the utilization of that food (Slansky and Scriber 1985). In addition, different nutritional requirements may be associated with different life cycle stages, which may dictate a change in diet. For these reasons, one would expect both conventional and life history omnivory to be quite common. Menge and Sutherland (1987) have suggested the possibility that the relative importance of omnivory differs between aquatic and terrestrial communities. Omnivory may be more common in aquatic communities and, because omnivory should increase connectance, there should thus be a greater potential for control of the community by consumers. Moreover, conventional omnivory is probably linked to seasonal changes in food availability whereas life history omnivory is more related to life cycles to which there is also a seasonal component.

The advantages of studying food webs range from a better understanding of community structure, ecology, and dynamics to providing a better understanding of, and solutions to, problems such as predicting biological concentration of contaminants, better strategies for integrated pest management, disease-causing vector control, wastewater treatment and wildlife conservation (Cohen et al. 1993). Yet the worth of food web studies has been questioned. This is surprising, especially in light of the need for more multispecies studies and their importance in the understanding and correct interpretation of higher order interactions in ecological systems (Kareiva 1994).

Schoener (1989) has found that certain web characteristics are specific to particular habitats and, although it has been suggested that inter-web comparisons of food web statistics are invalid because of the possible confounding effects of methodology (Closs and Lake 1994), inter-web/intra-habitat comparisons may prove useful. It is important to note that if such

comparisons are to be made, they should be made incorporating the recommendations of Cohen et al. (1993): studies should be from similar habitats using standardized or similar methodologies. We advocate adding temporal resolution of webs to the list of recommendations by Cohen et al. (1993). There is no doubt that collecting food web information of this calibre is labor intensive; however, the returns in terms of pure and applied knowledge of the dynamics of natural systems are potentially great.

The importance of looking at food webs temporally rather than statistically is reflected in the differences seen in the Duffin Creek summary web vs. the temporal webs. The summary web generated higher values for the total number of links per web, total number of species, intermediate-to-top links, linkage density, and linkage complexity. More importantly, variations in food web statistics, especially in any of the species proportions, predator-prey ratios, and link proportions were obscured when this information was calculated for the summary web alone. Our time-specific webs reveal that the incidence of omnivory, particularly life history omnivory is not rare in a detritus-based stream, information otherwise obscured by summarizing the data. Finally, the temporal perspective has given us insight into possible associations between trophic structure and life history effects, thus helping to unify food web structure and community ecology in the Duffin Creek system.

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APPENDIX I

Index of Relative Importance (IRI) values for the various food types found in the guts of Duffin Creek macroinvertebrates. Higher values indicate greater dietary importance.

Sampling date	Macroinvertebrate species	Body length (mm)	IRI value							N
			Detritus	Diatoms	Micro-inorgan-ics	Chitin	Fungal hyphae	Vascular plant	Other algae	
October 1985	<i>Antocha</i> sp.	1.0–2.0	17 050.0	32.0	2560.0	0	108.0	46.0	1.5	10
	<i>Antocha</i> sp.	3.0–4.0	16 177.8	400.0	2900.0	0	433.3	8.6	0	10
	<i>Antocha</i> sp.	4.0–5.0	14 381.3	60.9	4993.8	0	366.4	5.5	0	10
December 1985	<i>Antocha</i> sp.	1.0–2.0	16 760.0	21.0	2850.0	0	31.0	49.5	0	13
	<i>Antocha</i> sp.	4.0–5.0	13 720.0	344.0	5120.0	0	234.0	136.0	0	6
February 1986	<i>Antocha</i> sp.	5.0–6.0	14 885.0	28.0	4445.0	0	455.0	39.0	0	10
April 1986	<i>Antocha</i> sp.	2.0–3.0	14 350.0	0	5225.0	0	37.5	175.0	0	6
June 1986	<i>Antocha</i> sp.	0.0–1.0	15 100.0	0	4900.0	0	0	0	0	10
August 1986	<i>Antocha</i> sp.	1.0–2.0	16 061.0	41.7	3305.0	0	475.0	5.6	0	9
October 1986	<i>Antocha</i> sp.	*								
October 1985	<i>Nais simplex</i>	2.1–2.7	17 400.0	6.0	2130.0	0	280.0	54.0	0	5
December 1985	<i>N. simplex</i>	2.1–2.7	16 930.0	8.0	2580.0	0	60.0	0	24.0	5
February 1986	<i>N. simplex</i>	2.1–2.7	18 150.0	0	1700.0	0	150.0	0	0	5
April 1986	<i>N. simplex</i>	2.1–2.7	17 084.0	6.0	2736.0	0	8.0	22.0	0	5
June 1986	<i>N. simplex</i>	2.1–2.7	17 125.0	9.4	2475.0	0	37.5	9.4	0	5
August 1986	<i>N. simplex</i>	2.1–2.7	17 680.0	24.0	2150.0	0	66.0	0	0	5
October 1986	<i>N. simplex</i>	2.1–2.7	17 000.0	54.0	2730.0	0	108.0	0	0	5

