

Food web structure in a tropical stream ecosystem

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Abstract This study investigated the structure and properties of a tropical stream food web in a small spatial scale, characterizing its planktonic, epiphytic and benthic compartments. The study was carried out in the Potrerinho Creek, a second-order stream located in the south-east of Brazil. Some attributes of the three subwebs and of the conglomerate food web, composed by the trophic links of the three compartments plus the fish species, were determined. Among compartments, the food webs showed considerable variation in structure. The epiphytic food web was consistently more complex than the planktonic and benthic webs. The values of number of species, number of links and maximum food chain length were significantly higher in the epiphytic compartment than in the other two. Otherwise, the connectance was significantly lower in epiphyton. The significant differences of most food web parameters were determined by the increase in the number of trophic species, represented mainly by basal and intermediate species. High species richness, detritus-based system and high degree of omnivory characterized the stream food web studied. The aquatic macrophytes probably provide a substratum more stable and structurally complex than the sediment. We suggest that the greater species richness and trophic complexity in the epiphytic subweb might be due to the higher degree of habitat complexity supported by macrophyte substrate. Despite differences observed in the structure of the three subwebs, they are highly connected by trophic interactions, mainly by fishes. The high degree of fish omnivory associated with their movements at different spatial scales suggests that these animals have a significant role in the food web dynamic of Potrerinho Creek. This interface between macrophytes and the interconnections resultant from fish foraging, diluted the compartmentalization of the Potrerinho food web.

Key words: compartmentalized food web, food chain length, food web, omnivory, pyramid of number, spatial variation, taxonomic resolution, tropical stream.

INTRODUCTION

The main goal of food web theory is to understand the patterns exhibited by natural communities (Pimm *et al.* 1991). Early analyses of large collections of published food webs from many different habitats suggested that food webs show consistent structural patterns (Briand & Cohen 1984; Cohen *et al.* 1990; Pimm *et al.* 1991). However, these patterns were widely debated in the literature. The main points of debate were limitations in the collections of data used for these analyses, such as the poor quality of many food web data, the small subsets of species analysed (an average of 20 species or less), differences in the methodologies used, the definition of a link, the level and standardization of taxonomic resolution, and mathematical artifacts (Lawton 1989; Winemiller 1990; Hall & Raffaelli 1991; Martinez 1991, 1993; Closs *et al.* 1993; Thompson & Townsend 2000). In recent years food webs constructed with a higher taxonomic resolution (Hall & Raffaelli 1991; Martinez 1991; Tavares-Cromar & Williams 1996; Schmid-Araya *et al.* 2002a) invalidated

some earlier generalizations and showed that features such as long food chain and omnivory are common in food web structure.

Another aspect of food web studies is that, initially, most food webs were depicted as static representations of a cumulative web, lumping together species and interactions recorded within a habitat over a relatively long period of time (Winemiller 1990; Hall & Raffaelli 1991; Martinez 1991). However, static representations fail to capture the dynamic nature of communities, and may obscure significant temporal and spatial variation in their structure, resulting in food webs that are completely unrealistic (Closs & Lake 1994; Polis *et al.* 1996; Tavares-Cromar & Williams 1996; Woodward & Hildrew 2002). Thus, the determination of temporal and spatial scales is crucial given that they will influence the structure of the resultant web (Polis 1991; Closs & Lake 1994).

Despite widespread recognition of the dynamic nature of habitats, communities, and trophic interactions, relatively little attention has been given to the scale of variation involved in describing food web structure (Polis *et al.* 1996). In variable systems such as streams, some work showed temporal variation in food web structure (Closs & Lake 1994; Tavares-Cromar &

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Williams 1996; Carney *et al.* 1997; Thompson & Townsend 1999; Schmid-Araya *et al.* 2002a). However, few studies analysed spatial variation (Closs & Lake 1994; Corigliano & Malpassi 1998). The incorporation of spatial scale into stream food webs may influence the way species interact and result in functionally distinct food web (Warren 1989). Power (1992) showed an abrupt change over small spatial scale (centimetres) in the functional importance of predators in rivers. According to Woodward & Hildrew (2002), we might expect spatial compartmentalization to increase with increasing levels of habitat heterogeneity.

