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SPATIAL AND TEMPORAL VARIATION IN THE STRUCTURE OF AN INTERMITTENT-STREAM FOOD WEB¹

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Abstract. Food webs from the Lerderderg River, an intermittent stream in Victoria, Australia, were compiled with the aim of examining changes in food web structure in a highly variable habitat. Emphasis was placed on a high degree of taxonomic precision. Spatial and temporal variation in the food webs was assessed by partitioning the study area into three sites, located ≈ 1.5 km apart along the river. Sites differed in overall stream width and the length of the low streamflow period during summer. Three separate webs for each site were compiled for four different times of the year.

Relatively little spatial variation in community structure was observed. In contrast, temporal variation was considerable, with species composition and the number of species in the community changing considerably over the year. The number of species increased dramatically as the period of constant streamflow lengthened. Detritivores dominated the community, both in terms of species and individual numbers. The proportion of predators in the community increased slightly by the end of the year, suggesting that recolonization of the community by predators lags behind that of detritivores. The increase in the number of predator species also resulted in an increase in the mean food chain length through the year.

Patterns observed in the food webs tended to fall within the range of values reported from several previous studies, suggesting that underlying constraints may structure certain aspects of food webs. However, the constancy of certain food web statistics was attributable either to methodological decisions made during compilation, or to an inherent property of the statistic itself. The potential sensitivity of several food web statistics to the methodology used to compile a food web render between-web comparisons difficult due to the confounding effects of methodology. This suggests that comparisons between food webs should be restricted to webs derived from similar habitats using a comparable methodology.

Key words: connectance; disturbance; food-chain length; food chains; food web patterns; food webs; food web theory; intermittent streams; predator–prey ratios; spatial and temporal variation; succession; trophic interactions.

INTRODUCTION

Analyses of large collections of published food webs have suggested that food webs show consistent structural patterns (Cohen 1977, 1978, Pimm 1982, Briand and Cohen 1984, 1987, Cohen and Briand 1984, Briand 1985, Lawton and Warren 1988, Lawton 1989, Sugihara et al. 1989, Cohen et al. 1990, Pimm et al. 1991, Schoenly and Cohen 1991, Schoenly et al. 1991). These regular patterns include short food chains (Elton 1927, Pimm 1982); a constant number of links per species (Cohen and Briand 1984); an inverse relationship between web connectance and the number of species (May 1972, 1973, Rejmanek and Stary 1979, Pimm 1982); constant predator species to prey species ratios (Cohen 1977, 1978, Briand and Cohen 1984, Jeffries

and Lawton 1985, Lockwood et al. 1990, Warren and Gaston 1992); and constant proportions of top, intermediate, and basal species (Briand and Cohen 1984).

The observation of these patterns, and the possible reasons for their existence, have generated considerable debate. Views on the significance of different patterns have ranged from those who suggest that the patterns may be indicative of an underlying order in nature (e.g., Pimm et al. 1991) to those who view them as artifacts of food web compilation (e.g., Paine 1988) or mathematical artifacts (e.g., Closs et al. 1993). Several causative mechanisms for different patterns have been suggested, including the dynamics of predator–prey interactions (May 1972, 1973, Pimm 1982); inefficiencies in the transfer of energy between successive trophic levels (Elton 1927, Lindeman 1942, Yodzis 1981, 1984); biological size and design constraints (Elton 1927, Colinaux 1978, Pimm 1982, Warren and Lawton 1987); and topological or mathematical constraints (Auerbach 1984, Kenny and Loehle 1991, Closs et al. 1993).

Different aspects of these proposed mechanisms have been incorporated into theoretical food-web models,

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which predict observed patterns with varying degrees of success (see reviews by Pimm 1982, Lawton and Warren 1988, Lawton 1989, Pimm et al. 1991). Three groups of models, the dynamic model (Pimm 1982), the static cascade model (Cohen and Newman 1985), and the energetic constraints model (Yodzis 1981, 1984) suggest that biological constraints generate food web structure. Alternatively, the observation of similar patterns in random models has raised questions about the biological significance of several of the patterns (Auerbach 1984, Kenny and Loehle 1991, Closs et al. 1993), although the success of the different random models in predicting the various patterns varies. Random models can predict the observed values of Cohen's (1977) predator-prey ratio (Closs et al. 1993), and an inverse relationship between connectance and species number (Auerbach 1984, Kenny and Loehle 1991). In contrast, they tend to predict a higher proportion of long food chains than are observed in real webs (Pimm 1982), and proportions of top and basal species that are too low when compared with real webs (Cohen and Newman 1985). No single random model can quantitatively predict all the patterns observed in food webs.

Doubts as to whether certain patterns are real or merely artifacts present in poor-quality data have focussed on the variability in the quality of much food web data (Paine 1988, Peters 1988, Lawton 1989, Moore et al. 1989, Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991). A significant feature of the statistics used to examine food web structure is that they are based solely upon the presence/absence of taxa and feeding links within a web. Consequently, they can be calculated from any food web irrespective of its quality or the availability of any additional data such as species abundance or the significance of trophic links in energy flux (Paine 1988). The observation that food webs possess an inherent structure has been based upon analyses of several large collections of published food webs gleaned from a diverse range of sources (see Sugihara et al. 1989, Cohen et al. 1990, Schoenly and Cohen 1991, Schoenly et al. 1991). Few of these webs have been compiled for the expressed intention of being analyzed for their structure (Paine 1988, Lawton 1989). Factors such as the methodology used to collect data and the spatial and temporal scales of study vary enormously in the webs included in various food-web collections (Polis 1991). In particular, the incompleteness of many food-web descriptions may have contributed to the constancy of certain food-web patterns such as short food chains, and low levels of omnivory and connectance (Warren 1989, Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991). Recent analyses of large, detailed food webs have suggested that features such as long food chains and omnivory may actually be more common than has been previously observed (Hildrew et al. 1985, Warren 1989, Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991).

Intermittent streams and habitat variability

Defining appropriate spatial and temporal scales of study presents food web researchers with considerable difficulties given that all food webs are spatially and temporally open-ended. Determination of such scales is crucial given that they will influence the structure of the resultant web (Polis 1991). The great majority of food webs lump together species and interactions recorded within a habitat over a relatively long period of time, e.g., several months to a year (e.g., Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991). Such lumping may obscure significant temporal variation in structure, resulting in food webs that are completely unrealistic representations of the food web present at any one time (Kitching 1987, Warren 1989, Schoenly and Cohen 1991)—a potentially serious problem in food webs from highly variable habitats (Kitching 1987).

Intermittent streams, that is, streams which cease to flow on a regular and predictable basis (Boulton and Suter 1986, Boulton and Lake 1988), are an ideal environment in which to examine spatial and temporal variation in food web structure. Amplitudes in the physico-chemical conditions found in intermittent streams usually exceed those observed in permanent streams of a similar size (Boulton and Lake 1990). Depth and current may vary enormously, with conditions alternating seasonally between a swiftly flowing stream and still, stagnant pools (Boulton and Suter 1986). Dissolved oxygen declines with diminishing flow, often falling to values close to zero in stagnant pools (Boulton and Suter 1986). Temperatures in still summer pools may exceed 30°C (Lake et al. 1986, Boulton 1989, Boulton and Lake 1990). In Australian intermittent streams the difficult physical conditions may be further exacerbated by the fact that peak leaf fall in eucalypt forests is in summer, thus coinciding with periods of diminished streamflow (Towns 1985, Lake et al. 1986, Boulton and Lake 1992c).

The structure of intermittent stream communities changes markedly in response to variation in the physico-chemical regime (Boulton and Lake 1992a, b). Species richness and abundance generally increase the longer streamflow or permanent water persists (Boulton and Suter 1986, Lake et al. 1986, Smith and Pearson 1987, Boulton and Lake 1992b). Boulton and Lake (1990, 1992a) observed that patterns of faunal change closely matched changes in the physico-chemical regime of the Lerderderg and Werribee Rivers. Changes in community structure showed a cyclical sequence characterized by distinct pre-flow, early flow, main flow, diminishing flow, and post-flow phases. The sequence was broken only by the drying up of the stream (Boulton and Lake 1990, 1992a).

The inherent variability of intermittent stream communities allows examination of the effect of seasonal variation on aspects of food web structure, such as

predator–prey ratios and food chain length. In addition, changes in the physico-chemical environment also provide an opportunity to examine the predictions made by Sanders (1968), Slobodkin and Sanders (1969), May (1972, 1973), Menge and Sutherland (1976), and Peckarsky (1983) that communities should become simpler, and biological interactions weaker, as environmental conditions become less predictable. Theoretically, food webs dominated by many weak interactions should show little or no relationship between environmental predictability and structure (DeAngelis 1975, Pimm 1982), a pattern that may be typical of food webs based upon a basal resource of detritus (Pimm 1982). Stream food webs do tend to contain a high proportion of detritivorous species (e.g., Jones 1950, Cummins et al. 1966, Minshall 1967, Koslucher and Minshall 1973, Hildrew et al. 1985), a feature that may increase their resistance and resilience to environmental disturbance (see DeAngelis 1992). Hildrew et al. (1985) also observed high levels of connectance and omnivory in a stream food web, both patterns that are predicted to increase dynamic instability in a web dominated by strong predator–prey interactions (May 1972, 1973, Pimm 1982). Theoretically, such webs should be unlikely to persist in unstable, unpredictable habitats (May 1972, 1973, Pimm 1982).

In this paper we present the results of a detailed analysis of the food web of the upper Lerderderg River, an intermittent stream in central Victoria (Australia). This study examines spatial and temporal variation in food web structure, with four seasonal food webs collected from three separate sites being presented. Significantly, all of the detailed, stream community food webs that have been compiled to date have come from permanent streams (e.g., Jones 1950, Cummins et al. 1966, Hildrew et al. 1985) or from spring-fed streams (e.g., Minckley 1963, Minshall 1967, Tilly 1968, Koslucher and Minshall 1973, Collins et al. 1976). Many of these habitats are relatively stable and do not show great seasonal variation (e.g., Tilly 1968, Collins et al. 1976). In addition, relatively few detailed food-web studies from any habitat have examined temporal or spatial variation in food web structure (see Schoenly and Cohen 1991 for examples). Of those that have, none have been based on stream ecosystems (Cohen et al. 1990, Schoenly and Cohen 1991).