Sampling date	Macroinvertebrate species	Head capsule width (mm)	IRI value							N
			Detritus	Diatoms	Micro-inorgan-ics	Chitin	Fungal hyphae	Vascular plant	Other algae	
October 1985	<i>Agneta capitata</i>	2.0–3.0	9 316.0	9316.6	850.0	7916.7	0	0	0	8
	<i>Paracapnia angulata</i>	0.1–0.2	16 350.0	3.1	2357.1	1271.4	0	0	0	10
	<i>Brachyptera fasciata</i>	0.4–0.6	16 966.7	1441.7	1466.7	16.7	0	0	8.3	10
	<i>Paragnetina media</i>	1.0–2.0	13 575.0	4100.0	1662.5	234.4	0	121.9	140.6	3
December 1985	<i>P. media</i>	0.2–0.3	16 916.7	1025.0	1150.0	783.3	83.3	83.3	0	7
	<i>A. capitata</i>	1.0–2.0	13 500.0	700.0	1100.0	4700.0	0	0	0	3
	<i>P. angulata</i>	0.7–0.8	14 933.3	194.4	3208.3	1433.3	88.9	0	0	8
	<i>B. fasciata</i>	0.4–0.6	17 655.6	655.6	1672.2	1.9	0	0	0	10
	<i>P. media</i>	0.3–0.4†								4
February 1986	<i>A. capitata</i>	*								
	<i>P. angulata</i>	0.9–1.0	16 140.0	66.0	2070.0	1610.0	28.8	0	0	6
	<i>B. fasciata</i>	0.6–0.8	16 884.0	117.0	2445.0	396.9	81.0	0	0	10
	<i>P. media</i>	0.3–0.4†								2
April 1986	<i>A. capitata</i>	*								
	<i>P. angulata</i>	*								
	<i>B. fasciata</i>	0.2–0.4	17 275.0	12.5	2518.8	85.9	2.3	0	0	10
	<i>P. media</i>	0.3–0.4	16 355.7	48.9	1928.6	1342.8	4.1	12.2	32.7	7
June 1986	<i>A. capitata</i>	2.0–3.0	8 699.9	350.0	900.0	10050.0	0	0	0	3
	<i>P. angulata</i>	0.2–0.3	16 333.3	0	2666.7	850.0	50.0	0	0	10
	<i>B. fasciata</i>	*								
	<i>P. media</i>	0.4–0.5	16 433.2	16.7	1066.7		2383.3	0	22.2	7
August 1986	<i>A. capitata</i>	*								
	<i>P. angulata</i>	0.2–0.3	16 450.0	0	1920.0	1610.0	2.0	0	0	12
	<i>B. fasciata</i>	*								
	<i>P. media</i>	0.2–0.3	17 433.3	0	1433.3	1133.3	0	0	0	4
October 1986	<i>A. capitata</i>	2.0–3.0	10 650.0	2350.0	950	6050.0	0	0	0	2
	<i>P. angulata</i>	0.4–0.5	17 180.0	80.9	2280.0	385.0	2.0	0	0	11
	<i>B. fasciata</i>	0.2–0.4	16 570.0	411.0	2520.0	136.0	11.0	0	0	13
	<i>P. media</i>	0.2–0.3	15 925.0	225.0	2387.0	1175.0	18.8	0	34.4	6
October 1985	<i>Ephemerella subvaria</i>	0.4–0.6	16 490.0	238.5	3170.0	19.5	2.0	0	0	10
	<i>Paraleptophlebia adoptiva</i>	0.2–0.4	17 600.0	26.0	2190.0	5.5	54.0	0	0	11
December 1985	<i>Baetis tricaudatus</i>	0.2–0.4	17 775.0	34.5	2075.0	0	1.5	2.0	0	10
	<i>E. subvaria</i>	1.2–1.4	12 940.0	995.0	5630.0	15.0	324.0	0	0	10
	<i>P. adoptiva</i>	0.4–0.6	17 485.0	1.4	2386.0	0	68.9	0	0	11
	<i>B. tricaudatus</i>	0.4–0.6	16 770.0	63.0	3040.0	0	34.0	0	0	10

APPENDIX I. Continued.