Compartmentalization refers to the existence of 'subwebs' or 'blocks' within the larger food web of the entire community, a point of view not yet examined within a riverine context (Woodward & Hildrew 2002). Thus, the present study intends to analyse the food web of a small tropical stream using this compartmentalized context.

This stream, located in south-eastern Brazil, was analysed in a small spatial scale, considering the subwebs composed by planktonic, epiphytic and benthic compartments. Some attributes of the three subwebs and of the conglomerate food web, composed of the trophic links of the three compartments, plus the fish species, were determined. Comparisons of these attributes were made in an attempt to find spatial patterns and relate them to habitat characteristics.

METHODS

Study site

The study was carried out in Potrerinho Creek (23°03'S, 48°38'W), in the district of Itatinga, south-eastern Brazil, during the dry season of 1997. Potrerinho Creek is a second-order tributary of Pardo River and is located at an elevation of 850 m. During the study this creek had low mean values of current (0.33 m s^{-1}) and discharge ($0.09 \text{ m}^3 \text{ s}^{-1}$), and high mean values of oxygen ($9.06 \text{ mg O}_2 \text{ per litre}$) and saturated oxygen (103.8%). The stream can be characterized as a straight scour channel, 1.6 m wide and 0.2–0.6 m deep. The substrate consists of gravel, sand and silt. Riparian vegetation is present only on the left margin, although submerged vascular hydrophytes composed mainly of Poacea are abundant in the entire channel.

Sampling and laboratory procedures

Quantitative sampling was carried out within a 200-m stretch in August 1997. The open water, macrophytes

and streambed were sampled in one morning period. Six samples of the open water (200 L each) were collected using a plankton net (20 μm mesh). The plankton replicates were analysed by subsamples. From each subsample organisms were counted until 150 specimens were reached. The entire sample was analysed when the density of organisms was lower. Algae, Protozoa, Rotifera and the larval stage of Copepoda were counted in Sedgwick-Rafter chambers, by optic microscope; Cladocera, copepodites and adult stages of Copepoda were counted using a stereo-microscope. Six samples were taken from submerged vascular hydrophytes in the margin of the stream by cutting portions of the plant, enclosed within a square (900 cm^2), to a depth of 5 cm. In the laboratory, the vascular hydrophytes were washed and scraped. The epiphytic macroinvertebrates in these samples were sorted by sucrose flotation (Havens *et al.* 1996), identified and counted. After the removal of large invertebrates, the epiphytic algae and microinvertebrates were counted from the remaining material using the same methodology as for the plankton analysis. The epiphytic macroinvertebrates and associated fishes were collected with a sieve (3 mm mesh net) passed through the submerged vascular hydrophytes in a selected 75 m stretch of the stream. The benthos was sampled (six replicates) using a cylindrical PVC corer (10 cm^2 cross sectional area), sunk 10 cm into the substrate.

All samples were preserved in 4% formaldehyde solution and stained with fluoxin. Organisms were identified to the lowest possible taxonomic level and then their densities were determined and transformed in number per cubic metre. For fishes and epiphytic macroinvertebrates, sampled with a sieve, the density was calculated as a function of the volume of the sampled stretch. For planktonic, epiphytic and benthic macroinvertebrates the density was calculated as a function of the volume of the sampling devices used.

Consumer diet information

Diet of macroinvertebrates and fishes was determined through the analysis of gut contents, using a volumetric method. The macroinvertebrates were decapitated and their entire gut analysed. For Protozoa, Hydrozoa, Rotifera and Nematoda the diet was based on the literature (Pennak 1978; Pourriot & Meybeck 1995; Schmid-Araya & Schmid 2000). The fishes had their entire gut removed but only the stomach analysed. The gut contents were analysed in a counter chamber, under a microscope or stereo-microscope, with similar items grouped and the occupied area estimated (Esteves & Galetti 1995). The invertebrate gut contents were classified into six categories: organic matter, vascular plant, filamentous algae, unicellular algae,