METHODS

Study sites

The Lerderderg River rises ≈ 100 km northwest of Melbourne in the Wombat State Forest, and flows in a southeasterly direction before joining the Werribee River near Bacchus Marsh (Fig. 1). Vegetation in the study area consists of tall open eucalypt forest dominated by messmate (*Eucalyptus obliqua*), mountain grey gum (*E. cypellocarpa*), and manna gum (*E. viminalis*). The riparian understory consists of a variety of small

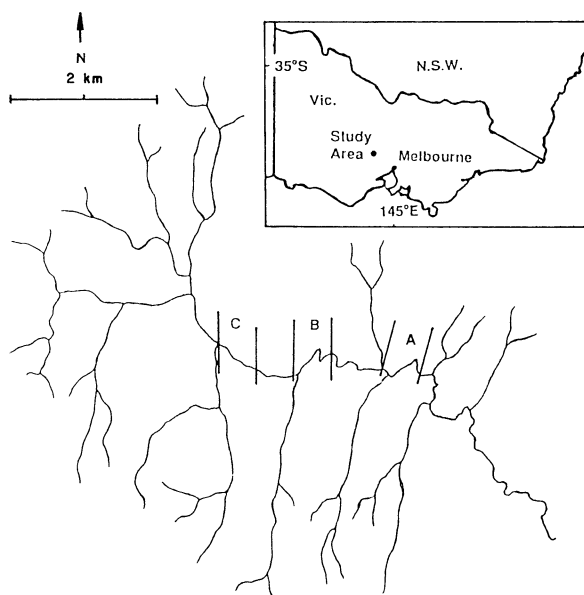


FIG. 1. Location of study sites A, B, and C in central Victoria, Australia.

trees and shrubs such as blackwood (*Acacia melanoxylon*) and mountain correa (*Correa lawrenciana*), with a dense ground cover of ferns (*Blechnum* sp.), blackberries (*Rubus* sp.), and forest wire grass (*Tetrarrhena juncea*). Human activity in the upper catchment of the Lerderderg River is restricted to recreation and some selective logging.

Mean monthly air temperature ranges from 25°C in February to 2°C in July. Extreme temperatures may exceed 40°C in summer and fall below freezing in winter. The area receives an average annual rainfall of 950 mm, the highest rainfall being in spring (Boulton 1988; M. A. Smith, *unpublished report* [1976] to the State Rivers and Water Supply Commission, Melbourne, Victoria, Australia). Flow is both relatively low and highly variable (Fig. 2). The mean discharge rate is $27.3 \times 10^3 \text{ m}^3/\text{d}$ with a coefficient of variation in annual flow of 62% at O'Brien's Crossing, a flow-measuring station ≈ 10 km downstream of the study area (Boulton and Lake 1990). On average, the river ceases to flow for two out of three summers (Boulton and Lake 1990), and on cessation of flow a series of isolated pools are formed. Flow usually resumes in April or May and peaks in late winter or early spring.

For the food web study we selected three sites along a 6-km reach of river (Fig. 1). Sites A, B, and C were at a mean altitude of 590, 620, and 650 m, respectively. Each site consisted of 24 small, usually permanent, pools spread along ≈ 1 km of the river. Pools were identified in March 1985 prior to the commencement of flow. The substrate at all sites was predominantly pebbles and cobbles, with some areas of boulders and bedrock. Pool size varied from 2 to 10 m long and up

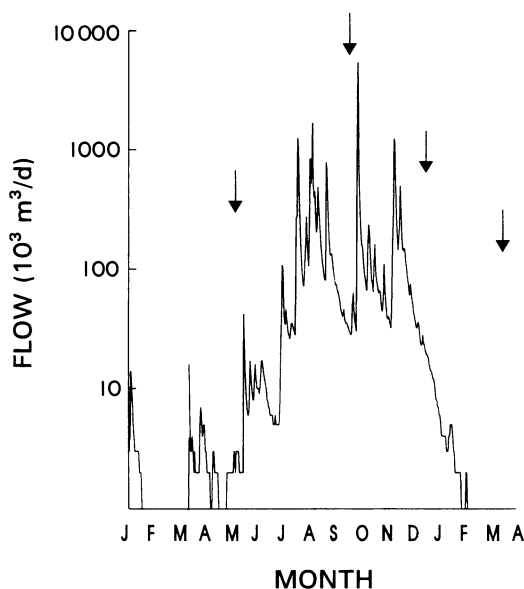


FIG. 2. Graph of daily discharge at O'Briens Crossing over the sampling period for the food web study January 1985–April 1986. Arrows indicate sampling dates.

to 0.6 m deep. The stream bed width varied from 3 to 8 m. Streamflow tended to cease for increasingly longer periods over summer moving upstream. Compared with site A, site C tended to experience longer periods of zero or very low flow, with remnant pools tending to be smaller and shallower by the end of summer.

Field procedures

We collected samples for food web analysis in May 1985, September 1985, December 1985, and March 1986, dates that corresponded approximately with the early flow, main flow, diminishing flow, and post-flow phases identified by Boulton and Lake (1990). Streamflow over the period of study is displayed in Fig. 2.

On each occasion we randomly selected six small pools from each of the three sites. Each pool was sampled only once during the study. Initially, a qualitative 'sweep' sample of the open water was collected using a dip net with a 300- μ m mesh. These samples were taken with the aim of collecting mobile animals and rarer predatory species, such as fish, nektonic beetles, and ecnomid caddis larvae, which might not have been collected in adequate numbers for determination of diet during subsequent quantitative sampling. The sweep samples were not used in any analysis of community structure, other than to supplement the numbers of animals available for gut content analysis.

Following collection of the sweep sample, a sample was collected from an area undisturbed by the prior dip-netting using a suction sampler, which allowed quantitative samples to be collected independently of streamflow conditions (Boulton 1985). Each sample covered an area of 0.05 m², collecting animals in the

water above the substrate and to a depth of ≈ 10 cm into the substrate.

Laboratory procedures

Each animal collected was identified to the lowest taxonomic division possible. We placed emphasis on a high degree of taxonomic resolution in an attempt to avoid one of the most common problems observed in many published food webs, that is, the differential lumping of species at different trophic levels (Paine 1988). Such lumping of species may influence the observation of patterns, such as constant predator-to-prey species ratios and constant links-per-species ratios (Pimm 1982, Paine 1988, Closs et al. 1993).

Following identification, we sorted representatives of each species into approximate size-classes. For non-predatory species (mostly detritivores), five animals from each class were selected for diet analysis. Such numbers adequately covered the range of food items observed in the guts of animals with relatively uniform diets, such as detritus. Predators had more diverse diets (G. P. Closs and P. S. Lake, *personal observation*), hence all available individuals from each predatory species were dissected and their gut contents examined (105 individuals in the case of *Hydra* sp.).

Each animal selected for dissection was measured, to the nearest 0.01 mm, along a particular body axis. Measurements of the head width of insects, the body width of crustaceans, the longest body axis of molluscs, and the total length of fish were taken. Soft-bodied animals such as flatworms and *Hydra* sp. were not measured due to the variable shrinkage that occurs following preservation.

Gut content analysis was the only method used to identify feeding interactions. We did not use literature records and feeding trials (e.g., Kitching 1987, Warren 1989), as we wished to avoid the possibility of including feeding interactions that do not actually occur in the habitat under study. Feeding trials could force species of predator and potential prey together that, under natural conditions, might never encounter each other at the microhabitat level. Similarly, feeding interactions observed in one habitat may not be representative of interactions that occur in other habitats. Food webs based on gut data alone represent, at best, a minimum estimate of the interactions occurring in the community at the time of sampling. However, such webs may also be biased in other ways. Information based on gut contents may underestimate the number of soft-bodied prey consumed (e.g., flatworms, molluscs), and cannot provide any information on the diet of fluid feeders (e.g., dytiscids, mites).

We obtained gut contents by either dissecting out the alimentary canal or, in the case of very small individuals such as copepods, early instar insects, etc., crushing under a coverslip as described by Fryer (1957). Whenever possible, only material from the foregut of detritivorous or herbivorous invertebrates was taken

for dietary examination. This reduced the effect of digestion on the proportions of the food categories ingested and recorded. We classified the gut contents from non-carnivorous species into six categories: amorphous detritus, dead cellular plant material (DCPM), filamentous algae, diatoms, fungi, and inorganic material.

Material collected from the guts of predators was counted and identified to species level where possible by comparing gut contents to a type collection of known invertebrates mounted on slides. We measured the size of the prey consumed if the head capsule or intact thorax of the prey was present in the gut. The gut contents of suctorial predators, such as the larvae of dytiscid and gyrid beetles and water mites, contained no identifiable remains. Consequently we could not determine their diets using gut content analysis. Observation of their feeding behavior was also impossible on account of their small size, hence the diets of these animals remained undetermined.

Community analysis

We summarized spatial and temporal variation in community structure using two indices, the mean species richness per sample and the mean number of individuals per square metre. We also compared overall spatial and temporal variation in community structure by ordinations of species abundance data from all sites for each sampling date.

Prior to ordination of the 72 samples collected, we deleted all species that occurred in <7 samples. All of the deleted species were rare, usually occurring in low numbers in one or two samples. This procedure retained the relatively common species, most of which occurred in all 18 samples collected from the three sites on any particular date. We $\log_{10}(x + 1)$ -transformed the remaining species abundances, then standardized them by dividing the abundance of each species in each sample by the maximum abundance attained by that species in any sample. This transformation and standardization prevented particularly abundant species from dominating the subsequent ordination (O'Connor 1991). We calculated compositional dissimilarity between each pair of samples using the Bray–Curtis dissimilarity coefficient (Minchin 1987, O'Connor 1991). We used multidimensional scaling (MDS) procedures for the ordination of species abundance data, initially performing global nonmetric MDS using 20 nonrandom starting configurations in two and three dimensions (Kruskal 1964, Minchin 1987, O'Connor 1991). A two-dimensional solution was used if there was only a small increase in stress over a three-dimensional solution, and if comparison by procrustean analysis suggested several identical configurations from the random starts (O'Connor 1991). The starting configuration for hybrid MDS was then selected from the minimum-stress configuration amongst the 20 global nonmetric MDS starts, thus constraining the final hybrid MDS

configuration and preventing the possibility of degenerate solutions arising (Minchin 1987, O'Connor 1991).