Sampling date	Macroinvertebrate species	Head capsule width (mm)	IRI value							N
			Detritus	Diatoms	Micro-inorgan-ics	Chitin	Fungal hyphae	Vascular plant	Other algae	
February 1986	<i>E. subvaria</i>	1.6–1.8	16 511.0	272.8	2660.0	26.4	320.0	0	0	10
	<i>P. adoptiva</i>	0.6–0.8	17 780.0	303.0	1606.0	0	54.5	0	0	10
	<i>B. tricaudatus</i>	0.6–0.8	17 065.0	104.0	2445.0	0	184.0	0	0	10
April 1986	<i>E. subvaria</i>	1.6–1.8	15 590.0	640.0	3605.0	0	115.5	0	0	10
	<i>P. adoptiva</i>	0.6–0.8	17 716.7	0	2077.8	0	182.7	0	0	11
	<i>B. tricaudatus</i>	0.4–0.6	17 765.0	34.5	1975.0	0	116.0	0	0	12
June 1986	<i>E. subvaria</i>	1.0–1.2	17 510.0	243.0	2010.0	0	147.0	0	0	10
	<i>P. adoptiva</i>	0.0–0.2	18 700.0	0	1150.0	0	200.0	0	0	3
	<i>B. tricaudatus</i>	0.2–0.4	18 390.0	48.0	1405.0	0	34.0	0	0	10
August 1986	<i>E. subvaria</i>	0.2–0.4	16 855.6	410.5	2527.8	0	34.6	0	0	10
	<i>P. adoptiva</i>	0.2–0.4	18 245.0	13.5	1640.0	0	28.0	0	0	10
	<i>B. tricaudatus</i>	0.2–0.4	18 150.0	16.5	1775.0	0	2.0	0	0	10
October 1986	<i>E. subvaria</i>	1.0–1.2	15 840.0	1570.5	2320.0	0	38.0	0	0	10
	<i>P. adoptiva</i>	0.4–0.6	18 400.0	57.5	1490.0	0	13.5	0	0	10
	<i>B. tricaudatus</i>	0.2–0.4	17 900.0	269.5	1655.0	0	18.0	0	0	10
October 1985	<i>Hydropsyche sparna</i>	0.4–0.6	16 775.0	270.0	2055.0	283.5	283.5	0	0	10
	<i>H. morosa</i>	0.4–0.6	17 262.5	333.6	1812.5	0	442.9	0	4.7	8
	<i>Cheumatopsyche</i> sp.	0.2–0.4	18 360.0	112.0	1415.0	0	42.5	0	0	11
December 1985	<i>Dolophilodes distinctus</i>	0.4–0.6	17 770.0	423.0	1665.0	0	52.5	0	0	10
	<i>Micrasema</i> sp.	0.3–0.4	15 675.0	1350.0	1610.0	0	62.0	208.0	0	16
	<i>Glossosoma nigrior</i>	0.2–0.3	18 559.0	396.9	1000.0	0	0	0	0	11
	<i>Glossosoma</i> sp. A	0.1–0.2	19 060.0	14.0	870.0	0	0	0	0	11
	<i>Rhyacophila fuscula</i>	0.2–0.4	18 800.0	600.0	650.0	0	0	0	0	3
	<i>H. sparna</i>	0.0–0.2	18 406.7	22.2	1466.7	0	20.0	0	0	10
	<i>H. morosa</i>	0.6–0.8	17 770.0	192.0	1420.0	0	430.0	0	12.0	5
	<i>Cheumatopsyche</i> sp.	0.2–0.4	18 020.0	91.0	1575.0	0	140.0	0	22.5	10
	<i>D. distinctus</i>	0.2–0.4	17 175.0	37.5	2750.0	0	0	0	0	2
	<i>Micrasema</i> sp.	0.3–0.4†								17
	<i>G. nigrior</i>	0.2–0.3	18 044.0	18.3	1780.0	0	0	1.5	0	11
	<i>Glossosoma</i> sp. A	0.1–0.2	18 670.0	0	1330.0	0	0	0	0	10
	<i>R. fuscula</i>	0.8–1.0	10 800.0	300.0	2700.0	6000.0	0	200.0	0	1
	<i>H. sparna</i>	0.2–0.4	18 255.0	80.5	1340.0	17.0	100.0	0	0	10
	<i>H. morosa</i>	0.8–1.0	17 150.0	200.0	1750.0	0	450.0	0	225.0	2
February 1986	<i>Cheumatopsyche</i> sp.	0.2–0.4	18 058.3	41.7	1508.3	0	45.8	4.2	77.8	6
	<i>D. distinctus</i>	*								
	<i>Micrasema</i> sp.	0.3–0.4	17 425.0	12.5	2525.0	0	0	0	0	14
	<i>G. nigrior</i>	0.2–0.3	18 235.0	42.0	1660.0	0	0	0	0	10
	<i>Glossosoma</i> sp. A	0.1–0.2	18 533.3	0	1433.3	0	5.6	0	0	15
	<i>R. fuscula</i>	0.2–0.4	16 733.3	133.3	2266.7	800.0	0	0	0	3
	<i>H. sparna</i>	0.2–0.4	17 900.0	203.0	1595.0	2.5	114.0	0	0	10
	<i>H. morosa</i>	*								
	<i>Cheumatopsyche</i> sp.	*								
	<i>D. distinctus</i>	0.0–0.2	18 105.0	15.0	1795.0	0	15.0	0	0	10
	<i>Micrasema</i> sp.	0.2–0.3	17 071.0	260.2	2050.0	14.3	107.1	20.4	0	8
	<i>G. nigrior</i>	0.4–0.5	17 344.4	71.6	2433.3	0	16.0	0	0	10
	<i>Glossosoma</i> sp. A	0.2–0.3	18 210.0	0	1790.0	0	0	0	0	10
	<i>R. fuscula</i>	1.2–1.4†								1
	<i>H. sparna</i>	1.0–1.2	14 791.0	179.1	1760.0	1000.8	1515.0	435.6	0	10
June 1986	<i>H. morosa</i>	1.0–1.2	15 600.0	700.0	2800.0	0	900.0	0	0	1
	<i>Cheumatopsyche</i> sp.	0.6–0.8	15 692.9	464.3	2642.9	52.0	985.7	26.5	0	7
	<i>D. distinctus</i>	0.4–0.6	16 870.0	68.9	2885.0	0	84.0	0	0	11
	<i>Micrasema</i> sp.	0.7–0.8†								3
	<i>G. nigrior</i>	0.1–0.2	18 620.0	24.0	1280.0	0	0	0	0	14
	<i>Glossosoma</i> sp. A	0.1–0.2	17 025.0	1156.3	625.0	0	9.4	0	0	4
	<i>R. fuscula</i>	0.2–0.4	16 500.0	0	2600.0	900.0	0	0	0	3
	<i>H. sparna</i>	0.2–0.4	18 760.0	0	1120.0	0	36.0	3.0	0	11
	<i>H. morosa</i>	0.6–0.8	14 050.0	103.1	1837.5	34.4	1887.5	975.0	0	5
	<i>Cheumatopsyche</i> sp.	*								
	<i>D. distinctus</i>	0.0–0.2	18 330.0	6.0	1640.0	0	0	0	0	8
	<i>Micrasema</i> sp.	0.1–0.2†								2
	<i>G. nigrior</i>	0.1–0.2	18 550.0	0	1430.0	0	2.0	0	0	12
	<i>Glossosoma</i> sp. A	0.1–0.2	18 740.0	10.0	1089.0	0	0	0	0	11
	<i>R. fuscula</i>	0.4–0.6	17 300.0	150.0	2550.0	0	0	0	0	1