Table 1. Composition, richness and density (ind. m⁻³, mean \pm 1SD) of taxa found at the planktonic, epiphytic and benthic compartments and at the cumulative Potrerinho Creek web

Taxa	Plankton		Epiphyton		Benthos		Potrerinho Creek	
	Richness	Density	Richness	Density	Richness	Density	Richness	Density
PROTOZOA	8	3988 \pm 505	8	1.4 \times 10 ⁶ \pm 147 529	9	1 \times 10 ⁹ \pm 97 158 848	12	1 \times 10 ⁹
INVERTEBRATES								
Hydrozoa	0	–	1	36 \pm 36	0	–	1	36
Turbellaria	0	–	1	36 \pm 36	0	–	1	36
Rotifera	6	2943 \pm 382	4	816 613 \pm 242 045	1	1.4 \times 10 ⁷ \pm 6 207 692	8	1.4 \times 10 ⁷
Nematoda	1	5 \pm 1	1	25 419 \pm 9334	1	171 573 \pm 113 222	1	196 997
Annelida	0	–	2	8378 \pm 2047	1	46 085 \pm 5521	2	54 463
Acari	0	–	1	7167 \pm 4543	1	885 \pm 1140	1	8052
Crustacea	4	27 \pm 2	6	55 409 \pm 10 714	2	4 814 530 \pm 4 814 530	7	4.8 \times 10 ⁶
AQUATIC	0	–	62	24 453 \pm 1226	21	29 487 \pm 1653	72	53 940
INSECTS								
Collembola	0	–	1	681 \pm 681	0	–	1	681
Ephemeroptera	0	–	1	609 \pm 609	0	–	1	609
Trichoptera	0	–	3	394 \pm 18	0	–	3	394
Lepidoptera	0	–	2	179 \pm 54	0	–	2	179
Odonata	0	–	11	110 \pm 15	1	877 \pm 11	11	987
Plecoptera	0	–	1	1398 \pm 1004	0	–	1	1398
Hemiptera	0	–	5	110 \pm 35	0	–	5	115
Coleoptera	0	–	9	1115 \pm 200	3	1302 \pm 9	11	2417
Diptera	0	–	30	19 785 \pm 617	17	29 487 \pm 1653	37	49 272
VERTEBRATES								
Fishes	0	–	0	–	0	–	7	1
TOTAL	19	6963	87	2.2 \times 10 ⁶	36	1 \times 10 ⁹	112	1 \times 10 ⁹

aquatic animals and terrestrial animals. Only the animal items of gut contents were identified to a lower taxonomic level. The gut contents of suctorial predators, such as hemipterans, could not be identified.

Food web analysis

A conglomerate food web of Potreirinho creek was constructed considering the basal resources, the species found in each set of sample (plankton, epiphyton and benthos), and the fishes. This entire food web was

reorganized into three subwebs composed of the organisms found in each compartment (plankton, epiphyton and benthos), except for the fishes. To compose the diagram of these food webs, we used the same methodology as Cohen *et al.* (1990) with the species grouped in trophic species or taxa with the exact same group of predators and prey. This procedure causes no loss of information because it was not used in calculating the food web parameters but only to simplify the illustration.

The food web was compiled by using the identified taxa as row and column headings in a binary matrix