Food web analysis

We compiled seasonal food webs for each site based on the abundance of animals in the quantitative suction samples. Rare species, defined as those that comprised <1% of the total abundance recorded from each site for any one season, were excluded from the food web for that site. Exclusion of rare species was considered necessary given the large number of species for which only a few individuals were recorded. Such rare species were unlikely to represent significant paths for energy transfer within the web.

Two problems quickly became apparent with this criterion for inclusion in the food webs. The cutoff point for inclusion excluded virtually every predator species, as most only occurred in relatively low numbers. Species otherwise defined as rare were also recorded in the guts of predators. To counter the first problem, a different definition of rarity was used for predators. Predators were included in the food webs if five or more were available for gut content analysis. The few rare species that were recorded in the guts of predators were simply included in the food webs for the sake of completeness. In addition, although *Galaxias olidus*, a small minnow-like fish, were not collected in any suction sample, they were included in the food web as they were obviously a key predator in the system. *G. olidus* were the only vertebrate predator observed feeding in the stream over the study period.

The prey of suctorial predators, such as dytiscid beetle larvae and water mites, could not be identified. Consequently, for the purposes of the calculation of statistics such as connectance (which requires the number of links per species as part of its calculation), we assumed they had the mean number of links per species for the web in which they were recorded. As noted previously, such an assumption may have biased the calculation of food web statistics, such as connectance and mean food chain length, in unknown ways.

We calculated connectance using the formula described by Beaver (1985),

$$C = L/[S(S - 1)/2],$$

where L is the number of observed links and S is the number of species in the web. The number of links per species was calculated by dividing L by S .

We used the different procedures described by Cohen (1977) and Jeffries and Lawton (1985) to calculate two separate predator–prey ratios for each web. The two ratios are calculated using different procedures, and hence give significantly different results (Closs 1991a). All categories (i.e., including detritus, diatoms, and algae) were included in the calculation of Cohen's predator–prey ratio and to calculate the proportions of basal, intermediate, and top species in the food web (Briand and Cohen 1984). Only those species included in

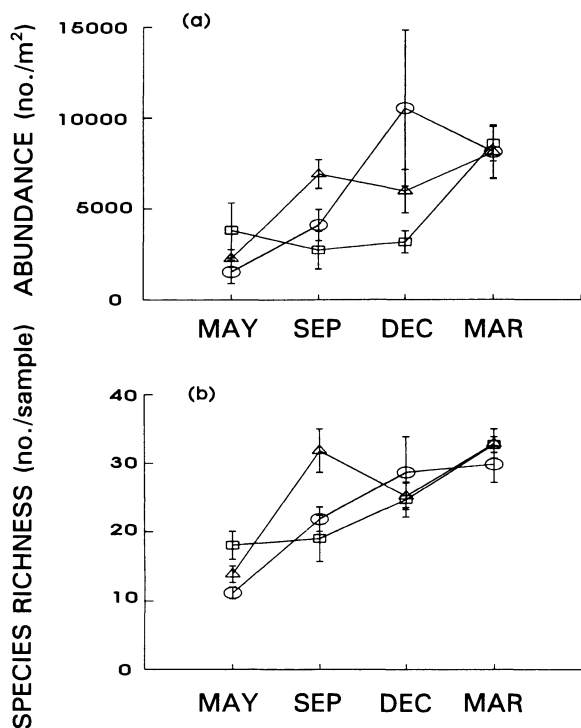


FIG. 3. Means of (a) abundance and (b) species richness for each site and sampling date. \square = site A, \circ = site B, \triangle = site C. Error bars show ± 1 SE.

the food webs were used to calculate Cohen's ratio. In contrast, no non-animal species were included, and the complete species list for the community, rather than the food web species list, was used to calculate Jeffries and Lawton's predator-prey ratio.

We calculated the longest and mean food-chain lengths using the methods described by Pimm (1982) and Cohen et al. (1986). The longest chain length refers to the single longest observed series of links between a top predator and a basal species in a food web. The mean chain length is estimated by determining the length of all food chains in a food web and then calculating a mean value from them.

RESULTS

Community analysis

A total of 110 taxa were collected during the quantitative benthic sampling program, with dipterans being the most diverse order (36 spp.), followed by trichopterans (19 spp.) and plecopterans (14 spp.). Numerically dipterans (mostly chironomids), molluscs (particularly *Angrobia* sp.) and oligochaetes (at least 3 spp.) were consistently amongst the most abundant taxa (Table 1). Total abundance (Fig. 3a) and species richness (Fig. 3b) varied through the year, with both indices being at their lowest in May 1985 and highest in March 1986.

Ordination of the species abundances suggested that

changes in community structure over time were much greater than any spatial differences between sites (Fig. 4). Samples taken in any one season at any site tended to be more alike than samples taken at the same site on different dates. There was no evidence to suggest that any one site was consistently different from any other site on any single date or over the course of the year. The trajectory of the clusters of points for each season (Fig. 4) suggested a cyclical pattern of community change similar to that described by Boulton and Lake (1992a). The lack of overlap between the clusters of points for each date probably reflects the length of time separating each sampling date. Despite the lack of overlap between the clusters, most of the more common species were recorded on more than one sampling date (Table 1). Several, such as the abundant molluscs *Angrobia* sp. and *Ferrissia* spp. and chironomids such as *Paramerina* sp., were recorded throughout the year at every site (Table 1).

Dietary analysis

The diet of non-predators.—Amorphous detritus and dead cellular plant material (DCPM) formed the basis of the Lerderberg River food web (Fig. 5). The significance of amorphous detritus in the diet of detritivores remained relatively constant throughout the year (Fig. 6), being observed in the guts of virtually every non-predatory individual examined. The importance of DCPM as a food source also remained relatively con-

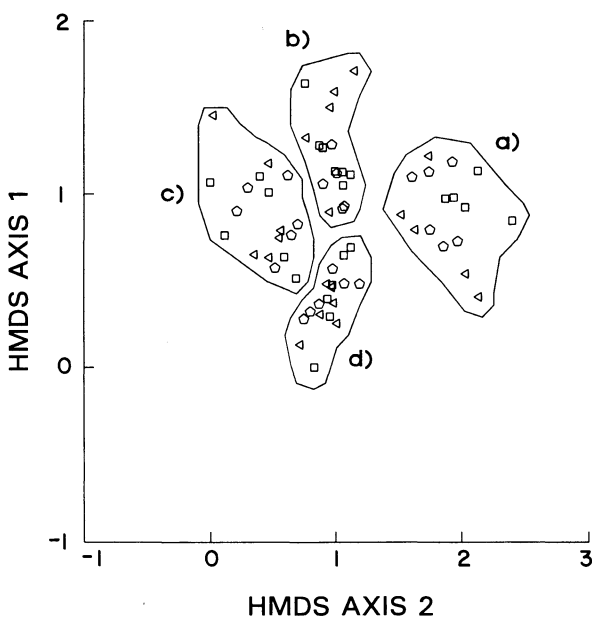


FIG. 4. Hybrid multidimensional scaling (HMDS) ordination of the benthic samples collected for the food web study. Polygons enclose samples collected on the same date. (a) May 1985, (b) September 1985, (c) December 1985, (d) March 1986. Sites identified by symbols: \square = site A, \circ = site B, \triangle = site C. Ordination axes scaled in half-change units (i.e., samples one half-change unit apart are $\approx 50\%$ similar).

stant over the course of the year, although there was a slight peak in the proportion of species consuming large amounts of DCPM during the low-flow periods (Fig. 6). This increase during the low-flow period can be attributed to the presence of large numbers of late-instar larvae, such as the cased-caddis larvae *Triplectides truncatus* and *Tamiasia acuta*, and the stonefly *Acruroperla atra* (Table 1).

The increased proportion of inorganic material (Fig. 6) in the diet of stream invertebrates in May 1985 and March 1986 was associated with an increase in the number of species that scraped material off the surface of hard substrates, such as the gastropod *Angrobis* sp. and the freshwater limpet *Ferrissia* spp. Algae and diatoms were frequently observed in the guts of these species (Fig. 5), although the amounts observed were rarely large.

The diet of predators.—The feeding of individual invertebrate predators tended to be concentrated on relatively few taxa, although collectively the range of prey was quite broad. Whilst the 18 recorded invertebrate predators ingested at least 27 species of prey, most species were observed feeding on <5 species (Fig. 5). Dipterans, mostly chironomids (15 sp.), were the most frequently recorded aquatic prey taxa (Fig. 7). Of those, the majority consisted of small individuals of a single species, the chironomid *Riethia* sp., a particularly common species for much of the year (Table 1, Fig. 5). In contrast, the range of prey taken by *Galaxias olidus* was much wider, with 33 species being recorded, and no one species being particularly favored (Fig. 5).

Prey size clearly played a role in determining the range of species preyed upon by a predator. The ability of *G. olidus* to consume prey across a wide size range (Fig. 8) probably contributed to the large number of species consumed by this species. In addition, engulfing predators, both fish and invertebrates, invariably took prey smaller than themselves (Fig. 8), a feature that suggests a size hierarchy of predator and prey.

Several species of invertebrate, such as cased caddis larvae (e.g., *Triplectides truncatus*) and the five species of molluscs, were rarely or never observed in the guts of any predator despite being abundant in the community (Figs. 5 and 7, Table 1). However, the possibility that, at least in the case of molluscs, predators ate the soft body and discarded the shell cannot be discounted.

Analysis of food web structure

Patterns of spatial and temporal variation in food web structure reflected the results of the community analysis in that spatial variation was considerably less than temporal variation (Figs. 5, 9, and 10). Spatial variation was restricted to relatively minor differences in the species composition of the web (Fig. 5). In contrast, temporal variation in web size was considerable, with the mean number of species included in the food

webs increasing from 24 species in May 1985 to 53 species in March 1986 (Fig. 5).

The relatively small spatial differences observed did not generally translate into substantial differences in the values of the derived food-web statistics (Fig. 9). However, in some instances the value of a statistic was sensitive to the presence or absence of a single species. *G. olidus*, a top predator, was only observed at site C in May 1985, an occurrence that resulted in longer food chains at that site for that particular date (Fig. 9d).

Whilst temporal changes in species composition and species richness were substantial, only the values of web connectance and the proportions of top, intermediate, and basal “species” changed markedly. Connectance declined in value (Fig. 10a) as the number of species per web increased, a consequence of the constancy of the number of links per species (Fig. 10a). This occurred despite the large number of links attributed to *G. olidus* (33 links) in March 1986. A significant factor contributing to that constancy was the increase in the number of species feeding on detritus over time (Fig. 5).