APPENDIX I. Continued.

Sampling date	Macroinvertebrate species	Head capsule width (mm)	IRI value							N
			Detritus	Diatoms	Micro-inorgan-ics	Chitin	Fungal hyphae	Vascu-lar plant	Other algae	
October 1986	<i>H. sparna</i>	0.6–0.8	15 681.3	2056.3	1825.0	2.3	53.1	2.3	0	14
	<i>H. morosa</i>	*								
	<i>Cheumatopsyche</i> sp.	0.4–0.6	14 116.7	4425.0	1316.7	4.2	11.1	0	8.3	6
	<i>D. distinctus</i>	1.0–1.2	11 050.0	7650.0	1300.0	0	0	0	0	2
	<i>Micrasema</i> sp.	0.4–0.5†								1
	<i>G. nigrior</i>	0.4–0.5	12 400.0	4650.0	2900.0	0	12.5	0	0	4
	<i>Glossosoma</i> sp. A	0.1–0.2	18 466.7	0	1533.3	0	0	0	0	4
	<i>R. fuscula</i>	0.6–0.8†								1
October 1985	<i>Stenelmis</i> nr. <i>bicari-nata</i>	0.1–0.2	17 840.0	320.0	1700.0	0	32.0	0	0	14
	<i>Promoresia elegans</i>	0.1–0.2	18 585.7	16.3	1271.4	0	39.7	0	0	16
	<i>Optioservus fastidi-tus</i>	0.5–0.6	14 400.0	2566.7	1900.0	0	366.7	0	0	3
	<i>S. nr. bicarinata</i>	0.1–0.2†								4
December 1985	<i>P. elegans</i>	0.4–0.5	17 800.0	600.0	1600.0	0	0	0	0	6
	<i>O. fastiditus</i>	0.3–0.4	18 870.0	21.0	960.0	0	50.0	0	0	12
	<i>S. nr. bicarinata</i>	0.1–0.2†								7
February 1986	<i>P. elegans</i>	0.2–0.3	18 966.7	50.0	933.3	0	0	0	0	10
	<i>O. fastiditus</i>	0.2–0.3	18 688.9	18.1	1223.3	0	3.7	0	0	11
	<i>S. nr. bicarinata</i>	0.2–0.3	17 300.0	0	2433.3	0	624.9	0	0	6
April 1986	<i>P. elegans</i>	0.3–0.4	17 977.8	553.1	1255.6	0	44.4	4.9	0	10
	<i>O. fastiditus</i>	0.1–0.2	19 010.0	10.0	939.9	0	0	0	0	11
	<i>S. nr. bicarinata</i>	0.3–0.4	17 533.3	0	1700	0	88.9	0	0	6
June 1986	<i>S. nr. bicarinata</i>	0.4–0.5	17 580.0	0	2120.0	0	32.0	48.0	0	5
	<i>P. elegans</i>	0.1–0.2	18 690.0	12.0	1230.0	0	0	0	0	15
	<i>O. fastiditus</i>	0.4–0.5	14 842.9	875.5	3678.6	0	162.2	11.2	0	10
August 1986	<i>S. nr. bicarinata</i>	0.1–0.2	18 175.0	18.8	1700.0	0	12.5	0	0	10
	<i>P. elegans</i>	0.1–0.2	18 755.6	22.2	1155.6	0	2.5	0	0	12
	<i>O. fastiditus</i>	0.4–0.5	15 750.0	100.0	4016.7	8.3	5.5	0	0	6
October 1986	<i>S. nr. bicarinata</i>	0.1–0.2†								3
	<i>S. nr. bicarinata</i>	0.4–0.5†								2
	<i>P. elegans</i>	0.2–0.3	18 275.0	262.5	1387.5	0	37.5	0	0	4
October 1985	<i>O. fastiditus</i>	0.1–0.2	18 350.0	71.9	1500.0	0	2.3	0	0	19
	<i>Thienemanniella</i> sp.	0.1–0.2	18 530.0	32.2	1355.0	0	5.1	0	0	11
	<i>Cricotopus</i> sp.	0.1–0.2	18 190.0	12.0	1560.0	0	93.0	7.0	0	10
	<i>E. brehmi</i> grp.	0.0–0.1	17 895.0	24.0	1610.0	0	64.0	102.0	0	10
	<i>E. gracei</i> grp.	0.1–0.2	17 615.0	8.0	1900.0	0	296.0	1.5	18.0	10
	<i>Parametriocnemus</i> sp.	0.0–0.1	17 668.8	12.5	1818.8	3.1	75.0	0	89.1	10
	<i>?Rheosmittia</i> sp.	*								
	<i>Tanytarsus</i> sp.	0.1–0.2	17 690.0	171.0	2065.0	0	8.0	1.5	0	10
	<i>Rheotanytarsus</i> sp.	*								
December 1985	<i>S. montivaga</i> grp.	0.2–0.3	16 483.0	120.0	3012.0	5.5	0	84.0	0	10
	<i>Thienemanniella</i> sp.	0.0–0.1	18 505.0	2.0	1245.0	0	0	69.0	0	10
	<i>Cricotopus</i> sp.	0.0–0.1	18 750.0	0	1240.0	0	0	0	0	10
	<i>E. brehmi</i> grp.	0.1–0.2	17 340.0	8.0	2515.0	0	34.0	102.0	0	10
	<i>E. gracei</i> grp.	0.1–0.2	16 770.0	15.0	2790.0	0	300.0	1.5	0	10
	<i>Parametriocnemus</i> sp.	0.0–0.1	16 833.3	0	2766.7	0	33.3	0	300.0	10
	<i>?Rheosmittia</i> sp.	0.1–0.2	18 222.2	2.5	1316.7	0	2.5	277.7	0	10
	<i>Tanytarsus</i> sp.	0.1–0.2	17 662.0	290.0	2023.0	0	2.0	0	0	10
	<i>Rheotanytarsus</i> sp.	0.1–0.2	18 027.0	25.6	1810.0	0	14.7	0	0	10
February 1986	<i>S. montivaga</i> grp.	*								
	<i>Thienemanniella</i> sp.	0.0–0.1	18 300.0	2.0	1690.0	0	21.0	2.0	0	10
	<i>Cricotopus</i> sp.	0.1–0.2	18 135.0	13.0	1499.0	0	0	1.5	0	10
	<i>E. brehmi</i> grp.	0.0–0.1	18 370.0	0	1455.0	0	77.5	2.0	0	10
	<i>E. gracei</i> grp.	0.1–0.2	17 595.0	1.5	1935.0	0	276.0	33.0	0	10
	<i>Parametriocnemus</i> sp.	0.0–0.1	17 900.0	0	1950.0	0	0	0	150.0	10
	<i>?Rheosmittia</i> sp.	0.0–0.1	18 575.0	27.0	1265.0	0	2.5	13.0	0	10
	<i>Tanytarsus</i> sp.	0.1–0.2	17 465.0	36.0	2325.0	0	36.0	8.0	0	10
	<i>Rheotanytarsus</i> sp.	0.1–0.2	18 514.3	4.1	1342.9	0	65.3	0	0	7
	<i>S. montivaga</i> grp.	0.1–0.2	16 188.9	133.3	3644.4	0	0	1.9	0	9

APPENDIX I. Continued.

Sampling date	Macroinvertebrate species	Head capsule width (mm)	IRI value							N
			Detritus	Diatoms	Micro-inorgan-ics	Chitin	Fungal hyphae	Vascu-lar plant	Other algae	
April 1986	<i>Thienemanniella</i> sp.	0.1–0.2	17 980.0	0	1755.0	0	87.0	24.0	0	10
	<i>Cricotopus</i> sp.	0.2–0.3	16 060.0	22.5	3405.0	0	24.0	238.0	0	10
	<i>E. brehmi</i> grp.	0.1–0.2	16 995.0	8.0	2660.0	0	232.0	1.5	0	10
	<i>E. gracei</i> grp.	0.1–0.2	16 845.0	18.0	2830.0	0	265.0	0	0	10
	<i>Parametriocnemus</i> sp.	0.2–0.3	17 975.0	0	1790.0	2.5	168.0	0	0	10
	<i>?Rheosmittia</i> sp.	0.1–0.2	17 200.0	16.5	2595.0	0	47.5	16.5	0	10
	<i>Tanytarsus</i> sp.	0.1–0.2	17 800.0	6.0	2060.0	0	33.0	0	0	10
	<i>Rheotanytarsus</i> sp.	0.1–0.2	17 980.0	0	1830.0	0	140.0	1.5	0	10
	<i>S. montivaga</i> grp.	0.1–0.2	17 240.0	32.0	2680.0	0	0	0	0	10
	<i>Thienemanniella</i> sp.	0.0–0.1	17 555.0	226.8	2136.0	0	1.4	4.3	0	10
June 1986	<i>Cricotopus</i> sp.	0.1–0.2	17 460.0	0	2100.0	0	40.0	88.5	0	10
	<i>E. brehmi</i> grp.	0.1–0.2	18 110.0	2.0	1414.0	0	18.3	19.0	30.0	10
	<i>E. gracei</i> grp.	0.1–0.2	17 180.0	16.5	2300.0	0	418.5	0	0	10
	<i>Parametriocnemus</i> sp.	0.2–0.3	17 322.2	1.9	2277.8	0	327.8	0	0	11
	<i>?Rheosmittia</i> sp.	0.0–0.1	17 005.0	60.0	1900.0	0	21.0	91.5	0	10
	<i>Tanytarsus</i> sp.	0.1–0.2	17 680.0	16.5	2155.0	0	28.0	2.0	0	10
	<i>Rheotanytarsus</i> sp.	0.1–0.2	18 475.0	0	1400.0	2.0	27.0	1.5	0	10
	<i>S. montivaga</i> grp.	0.2–0.3	17 633.3	16.7	2316.7	0	0	0	0	3
	<i>Thienemanniella</i> sp.	0.0–0.1	17 850.0	30.0	1895.0	0	0	72.0	0	10
	<i>Cricotopus</i> sp.	0.0–0.1	18 300.0	2.0	1570.0	0	0	44.0	0	10
August 1986	<i>E. brehmi</i> grp.	0.1–0.2	16 345.0	12.0	3450.0	0	50.0	2.0	0	10
	<i>E. gracei</i> grp.	0.1–0.2	17 230.0	2.0	2555.0	0	77.5	0	0	10
	<i>Parametriocnemus</i> sp.	0.1–0.2	17 141.7	5.6	1333.3	0	1256.9	0	0	6
	<i>?Rheosmittia</i> sp.	0.0–0.1	18 220.0	8.0	1680.0	0	0	12.0	0	8
	<i>Tanytarsus</i> sp.	0.1–0.2	16 300.9	1.5	3619.1	0	23.1	0	0	11
	<i>Rheotanytarsus</i> sp.	0.2–0.3	16 600.0	11.5	2987.5	1.0	215.3	30.6	0	12
	<i>S. montivaga</i> grp.	0.1–0.2	16 262.5	3.1	3712.5	0	0	0	0	8
	<i>Thienemanniella</i> sp.	0.0–0.1	18 700.0	55.6	1050.0	0	13.9	0	0	10
	<i>Cricotopus</i> sp.	0.0–0.1	18 510.0	1.6	1410.0	0	1.6	4.0	0	10
	<i>E. brehmi</i> grp.	0.0–0.1	17 890.0	11.0	2415.0	0	74.0	67.5	0	10
October 1986	<i>E. gracei</i> grp.	0.1–0.2	15 361.1	762.9	2005.6	0	98.8	37.0	0	9
	<i>Parametriocnemus</i> sp.	0.1–0.2	18 550.0	0	1500.0	0	10.0	0	0	11
	<i>?Rheosmittia</i> sp.	0.0–0.1	18 638.9	19.8	1183.3	0	0	9.9	0	10
	<i>Tanytarsus</i> sp.	0.0–0.1	18 022.7	51.2	1759.1	0	14.9	2.1	0	11
	<i>Rheotanytarsus</i> sp.	0.0–0.1	18 700.0	0	1300.0	0	0	0	0	10
	<i>S. montivaga</i> grp.	0.1–0.2	16 878.0	1.5	3047.0	0	18.0	0	0	10