The proportions of top, intermediate, and basal species changed as species number increased, and were clearly influenced by the patterns of linkage within the web. The large number of links attributed to *G. olidus* in March 1986 had a significant impact on the proportions of top and intermediate species (Fig. 5). Their presence in March 1986 greatly increased the number of species that were recorded as having a predator. Consequently, the proportion of species recorded as intermediate rose at the expense of the proportion of top species (Fig. 10b). The high number of links attributed to *G. olidus* in March 1986 also caused the value of Cohen’s predator–prey ratio to decline slightly since *G. olidus* increased the number of species counted as prey. In contrast to the changes in the numbers of top and intermediate predators observed over time, the number of basal “taxa” remained constant (Fig. 5), resulting in a decline in the proportion of basal taxa observed over time (Fig. 10b). In contrast the value of Jeffries and Lawton’s predator–prey ratio was at its highest in March 1986 (Fig. 10c). Increasing numbers of predator species in the community over time also appeared to contribute, in part, to the increase in mean food-chain length (Fig. 10d) that occurred during the study period.

DISCUSSION

Community structure and trophic interactions in the Lerderderg River

The results of this study are closely comparable to the results of Boulton (1988). The community of the Lerderderg River was characterized by considerable cyclical change in species composition and abundance. Species composition of the community was characteristic of certain flow phases (i.e., pre-flow, main flow,

TABLE 1. Abundance of common species at all three sites (A, B, C) by date (no./m², means \pm 1 SD). Species abundances indicated by question marks refer to mobile species that could not be quantitatively sampled but were commonly observed. Predators are highlighted in bold type. "(A)" following a species name indicates adult insect.

Species	May 1985			September 1985	
	A	B	C	A	B
<i>Oligochaeta</i> sp.	480 \pm 96	672 \pm 128	128 \pm 48	304 \pm 80	544 \pm 48
Cnidaria					
<i>Hydra</i> sp.	96 \pm 48	48 \pm 32			
Turbellaria					
<i>Cura pinguis</i>	32 \pm 32	48 \pm 32	16 \pm 16	32 \pm 16	48 \pm 32
Mollusca					
<i>Ferrissia</i> sp.	1296 \pm 176	48 \pm 32	16 \pm 32	16 \pm 16	32 \pm 32
<i>Angrobia</i> sp.	96 \pm 48	48 \pm 32	48 \pm 32	513 \pm 144	1024 \pm 96
<i>Sphaerium tasmanicum</i>	16 \pm 16	432 \pm 80	608 \pm 144	16 \pm 16	560 \pm 96
<i>Physastra gibbosa</i>	176 \pm 64	272 \pm 48	32 \pm 16	32 \pm 16	224 \pm 48
<i>Glacidorbis hedleyi</i>	256 \pm 512			32 \pm 16	64 \pm 32
Diptera					
<i>Chironomus</i> sp.	416 \pm 96	352 \pm 64	272 \pm 48		48 \pm 32
<i>Paramerina</i> sp.	128 \pm 64	16 \pm 16	128 \pm 48	32 \pm 32	64 \pm 32
<i>Coelopynia</i> sp.				4 \pm 5	3 \pm 9
<i>Riethia</i> sp.	400 \pm 128			240 \pm 64	1136 \pm 96
<i>Cricotopus annuliventris</i>				16 \pm 16	48 \pm 16
<i>Rheotanytarsus</i> sp.					
<i>Parakiefferiella</i> sp.					
<i>Thienmaniella trivittata</i>					
<i>Tanytarsus inextensus</i>	16 \pm 16		16 \pm 16		
nr. <i>Halocladius</i> sp.					
<i>Stempellina</i> sp.					
<i>Austrosimulium</i> sp.					32 \pm 32
Tipulidae sp. 1	16 \pm 16		16 \pm 16	16 \pm 16	
Ceratopogonidae sp.					32 \pm 32
Tipulidae sp. 2	32 \pm 48				
Empididae sp. 1					
Trichoptera					
<i>Triplectides truncatus</i>	64 \pm 32	64 \pm 32	48 \pm 16	48 \pm 32	192 \pm 64
<i>Triplectides ciuskeus</i>	96 \pm 48	16 \pm 16	16 \pm 16		
<i>Helicopsyichidae</i> sp.	144 \pm 64	16 \pm 16		112 \pm 32	32 \pm 16
<i>Leptorussa darlingtoni</i>	16 \pm 16	128 \pm 48	160 \pm 48		48 \pm 32
<i>Agapetus kimminsii</i>				112 \pm 64	16 \pm 16
<i>Tasmasia acuta</i>	16 \pm 16		32 \pm 32	16 \pm 16	64 \pm 32
<i>Ecnomus russellius</i>	16 \pm 16			16 \pm 16	
<i>Oecetis</i> sp.				16 \pm 16	
<i>Apsilochorema</i> sp.					
Ephemeroptera					
<i>Nousia fuscula</i>	16 \pm 32	16 \pm 16			
<i>Koorononga pilosa</i>				256 \pm 80	1136 \pm 128
Plecoptera					
<i>Leptoperla bifida</i>				16 \pm 32	112 \pm 48
<i>Riekoperla rugosa</i>				176 \pm 48	208 \pm 64
<i>Illiesoperla australis</i>				16 \pm 32	160 \pm 48
<i>Austrocerca tillyardi</i>	16 \pm 16				
<i>Acruroperla atra</i>	16 \pm 16	16 \pm 16	16 \pm 16	48 \pm 32	32 \pm 16
<i>Dinotoperla serricauda</i>					48 \pm 32
Coleoptera					
<i>Necterosoma penicillatus</i> (A)	?	16 \pm 16	16 \pm 16	?	?
<i>Necterosoma penicillatus</i>					
<i>Macrogyrus oblongus</i>					
<i>Macrogyrus oblongus</i> (A)		?	?		
Crustacea					
<i>Eucyclops</i> sp.	80 \pm 48	16 \pm 32		16 \pm 32	192 \pm 48
<i>Macrocylops albidus</i>	48 \pm 48			16 \pm 16	48 \pm 32
<i>Ilyocypris australiensis</i>				64 \pm 32	320 \pm 80
<i>Afrochiltonia australis</i>				16 \pm 16	32 \pm 16
<i>Pleuroxus</i> sp.					

TABLE 1. Continued.

September 1985	December 1985			March 1986		
C	A	B	C	A	B	C
496 ± 96	224 ± 48	288 ± 48	304 ± 80	240 ± 32	272 ± 64	224 ± 48
				64 ± 32	80 ± 32	64 ± 32
48 ± 16	112 ± 32	64 ± 32	112 ± 32	80 ± 48	32 ± 16	80 ± 32
16 ± 16	16 ± 16	128 ± 64		688 ± 96	352 ± 48	176 ± 48
736 ± 96	160 ± 32	720 ± 128	1072 ± 144	528 ± 96	1712 ± 160	192 ± 64
352 ± 128	16 ± 16	80 ± 48	624 ± 128	16 ± 16	192 ± 64	384 ± 96
128 ± 486		64 ± 48	64 ± 48	32 ± 16	192 ± 48	256 ± 64
32 ± 32		16 ± 16	16 ± 16	32 ± 16	16 ± 16	32 ± 16
		32 ± 32	96 ± 64	224 ± 80	160 ± 48	704 ± 96
32 ± 32	96 ± 32	96 ± 32	192 ± 64	400 ± 64	656 ± 80	528 ± 64
4 ± 5						
304 ± 64	352 ± 64	764 ± 128	1328 ± 160	2432 ± 144)	1520 ± 128	2416 ± 144
80 ± 32	80 ± 32	384 ± 96	544 ± 80		80 ± 32	
	32 ± 16	32 ± 32	96 ± 48			
		16 ± 16	16 ± 16			
			16 ± 16	96 ± 48	16 ± 16	16 ± 16
	80 ± 32	384 ± 96	544 ± 80	128 ± 64	160 ± 80	128 ± 48
				32 ± 32	192 ± 48	48 ± 32
	16 ± 16		32 ± 32	64 ± 32	64 ± 32	80 ± 32
16 ± 16			16 ± 32			
	16 ± 16			16 ± 16	16 ± 16	16 ± 16
	16 ± 16	16 ± 16	16 ± 16	16 ± 16	64 ± 32	48 ± 32
32 ± 16		16 ± 16	112 ± 64	176 ± 64	160 ± 48	272 ± 64
				32 ± 16	16 ± 16	
32 ± 16	32 ± 32	16 ± 16	16 ± 16	272 ± 64	144 ± 48	48 ± 32
48 ± 32						
48 ± 32	96 ± 32	416 ± 112	512 ± 96			
16 ± 16			16 ± 16	624 ± 80	240 ± 64	192 ± 64
	16 ± 16	16 ± 16	16 ± 16	160 ± 64	144 ± 48	48 ± 32
				48 ± 32	48 ± 32	16 ± 16
				48 ± 32		
272 ± 64	1248 ± 128	2176 ± 144	2944 ± 208	1088 ± 96	272 ± 48	336 ± 64
128 ± 64	16 ± 16	16 ± 16	64 ± 32	32 ± 32	64 ± 32	16 ± 16
400 ± 96			16 ± 16			
32 ± 16	16 ± 16	16 ± 16	32 ± 32	16 ± 16		
	160 ± 48	256 ± 64	592 ± 112	16 ± 16	144 ± 48	16 ± 16
16 ± 16	144 ± 48	64 ± 32	304 ± 64	128 ± 32	112 ± 48	112 ± 48
16 ± 16	16 ± 16	16 ± 16	240 ± 64			16 ± 16
?	?			?	16 ± 16	
				32 ± 16	48 ± 32	48 ± 32
	?	?			?	?
32 ± 32	64 ± 32		32 ± 32	32 ± 32	80 ± 32	16 ± 16
	16 ± 16	16 ± 16	16 ± 16	96 ± 32	320 ± 64	80 ± 48
160 ± 48	16 ± 16	32 ± 32	192 ± 80			
48 ± 32	16 ± 16	16 ± 16	512 ± 112			
				53 ± 211		

TABLE 1. Continued.

Species	May 1985			September 1985	
	A	B	C	A	B
Hydracarina					
<i>Frontiopodopsis</i> sp.	16 ± 16	32 ± 32	16 ± 16		16 ± 16
<i>Limnesia</i> sp. 2	16 ± 16				
<i>Aspidiobates</i> sp.	16 ± 16	16 ± 16			
<i>Hydracarina</i> sp.					
<i>Limnesia</i> sp. 1					
Pisces					
<i>Galaxias olidus</i>			?		

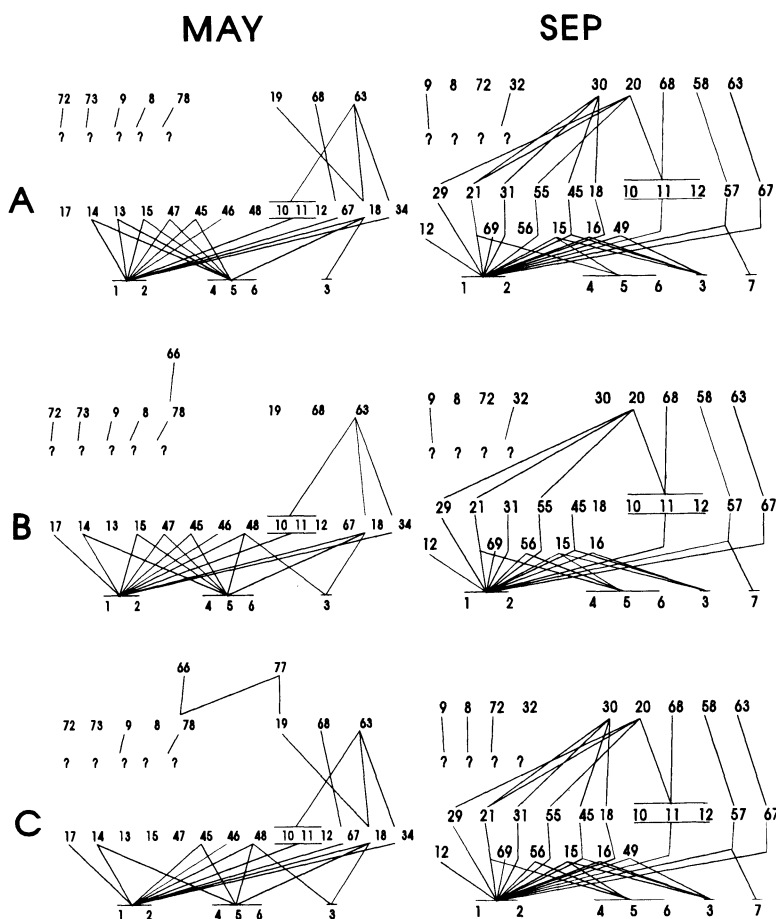
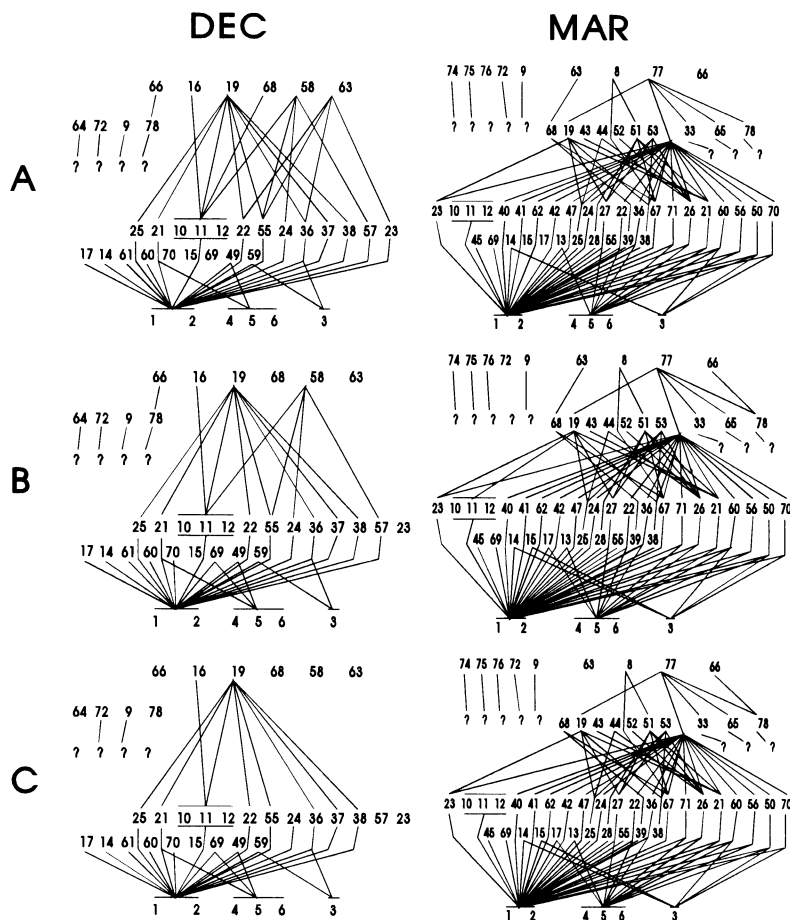


FIG. 5. Food web diagrams for each site-date combination. Species indicated without prey are suctorial predators for which no prey could be identified. Species names are denoted by numbers corresponding to accompanying key. Numbers missing from food web indicate species were not recorded for that particular site-date combination. Letters following names give additional taxonomic information according to the following key: Tu = Turbellaria, O = Oligochaeta, M = Mollusca, G = Gastropoda, B = Bivalvia, D = Diptera, C = Chironomidae, S = Simuliidae, T = Trichoptera, Le = Leptoceridae, Gs = Glossomatidae, Ca = Calocidae, E = Ecnomidae, Hb = Hydrobiosidae, Ep = Ephemeroptera, Lp = Leptophlebiidae, P = Plecoptera, Gr = Gripopterygidae, Au = Austroperlidae, Cl = Coleoptera, Dy = Dytiscidae, Gy = Gyridae, Cr = Crustacea, Co = Copepoda, Os = Ostracoda, Am = Amphipoda, Cd = Cladocera, Hy = Hydracarina, P = Pisces, Ga = Galaxidae; (A) means adult insect.

(1) Amorphous detritus; (2) Dead cellular plant material; (3) Algae spp.; (4) *Tetraedron* sp.; (5) *Tabellaria* sp.; (6) *Navicula* sp.; (7) Fungi; (8) *Hydra* sp. C; (9) *Cura pinguis* Tu; (10) Tubificidae sp. O; (11) Naididae sp. O; (12) Lumbricidae sp. O; (13) *Ferrissia* sp. M G; (14) *Angrobia* sp. M G; (15) *Physastra gibbosa* M G; (16) *Glacidorbis hedleyi* M G; (17) *Sphaerium tasmanicum* M B; (18) *Chironomus* sp. D C; (19) *Paramerina* sp. D C; (20) *Coelopynia* sp. D C; (21) *Riethia* sp. D C; (22)

TABLE 1. Continued.

September 1985	December 1985			March 1986		
C	A	B	C	A	B	C
32 ± 16	96 ± 48 16 ± 16 16 ± 16	32 ± 32 16 ± 16	32 ± 32	32 ± 32 144 ± 32 48 ± 32 ?	112 ± 48 80 ± 32 ?	16 ± 16 16 ± 16 144 ± 64 144 ± 64 ?



Cricotopus annuliventris D C; (23) *Rheotanytarsus* sp. D C; (24) *Parakiefferiella* sp. D C; (25) *Thienmaniella trivittata* D C; (26) *Tanytarsus inextensus* D C; (27) nr. *Halocladius* sp. D C; (28) *Stempellina* sp. D C; (29) *Austrosimulium* sp. D S; (30) Tipulidae sp. 1 D; (31) Tipulidae sp. 2 D; (32) Ceratopogonidae sp. D; (33) Empididae sp. 1 D; (34) Orthoclaadiinae sp. 1 C D; (36) Chironomidae sp. C D; (37) Orthoclaadiinae sp. 8 C D; (38) Tanypod sp. C D; (39) *Eukiefferiella* sp. C D; (40) *Brillia* sp. C D; (42) *Polypedilum* sp. C D; (43) *Larsia* sp. C D; (44) *Ablabesmyia* sp. C D; (45) *Triplectides truncatus* T Le; (46) *Triplectides ciuskeus* T Le; (47) *Helicopsyche* sp. T; (48) *Leptorussa darlingtoni* T Le; (49) *Agapetus kimmisii* T Gs; (50) *Tasmania acuta* T Ca; (51) *Ecnomus russellii* T E; (52) *Oecetis* sp. T Le; (53) *Apsilochorema* sp. T Hb; (54) *Nousia fuscata* Ep Lp; (55) *Koorononga pilosa* Ep Lp; (56) *Leptoperla bifida* P Gr; (57) *Riekoperla rugosa* P Gs; (58) *Illiesoperla australis* P Gs; (59) *Austrocercia tillyardi* P Gr; (60) *Acruperla atra* P Au; (61) *Dinotoperla serricauda* P Gr; (62) *Dinotoperla* sp. P Gr; (63) *Necterosoma penicillatus* (A) C Dy; (64) *Necterosoma penicillatus* (A) C Dy; (65) *Macrogyrus oblongus* C Gy; (66) *Macrogyrus oblongus* (A) C Gy; (67) *Eucyclops* sp. Co; (68) *Macrocylops albidus* Co; (69) *Ilyocypris australiensis* Cr Os; (70) *Afrochiltonia australis* Cr Am; (71) *Pleuroxus* sp. Cr Cd; (72) *Frontiopodopsis* sp. Hy; (73) *Limnesia* sp. 2 Hy; (74) *Aspidiobates* sp. Hy; (75) *Hydracarina* sp. Hy; (76) *Limnesia* sp. Hy; (77) *Galaxias olidus* P Ga; (78) Terrestrial insects.