* Indicates that no individuals were collected at that sampling date; † indicates that all individuals examined had empty guts.

APPENDIX II

(A) Food web matrix for the Duffin Creek riffle community summary web. A 0 at the intersection of row and column indicates no trophic interaction; 1 indicates a trophic interaction (after Briand 1983). (B) Species identification key, by assigned number.

A) Food web matrix

Resource species (assigned number)	Consumer species (assigned number)																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	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
14	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	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	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	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
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
38	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
39	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
40	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
41	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	1	1	1	1	0	0	0	1
42	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
43	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0
44	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1

[illegible]

APPENDIX II. Continued.

B) Species identification

Assigned number	Species
1.	<i>Agnatina capitata</i> (1.0–2.0 mm HCW)
2.	<i>A. capitata</i> (2.0–3.0 mm HCW)
3.	<i>Paragnetina media</i> (0.2–0.4 mm HCW)
4.	<i>P. media</i> (0.4–0.5 mm HCW)
5.	<i>P. media</i> (1.0–2.0 mm HCW)
6.	<i>Rhyacophila fuscula</i> (0.2–0.5 mm HCW)
7.	<i>R. fuscula</i> (0.8–1.0 mm HCW)
8.	<i>Optioservus fastiditus</i>
9.	<i>Stenelmis</i> nr. <i>bicarinata</i>
10.	<i>Promoresia elegans</i>
11.	<i>Ephemerella subvaria</i>
12.	<i>Paraleptophlebia adoptiva</i>
13.	<i>Brachyptera fasciata</i>
14.	<i>Baetis tricaudatus</i>
15.	<i>Paracaphia angulata</i>
16.	<i>Cheumatopsyche</i> sp. (0.2–0.4 mm HCW)
17.	<i>Cheumatopsyche</i> sp. (0.4–0.8 mm HCW)
18.	<i>Hydropsyche sparna</i>
19.	<i>H. morosa</i>
20.	<i>Dolophilodes distinctus</i> (0–0.4 mm HCW)
21.	<i>D. distinctus</i> (0.4–0.6 mm HCW)
22.	<i>D. distinctus</i> (1.0–1.2 mm HCW)
23.	<i>Micrasema</i> sp.
24.	<i>Glossosoma</i> sp. A
25.	<i>G. nigrior</i>
26.	<i>Nais simplex</i>
27.	<i>Tanytarsus</i> sp.
28.	<i>Cricotopus</i> sp.
29.	<i>Thienemanniella</i> sp.
30.	<i>Rheotanytarsus</i> sp.
31.	? <i>Rheosmittia</i> sp.
32.	<i>Parametriocnemus</i> sp.
33.	<i>Eukiefferiella brehmi</i> grp.
34.	<i>Stempellina montivaga</i> grp.
35.	<i>Eukiefferiella gracei</i> grp.
36.	<i>Antocha</i> sp.
37.	fungal hyphae
38.	diatoms
39.	detritus
40.	microinorganic particles
41.	vascular plant material
42.	other algae
43.	chitin fragments
44.	soft body parts
45.	chironomids