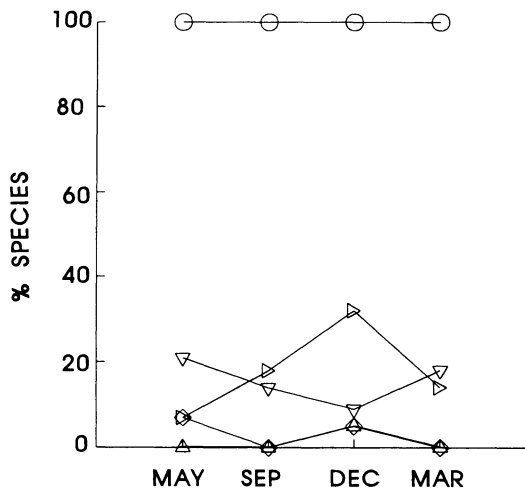


FIG. 6. The proportion of species observed to contain >20%, by gut volume, of any food category for each sampling date. Amorphous detritus (O), dead cellular plant material (DCPM, >), inorganic material (▽), algae (◇), diatoms (△).

etc.), although there was considerable overlap between phases. In May 1985 (early flow), species highly tolerant of the harsh physico-chemical conditions found in drying pools, (e.g., the gastropod *Physastra gibbosa* and the chironomid *Chironomus* sp.) and species more typical of the diminishing-flow phase (e.g., cased-caddis larvae, *Hydra* sp., and the stonefly *Austrocerca tasmanica*) were common. Early-colonizing species (e.g., the water mite *Aspidiobates* sp. and the cased caddis *Leptorussa darlingtoni*), typical of the early-flow phase were also abundant (Table 1; Towns 1985, Boulton 1988, Boulton and Lake 1992a). Species common in the March 1986 samples (post-flow), included species typical of the diminishing-flow phase (e.g., the amphipod *Afrochiltonia australis* and the stonefly *Austrocerca tasmanica*) and the post-flow phase (e.g., the dipterans *Riethia* sp. and Empididae sp. 1, and the freshwater limpet *Ferrissia* spp.) (Table 1; Boulton 1988, Boulton and Lake 1992a). Similar patterns of overlap could also be seen in the samples taken in September and December 1985.

Not all the changes in species composition appeared to be strictly seasonal. The only fish species recorded, *Galaxias olidus*, had a patchy distribution in May 1985. However, by March 1986 they were recorded from most pools at all three sites. This increase in abundance appeared to be related to a particularly successful spawning season in September–October 1985 that enabled them to repopulate sections of the stream from which they had been eliminated by trout prior to or during the 1982–1983 drought (Boulton 1988). Another species, the cased caddis *Leptorussa darlingtoni*, was relatively abundant in the summer of 1985, but was not recorded in the summer of 1986. Their eggs are deposited in bankside vegetation (Towns 1985,

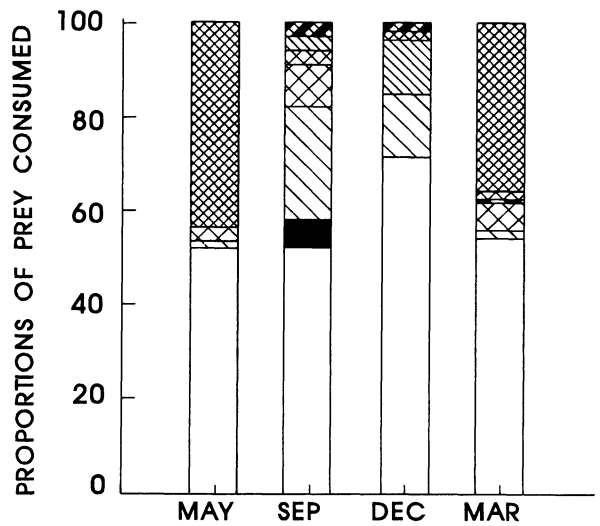


FIG. 7. The proportions of prey, by order, in predator guts as a percentage of the total number of items recorded.

1991, Boulton 1988), and may have been washed away in a major flood that occurred in October 1985.

Although many factors must influence the structure of the community in the Lerderderg River, physico-

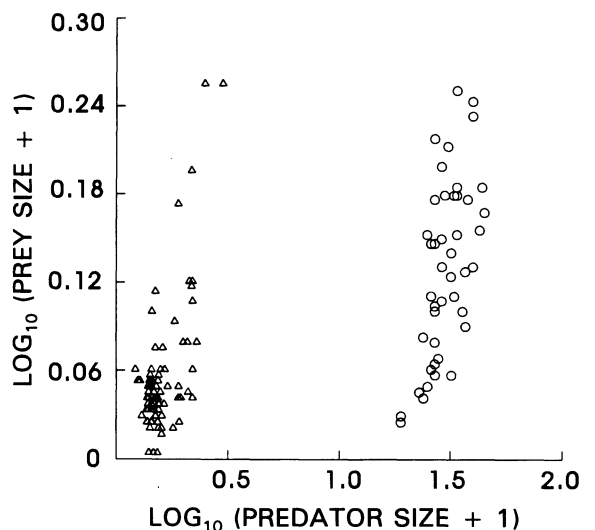


FIG. 8. Scatterplot of predator size vs. prey size. Δ = invertebrate predators, O = fish. Invertebrate size refers to head-capsule width; fish size refers to total length.

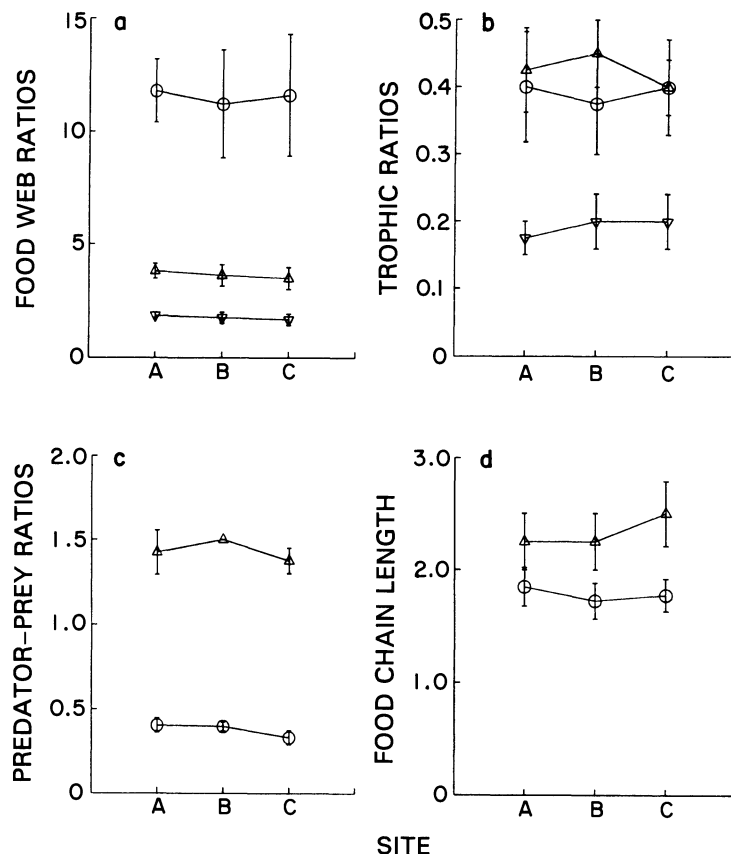


FIG. 9. Spatial comparisons of food web statistics: (a) mean number of links per species (▽), mean connectance (○), and the mean of the product of species and connectance (△); (b) mean proportions of top (△), intermediate (○), and bottom species (▽); (c) Jeffries and Lawton's ratio (○), Cohen's ratio (△); (d) longest (△) and mean (○) food chain length. Error bars show ± 1 SE.

chemical factors related to streamflow appeared to play a key structuring role. Many species showed physiological or life-history strategies to enable them to cope with the difficulties of living in an intermittent stream, a pattern also observed by Boulton (1988, 1989). Many of the species surviving in still summer pools were air breathers (e.g., adult dytiscid beetles) or contained hemoglobin (e.g., *Chironomus* sp., *Riethia* sp.). Many of the species requiring flowing water for survival had relatively short life cycles, such as the blackfly larvae *Austrosimulium* sp., which enabled them to complete their larval stages before flow ceased. The post-flow period appeared to act as a "filter" that determined the species composition of the community in the Lerderderg River from year to year. For example, long-lived predatory species typically found in permanent streams, such as the megalopteran *Archichauliodes* sp., were not recorded. *Archichauliodes* sp. was, however, found further downstream where streamflow persists for longer periods (G. P. Closs, *personal observation*).

Patterns of trophic interactions in the Lerderderg River were qualitatively similar to those observed in other food webs from small streams (Jones 1950,

Minckley 1963, Cummins et al. 1966, Minshall 1967, Hildrew et al. 1985, Bottorff and Knight 1988, Boulton 1988). Organic detritus formed the primary basis of the food web, being fed upon by all non-predatory invertebrates. Detritivorous species, feeding on both amorphous detritus and dead cellular plant material (DCPM), numerically comprised the bulk of the stream community at all times of the year. Variation in the availability of amorphous detritus did not appear to be an important factor in determining the abundance of detritivorous species given that the use of amorphous detritus as a food resource remained consistently high throughout the year (Fig. 6). This was despite the considerable fluctuations that occur in the stocks of amorphous detritus available throughout the year (Boulton and Lake 1992c). Boulton and Lake (1992c) observed few significant correlations between detritivores and detritus in the Lerderderg and Werribee Rivers, suggesting that detritus is not generally a limiting resource. Weak correlations between detritivores and detritus have also been observed in permanent streams (e.g., Barmuta 1988), although such patterns are likely to be habitat specific (see Dobson and Hildrew 1992).