APPENDIX III

(A) Food web matrices for the Duffin Creek time-specific webs. A 0 at the intersection of row and column indicates no trophic interaction; 1 indicates a trophic interaction (after Briand 1983). (B) Species identification key, by assigned number.

A) Food web matrices

Resource
species
(assigned
number)

Consumer species (assigned number)

OCTOBER 1985

	1b	2a	3b	4d	4a	5b	6b	7a	8c	9a	10a	11c	12b	13b	14a	15a	16a	17a	18e	19b	20b	21a	22	23a	25b	27b	28	29b	29d	29e
5b	1	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
7a	1	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
8c	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
30	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1
31	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
32	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
33	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
34	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1
35	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
36	0	1	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
37	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
38	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

DECEMBER 1985

	1a	2d	3b	5d	6c	7b	8a	9b	10a	11b	13b	14a	15c	17d	18c	19a	20a	21b	22	23a	24b	25b	26b	28	29b	29e
30	0	1	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
31	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0	1	1	1	1	1	1	1
32	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
33	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
34	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1
35	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
36	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
37	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
38	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

FEBRUARY 1986

	2e	3c	5e	6d	7c	8b	9c	10a	12b	13b	14a	15a	17b	18b	19a	20b	21a	22	23a	24a	25b	26b	27a	28	29f
30	1	1	1	1	1	1	1	1	0	0	1	0	0	1	1	0	1	1	0	1	1	1	0	1	1
31	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	1	1	1	1	0	1
32	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
33	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
34	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	0	1
35	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
36	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

APRIL 1986

	3a	4b	5e	6d	7b	8b	11a	12a	13c	14b	16b	17c	18a	19b	20c	21b	22	23c	24b	25b	26b	27a	28	29c
30	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1
31	1	1	1	0	1	1	1	1	1	0	0	1	1	0	1	1	1	0	1	1	0	1	1	0
32	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
33	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
34	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	0	1	0	1	1
35	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

JUNE 1986

	1b	2b	4c	5c	6a	7a	8e	9d	10c	11c	13a	14a	15a	16c	16d	17a	18d	19a	20b	21a	22	23c	24a	25b	26b	27b	28	29a
5c	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
7a	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
30	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0
31	1	0	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
32	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
33	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
34	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	1	1	0	1	0
35	0	0	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
36	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
37	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
38	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

APPENDIX III. Continued.

AUGUST 1986																										
	2b	4a	5a	6b	7a	8b	9b	11a	13a	14a	15b	16a	17a	18d	19a	20a	21b	22	23b	24a	25b	26c	27a	28	29b	
30	1	0	1	1	1	1	1	0	1	0	0	1	1	1	0	0	1	1	1	0	1	1	0	1	1	
31	0	0	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	
32	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
33	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
34	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	1	
35	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	
OCTOBER 1986																										
	1b	2c	3a	4a	5c	6c	7a	8d	10b	11d	13c	14a	17b	18a	19a	20a	21a	22	23a	24a	25a	26a	27a	28		
30	0	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0	1	0	1	1		
31	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1		
32	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
33	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
34	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0		
35	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
36	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
37	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		

APPENDIX III. Continued.

B) Species identification key

Assigned number	Species	HCW* (mm)
1a	<i>Agnetina capitata</i>	1.0–2.0
1b	<i>A. capitata</i>	2.0–3.0
2a	<i>Paracaphnia angulata</i>	0.1–0.2
2b	<i>P. angulata</i>	0.2–0.3
2c	<i>P. angulata</i>	0.4–0.5
2d	<i>P. angulata</i>	0.7–0.8
2e	<i>P. angulata</i>	0.9–1.0
3a	<i>Brachyptera fasciata</i>	0.2–0.4
3b	<i>B. fasciata</i>	0.4–0.6
3c	<i>B. fasciata</i>	0.6–0.8
4a	<i>Paragnetina media</i>	0.2–0.3
4b	<i>P. media</i>	0.3–0.4
4c	<i>P. media</i>	0.4–0.5
4d	<i>P. media</i>	1.0–2.0
5a	<i>Ephemerella subvaria</i>	0.2–0.4
5b	<i>E. subvaria</i>	0.4–0.6
5c	<i>E. subvaria</i>	1.0–1.2
5d	<i>E. subvaria</i>	1.2–1.4
5e	<i>E. subvaria</i>	1.6–1.8
6a	<i>Paraleptophlebia adoptiva</i>	0.0–0.2
6b	<i>P. adoptiva</i>	0.2–0.4
6c	<i>P. adoptiva</i>	0.4–0.6
6d	<i>P. adoptiva</i>	0.6–0.8
7a	<i>Baetis tricaudatus</i>	0.2–0.4
7b	<i>B. tricaudatus</i>	0.4–0.6
7c	<i>B. tricaudatus</i>	0.6–0.8
8a	<i>Hydropsyche sparna</i>	0.0–0.2
8b	<i>H. sparna</i>	0.2–0.4
8c	<i>H. sparna</i>	0.4–0.6
8d	<i>H. sparna</i>	0.6–0.8
8e	<i>H. sparna</i>	1.0–1.2
9a	<i>Hydropsyche morosa</i>	0.4–0.6
9b	<i>H. morosa</i>	0.6–0.8
9c	<i>H. morosa</i>	0.8–1.0
9d	<i>H. morosa</i>	1.0–1.2
10a	<i>Cheumatopsyche</i> sp.	0.2–0.4
10b	<i>Cheumatopsyche</i> sp.	0.4–0.6
10c	<i>Cheumatopsyche</i> sp.	0.6–0.8
11a	<i>Dolophilodes distinctus</i>	0.0–0.2
11b	<i>D. distinctus</i>	0.2–0.4
11c	<i>D. distinctus</i>	0.4–0.6
11d	<i>D. distinctus</i>	1.0–1.2
12a	<i>Micrasema</i> sp.	0.2–0.3
12b	<i>Micrasema</i> sp.	0.3–0.4
13a	<i>Glossosoma nigrior</i>	0.1–0.2
13b	<i>G. nigrior</i>	0.2–0.3
13c	<i>G. nigrior</i>	0.4–0.5
14a	<i>Glossosoma</i> sp. A	0.1–0.2
14b	<i>Glossosoma</i> sp. A	0.2–0.3
15a	<i>Rhyacophila fuscula</i>	0.2–0.4
15b	<i>R. fuscula</i>	0.4–0.6
15c	<i>R. fuscula</i>	0.8–1.0

APPENDIX III. Continued.

Assigned number	Species	HCW* (mm)
16a	<i>Stenelmis</i> nr. <i>bicarinata</i>	0.1–0.2
16b	<i>S.</i> nr. <i>bicarinata</i>	0.2–0.3
16c	<i>S.</i> nr. <i>bicarinata</i>	0.3–0.4
16d	<i>S.</i> nr. <i>bicarinata</i>	0.4–0.5
17a	<i>Promoresia elegans</i>	0.1–0.2
17b	<i>P. elegans</i>	0.2–0.3
17c	<i>P. elegans</i>	0.3–0.4
17d	<i>P. elegans</i>	0.4–0.5
18a	<i>Optioservus fastiditus</i>	0.1–0.2
18b	<i>O. fastiditus</i>	0.2–0.3
18c	<i>O. fastiditus</i>	0.3–0.4
18d	<i>O. fastiditus</i>	0.4–0.5
18e	<i>O. fastiditus</i>	0.5–0.6
19a	<i>Thienemanniella</i> sp.	0.0–0.1
19b	<i>Thienemanniella</i> sp.	0.1–0.2
20a	<i>Cricotopus</i> sp.	0.0–0.1
20b	<i>Cricotopus</i> sp.	0.1–0.2
20c	<i>Cricotopus</i> sp.	0.2–0.3
21a	<i>Eukieferiella brehmi</i> grp.	0.0–0.1
21b	<i>E. brehmi</i> grp.	0.1–0.2
22	<i>E. gracei</i> grp.	0.1–0.2
23a	<i>Parametriocnemus</i> sp.	0.0–0.1
23b	<i>Parametriocnemus</i> sp.	0.1–0.2
23c	<i>Parametriocnemus</i> sp.	0.2–0.3
24a	<i>Rheosmittia</i> sp.	0.0–0.1
24b	<i>Rheosmittia</i> sp.	0.1–0.2
25a	<i>Tanytarsus</i> sp.	0.0–0.1
25b	<i>Tanytarsus</i> sp.	0.1–0.2
26a	<i>Rheotanytarsus</i> sp.	0.0–0.1
26b	<i>Rheotanytarsus</i> sp.	0.1–0.2
26c	<i>Rheotanytarsus</i> sp.	0.2–0.3
27a	<i>Stempellina montivaga</i> grp.	0.1–0.2
27b	<i>S. montivaga</i> grp.	0.2–0.3
28	<i>Nais simplex</i>	2.1–2.7 (length)
29a	<i>Antocha</i> sp.	0.0–1.0 (length)
29b	<i>Antocha</i> sp.	1.0–2.0 (length)
29c	<i>Antocha</i> sp.	2.0–3.0 (length)
29d	<i>Antocha</i> sp.	3.0–4.0 (length)
29e	<i>Antocha</i> sp.	4.0–5.0 (length)
29f	<i>Antocha</i> sp.	5.0–6.0 (length)
30	Fungal hyphae	
31	Diatoms	
32	Detritus	
33	Microinorganic particles	
34	Vascular plant material	
35	Other algae	
36	Chitin fragments	
37	Soft body parts	
38	Chironomids	

* Unless otherwise indicated.