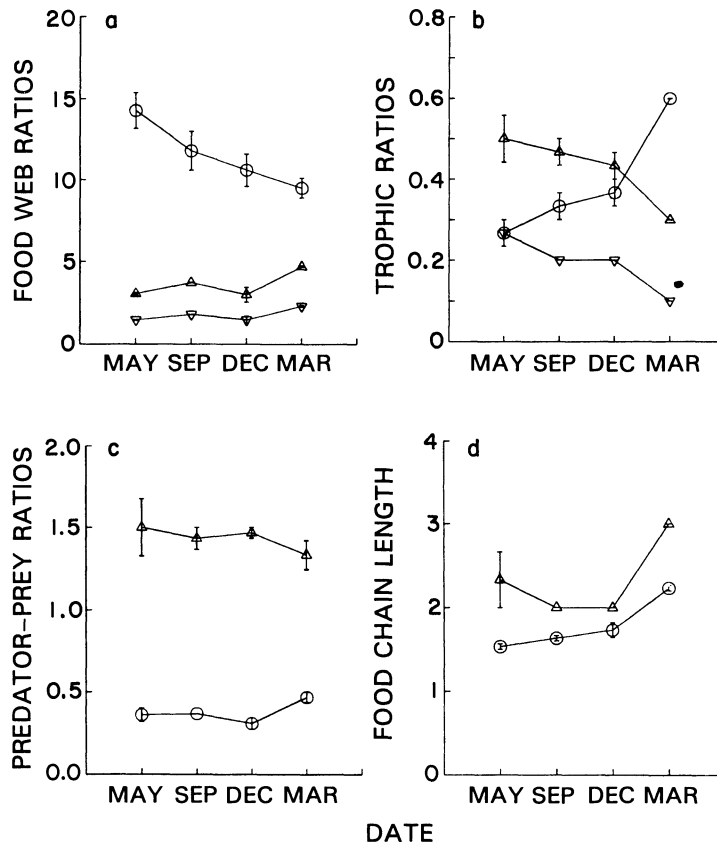


FIG. 10. Temporal comparisons of food web statistics: (a) mean number of links per species (∇), mean connectance (\circ), and the mean of the product of species and connectance (Δ); (b) mean proportions of top (Δ), intermediate (\circ), and bottom species (∇); (c) Jeffries and Lawton's ratio (\circ), Cohen's ratio (Δ); (d) longest (Δ) and mean (\circ) food chain length. Error bars show ± 1 SE.

The bulk of the DCPM in the stream was allochthonous leaf litter and detritus shed by riparian vegetation. Many typical shredding species, such as the cased-caddis *Tamasia acuta* and the stonefly *Acruroperla atra*, were observed feeding on whole leaves that had fallen into the stream. The final instars of these species coincided with the period of peak summer leaf fall. Although suggestive of a relationship between food availability and community structure, such a pattern is confounded with many other seasonal factors. The commencement of flow and the triggering of hatching in autumn may be a more important determinant of life-cycle timing than a peak in the availability of DCPM the following summer. Towns (1991) found that physical factors, such as rainfall, played a critical role in the timing of the life cycle of two South Australian Leptocerid caddis larvae.

The number of species scraping epilithon from various substrates, such as the snails *Angrobia* sp. and *Ferrissia* spp., was also higher in December 1985 and March 1986. An increase in the abundance of grazing species could be associated with higher rates of algal growth due to longer hours of daylight and higher temperatures during summer (Grimm and Fisher 1989).

Alternatively, changes in the abundance of grazing species, such as snails, may also be linked to changes in patterns of disturbance. Sedentary species, such as snails, may be poorly equipped to cope with the substrate disturbance associated with high flow levels. Brooks and Boulton (1991) observed that molluscs were rare in a South Australian intermittent stream following artificial and natural substrate disturbances. Disturbance may also reduce the availability of food for grazing species, as the scouring and substrate disturbance associated with high streamflow tends to remove growths of epilithic algae (Boulton et al. 1988, Grimm and Fisher 1989).

Detritus, and its role in food web dynamics

Detritus typically forms a key basal resource in freshwater food webs (Jones 1950, Minckley 1963, Cummins et al. 1966, Minshall 1967, Tilly 1968, Koslucher and Minshall 1973, Hildrew et al. 1985, Kitching 1987, Warren 1989, Winemiller 1990, Martinez 1991, this study). In many of these webs, particularly those from small shaded streams such as the Lerderderg River, various forms of detritus are the primary food source for most of the non-predatory species in the commu-

nity. In the Lerderderg River detritivorous species comprised the bulk of the community by number (see also Boulton and Lake 1992a, c), a pattern probably typical of most other upland stream communities (e.g., Cummins et al. 1966, Koslucher and Minshall 1973, Barmuta 1988, 1989).

The observation that many food webs from freshwater habitats are based upon a detrital resource suggests that a large proportion of interactions in such webs are weak, and are hence donor controlled (DeAngelis 1975, Pimm 1982). Such a scenario is particularly likely for food webs in upland streams, given that a very large proportion of their energy base is derived from allochthonous detrital inputs from the surrounding riparian forest (Hildrew et al. 1985, Cummins 1986, Kitching 1987). Theoretical simulations suggest that a large pool of detritus in a food web should increase community resistance and resilience to disturbance (DeAngelis 1992). Webs containing a high proportion of weak links, such as those between detritus and detritivores, are also unlikely to show strong relationships among web stability, web complexity, and environmental harshness (May 1973, DeAngelis 1975, Pimm 1982). Such a feature may partly explain the resistance of upland stream communities, such as the Lerderderg River, to disturbances such as flooding (see Boulton and Lake 1992b). Considerable amounts of organic detritus usually remain buried in stream substrates even after severe floods (Metzler and Smock 1990, Boulton and Lake 1992c, Hill et al. 1992a, b). Provided supplies of detritus are not significantly reduced during floods, survival and recolonization by detritivores will not be limited by a lack of food (see Boulton and Lake 1992c). Rapid recolonization of the Lerderderg River, largely by detritivorous species, also occurs following low-flow or drought periods (Boulton and Lake 1992a, this study), a pattern that may also be considerably aided by the presence of abundant detritus. Similar patterns of recolonization can also be seen in temporary ponds and water-filled tree hollows, where detritivores tend to be the first colonists after pool refilling (Lake et al. 1989, Jenkins and Kitching 1990, Jenkins et al. 1992).

In contrast to the rapid recovery of species feeding upon detritus, the recolonization of species dependent upon epilithic periphyton (e.g., snails) tends to occur at a slower rate following disturbance in both permanent and intermittent streams (Boulton et al. 1988, Brooks and Boulton 1991, Boulton and Lake 1992a, this study). As discussed previously, the increase in snail numbers during the diminishing flow period in the Lerderderg River could be associated with either reduced substrate disturbance and/or reduced food availability. At a community level, increasing levels of autochthonous production of algae in a stream may be associated with a reduced level of community resistance to disturbance. Autochthonous production of algae is often considerable in desert streams, with algae

forming a primary food resource for many consumers (Fisher et al. 1982, Fisher 1986). Such communities show a low level of resistance to flood disturbance, a result partly due to the detrimental effects of scouring and substrate disturbance on the density of attached algae (Fisher et al. 1982, Fisher 1986). Recovery of the algae from such floods is rapid in the high-light, high-temperature environment of the desert; however, macroinvertebrate recolonization does lag behind that of the algae (Fisher et al. 1982, Fisher 1986). In environments not so conducive to the rapid growth of algae, a slow rate of algal regrowth following a flood can delay invertebrate recolonization. In a stream receiving minimal inputs of allochthonous detritus, Siegfried and Knight (1977) observed that the recovery of the macroinvertebrate community after winter flooding was delayed until the occurrence of spring blooms of filamentous algae.

Weak interactions at higher trophic levels may also contribute to the long-term resilience of the Lerderderg River food webs by enabling long-lived predators, such as fish, to survive the continuous variation in the abundance and availability of their prey. Manipulation of the densities of the dominant predator, *Galaxius olidus*, had little impact upon the abundance of benthic invertebrates (Closs 1991b). In addition, a significant proportion of the diet of *G. olidus* was in the form of detrital inputs of terrestrial insects, a common pattern of feeding for many aquatic predators, both invertebrates and fish (e.g., Hildrew et al. 1985, Winemiller 1990). Many invertebrate predators, such as tanyptodine chironomids, also supplement their diet with detritus (Minshall 1967, Koslucher and Minshall 1973, Hildrew et al. 1985). The ability to utilize an ever-present food resource such as detritus must be particularly advantageous in highly variable and unstable habitats, such as small streams.

The primacy of detritus as a basal resource, together with the speciose nature of upland stream food webs, may also contribute to the apparent scarcity of strong top-down trophic cascades in upland streams (see Cooper et al. 1989, Hildrew 1992). Strong top-down trophic cascades generally occur in relatively simple food webs based upon an algal resource, e.g., planktonic communities in lakes (Strong 1992). In such webs the regulatory impact of a top predator cascades down a narrow "trophic ladder," exerting a strong level of control upon autochthonous production in the system (Strong 1992). In contrast, typical stream food webs are generally highly speciose and based in detritus (Cummins et al. 1966, Minshall 1967, Koslucher and Minshall 1973, Hildrew et al. 1985, Winemiller 1990, this study). In such habitats the speciose nature of food webs may tend to dissipate the impact of top predators such as fish (see Polis 1991, Strong 1992). Furthermore, the bulk of the detritus in the system is of terrestrial origin, the supply of which is independent of the density of detritivorous invertebrates. Such a factor must

reduce the capacity of detritivorous invertebrates to regulate the availability of the web's basal resource. Strong top-down trophic cascades have been described from lotic systems, the most unequivocal examples being those from lowland streams (see Power 1990, 1992). In these lowland stream webs, the effect of a top predator cascades down a relatively narrow ladder of interactions ending in an algal base, a pattern similar to that found in many lentic systems (see Strong 1992).

Food web statistics and structure

Considerable temporal variation was a feature of the food webs from the Lerderderg River. Variation in food web structure reflected the changes observed in overall species composition and in the results of the ordination. Rebuilding of the food web following the summer low-flow period resembled patterns of succession observed in most other temporary habitats, with species number and the overall complexity of feeding interactions increasing dramatically over time (see Kitching 1987, Lake et al. 1989, Jenkins and Kitching 1990, Boulton and Lake 1992a). The mean food-chain length and the proportion of predators in the community (as measured by the Jeffries and Lawton predator-prey ratio) increased slightly over time, suggesting that predators tended to colonize the habitat at a slower rate than species at lower trophic levels, a pattern also observed in other aquatic communities rebuilding after a major disturbance (e.g., Pimm and Kitching 1987, Lake et al. 1989). Such a pattern suggests that the regulation of predator diversity is "bottom-up," i.e., the abundance and/or diversity of prey tends to determine predator diversity. Warren and Gaston (1992) discussed evidence for five hypotheses proposed to explain the observation of constant predator-prey ratios in community data. Bottom up regulation of predator diversity would appear to be more consistent with the prey-niche hypothesis (more prey species provide more predator niches) and the energy-ratio hypothesis (increased availability of energy at lower trophic levels provides more energy for predators) compared with the random-draw hypothesis, the enemy-free space hypothesis (predator diversity limits prey diversity) and the common-determinants hypothesis (similar factors determine both predator and prey diversity).

The values of several other food web statistics also varied temporally, although the significance of such variation is difficult to ascertain. The values of several statistics, such as connectance and the proportions of top, intermediate, and basal species, may have been influenced by methodological decisions; hence any observed changes in value are somewhat confounded. Such a problem highlights the criticism of Paine (1988), who pointed out that whilst food web statistics may be objectively calculated from any food web, their value is highly dependent upon the often-subjective decisions made during web compilation. The persistence

of certain food-web patterns was also evident, with most of the food web statistics derived from the Lerderderg River food webs falling within the range of values reported from analyses of large collections of food webs (Cohen 1977, 1978, Briand 1983, Briand and Cohen 1984, Jeffries and Lawton 1985, Schoenly and Cohen 1991, Schoenly et al. 1991). Some of these constant patterns either appear to be a consequence of the methodology used to compile the food web (e.g., links per species), or may be an intrinsic property of the statistic itself (e.g., Cohen's predator-prey ratio, see Closs et al. 1993).

Defining a food web

The food webs in this study and others (e.g., Kitching 1987, Warren 1989) represent one approach to describing temporal variation in food web structure, that is, only those interactions occurring at a point in time are depicted. However, a food web compiled at one point in time may not be an accurate portrayal of the community 1 wk later, particularly in a system as variable as the Lerderderg River. Such problems may be compounded when a key mobile predator, such as *G. olidus*, occurs in the system. The abundance of such a species at any one location can change rapidly, resulting in their possible omission from a food web should they be absent at the time of sampling, e.g., September and December in the Lerderderg River. The omission of mobile predators from webs may have contributed to the observation that food chains are generally shorter in webs from two-dimensional habitats compared with three-dimensional habitats (Edwards et al. 1982). Alternatively, all the interactions occurring over an extended period of time, perhaps as long as several years, can be included (e.g., Hall and Raffaelli 1991, Martinez 1991, Polis 1991). Not surprisingly, such webs often contain many more species and interactions, differences that are likely to influence the values of any derived food-web statistics (e.g., Polis 1991). Significantly, elements of both approaches can be seen in many of the different studies represented in collections of published food webs (see Sugihara et al. 1989, Cohen et al. 1990).

Similar problems can be envisaged in defining appropriate spatial scales of study. Food web descriptions are usually defined by the habitat under study (Cohen 1978, Pimm 1982). However, even the most circumscribed habitats, such as water-filled tree hollows (e.g., Kitching 1987), possess trophic links with the surrounding environment. Restricting a food web study to a defined habitat is a virtual impossibility given that the niches of at least some of the animals being sampled will almost always extend beyond the spatial scale of the habitat being sampled. In the Lerderderg River only the rocky substrate of the stream was sampled, a spatial scale that adequately covers the feeding range of most invertebrates. However, mobile predators such as *G. olidus* feed over a wide area within the stream, and

hence are likely to pick up foods from sub-habitats not sampled, e.g., bankside vegetation and woody debris. Consequently, "rare" species, such as the chironomid *Brillia* sp., are more likely to be recorded in the diet of a wide-ranging species. Such rare species may well be very common in some unsampled sub-habitat within the stream. In upland streams such problems are obviously compounded by the considerable inputs of terrestrial material that inevitably blur any distinction between stream and terrestrial food webs. The food web of the Lerderderg River can be viewed as a sub-web contained within the overall Lerderderg River valley food web. Linkage of the aquatic web to the surrounding terrestrial environment would undoubtedly result in the observation of longer food chains due to the inclusion of terrestrial predators, such as insectivorous birds and hawks. Defining an appropriate spatial scale that would allow comparisons between webs derived from any habitat would seem to be virtually impossible given the major differences that exist between different habitats.

The methods used to identify trophic links can also influence the value of several statistics. Warren's (1989) observation of high levels of connectance and omnivory in a pond food web may be a consequence of using literature records, feeding trials, and gut analysis to identify feeding links. The use of all three approaches must increase the probability of recording an interaction between species compared with a study in which a single method is used. In the present study we only used gut content analysis to identify trophic links. Consequently our webs depict, at best, a minimum estimate of the feeding interactions (and hence web connectance) within the habitat. In addition, the webs may also have been biased in unknown ways by not identifying the diet of suctional prey, and by possible underestimates of soft-bodied prey. Significantly, connectance, although falling within the range of previous values reported (cf. Sugihara et al. 1989, Cohen et al. 1990, Schoenly et al. 1991), was comparatively low when compared with several detailed food webs based on gut data, feeding trials, and literature records (cf. Beaver 1985, Kitching 1987, Warren 1989). Relying entirely on gut analysis to identify links avoided the risk of depicting interactions not actually occurring in the habitat. However, this somewhat conservative approach inevitably means that some interactions will go undetected, a practical necessity given that the effort required to detect an ever higher proportion of the trophic interactions in a community increases exponentially (Kenny and Loehle 1991, Polis 1991).

The aggregation of species into larger groups, i.e., taxonomic lumping, also poses significant problems for food web research given that such practices can distort observed food-web structure significantly (Paine 1988, Lawton 1989, Winemiller 1990, Polis 1991). Even those compiling detailed food webs usually aggregate species at some level with the use of categories such as detritus

(e.g., Beaver 1985, Hildrew et al. 1985, Walker 1985, Kitching 1987, Warren 1989, Winemiller 1990, Hall and Raffaelli 1991, this study). Unfortunately, it can be almost impossible to avoid this problem, given the difficulties associated with the detection of interactions among microscopic species (Berrie 1976, Walker 1985, Pomeroy and Wiebe 1988, Walter et al. 1991). Differing degrees of taxonomic resolution at different levels within a web will affect the observed length of food chains, Cohen's predator-prey ratio, and the number of links per species and proportions of species in top, intermediate, and basal trophic levels (Pimm 1982, Paine 1988, Warren 1989, Hall and Raffaelli 1991, Martinez 1991, Polis 1991, Schoenly et al. 1991, Closs et al. 1993). Food chains will be observed to be shorter if lower trophic levels are aggregated into large taxonomic groups such as insects, herbivores, or detritus (e.g., Twomey 1945, Harrison 1962, Hildrew et al. 1985, Warren 1989, Winemiller 1990, this study). The number of basal species will also tend to remain constant, resulting in a decline in the proportion of basal species as species number increases, a pattern observed in the Lerderderg River. The number of links per species may also change as the number of lumped taxa increases and the detail of feeding interactions between species is lost. Whilst the category "detritus" may in fact include many species (e.g., Walker 1985), only a single link can be drawn between it and any detritivorous species, hence biasing the observed number of links per species downwards. In the Lerderderg River, aggregation of the lower trophic levels into categories such as detritus undoubtedly contributed to the constancy of the number of links per species through time.

CONCLUSIONS

Food web diagrams represent valuable road maps to the patterns of interactions and energy flow within communities. The food webs derived from the Lerderderg River clearly demonstrate the importance of detritus as a basal food resource within the system, the dramatic changes in community structure and feeding interactions over time, the importance of *Galaxius olidus* as a dominant predator, etc. Such observations are useful, and can be compared, in a qualitative sense, with patterns of energy flow and feeding interactions observed in other streams. Comparisons of the food webs obtained in this study with webs derived from other streams highlight the importance of detritus in lotic systems, and the possible role that the detrital pool has in buffering the community against disturbance. Food webs can also form the basis for many further comparative and experimental investigations into the dynamics of community and food web structure (e.g., Closs 1991b, Polis 1991, Jenkins et al. 1992).

The persistence of certain food-web patterns, such as constant predator-prey ratios, in a wide variety of food webs is quite remarkable, particularly so when considering the degree of variation observed in the

species composition of webs, the range of habitats sampled, and the different methods used to compile them. Such persistence would appear to suggest an underlying order to nature (e.g., Pimm et al. 1991). Such order also extends beyond the descriptions of real food webs, with theoretical food-web models exhibiting many of the same patterns (Lawton and Warren 1988, Lawton 1989, Pimm et al. 1991). Martinez (1991) suggested that patterns that remain consistent over different degrees of taxonomic resolution are more likely to be attributes of the system rather than artifacts of poor-quality data. Alternatively, Hall and Raffaelli (1991) suggested that the insensitivity of certain food-web statistics to variation in data quality must bring into question their value as descriptors of biological systems.

The observation of persistent patterns in real and theoretical webs should, at the very least, introduce a sense of caution when attempting to infer that such features are invariably of biological significance. Constant patterns in food webs can be caused by common cultural practices among food web researchers (Paine 1988), e.g., the tendency to lump microscopic species into a detrital category, thus contributing to a constant links-per-species ratio. Regular patterns in both real and theoretical food webs can also be the product of mathematical artifacts. Double counting of taxa as both predators and prey appears to underpin the constancy of Cohen's (1977) predator-prey ratio (Closs et al. 1993). Quantitative comparisons of food web structure using food web statistics, particularly where the food webs have been derived from different habitats are also dogged by the sensitivity of several of the statistics to the methodology used to compile the web. Statistics, such as the number of links per species, the longest food chain, and the proportions of top, intermediate, and basal species, are particularly sensitive to methodological differences. In many instances it is impossible to determine the biological significance of differences in web structure as measured by the statistics, given that such comparisons are obviously confounded by the different approaches used during web compilation. In addition, food web analyses based solely upon the various "presence/absence" food-web statistics can be difficult to place in a meaningful ecological context given that they disregard so much ecological information, such as relative species abundances and the strength of individual trophic links (see Paine 1988, Polis 1991).

The degree of variation in the methodology used to compile food webs, and the sensitivity of food web statistics to that variation, might appear to suggest that inter-web comparisons are almost inevitably confounded, and hence, pointless. However, food webs can be compared, and useful observations made, if the habitats sampled are similar and the methodology used is consistent. The significance of such studies is further enhanced when an analysis of a web is accompanied by a consideration of additional community param-

eters that help place a web in an ecological context. Such an approach has been used by Beaver (1985), Kitching (1987), and Jenkins and Kitching (1990) to study food webs in *Nepenthes* pitcher plants and water-filled tree hollows, respectively. These studies revealed interesting and potentially significant patterns and differences in web structure that cannot be queried on the grounds of methodological differences. Likewise, patterns observed in the development of the community over time in the Lerderderg River suggest interesting relationships between the basal resource of the web and community resistance to disturbance. Limiting comparisons to studies conducted in the same type of habitats using similar methodology will greatly reduce the range of comparisons that can be made. However, those comparisons will have the potential to yield meaningful information.

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