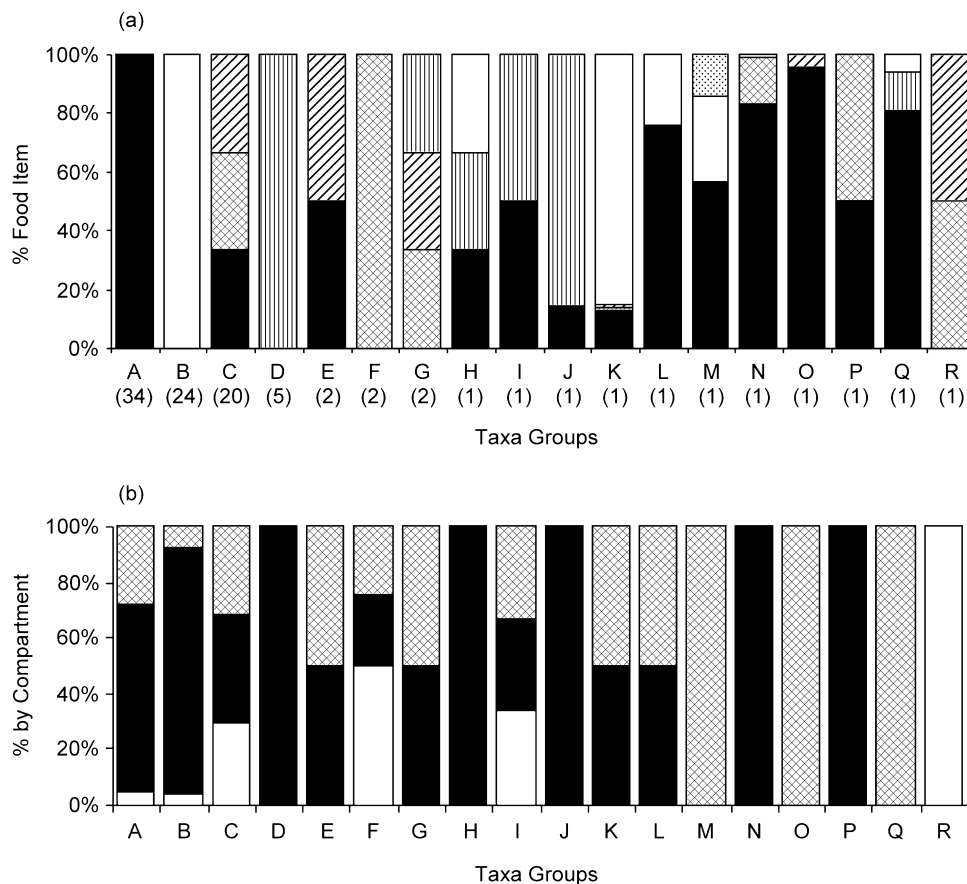


Fig. 1. (a) Taxa groups analysed in relation to the percentage of food items ingested. The resources categories are: (■) organic matter; (▨) filamentous algae; (▧) unicellular algae; (▩) vascular hydrophytes; (□) aquatic animals; and (▦) terrestrial animals. (b) Taxa groups analysed in relation to the percentage of occurrence by compartment: (□) plankton; (■) epiphyton; and (▦) benthos. Taxa with similar diet were grouped in the same letter (number of taxa): **Group A**, *Vorticella*, *Keratella*, *Oligochaeta*, *Hirudinea*, *Ostracoda*, *Paracyclops*, *Baetis*, *Tupiperla*, *Gyretes* (larvae), *Megadytes* (larvae), *Tropisternus*, *Heterelmis*, *Hydrothassa*, *Brachycera*, *Ceratopogonidae* sp.1, *Ceratopogonidae* sp.2, *Procladius*, *Cricotopus* sp.1, *Corynoneura*, *Thienemanniella*, *Limnophyes*, *Parametriocnemus*, *Chironominae*, *Xestochironomus*, *Polypedium* (*Tripodura*)*, *Saetheria* sp.2, *Phaenopsectra*, *Goeldichironomus*, *Constempellina*, *Tanytarsini* Genus A*, *Tanytarsini* Genus B*, *Tanytarsini* Genus D*, *Dixella*, *Nimbochera paulensis*; **Group B**, *Heliozoa*, *Cephalodella*, *Ploesoma*, *Hydrozoa*, *Turbellaria*, *Acarina*, *Eucyclops*, *Trichodactylus*, *Aphylla*, *Progomphus*, *Zonophora*, *Castoraeschma*, *Erythrodiplax*, *Libellulidae*, *Megapodagrionidae* sp.1, *Megapodagrionidae* sp.2, *Hetaerina*, *Enallagma*, *Corduliidae*, *Gyrinus*, *Gyretes* (adult), *Megadytes* (adult), *Laccophilus*, *Labrundinia*; **Group C**, *Arcella*, *Nebela*, *Quadrullella*, *Heleopera*, *Euglypha*, *Trinema*, *Cyphoderia*, *Euchlanis*, *Lepadella*, *Monommata*, *Lecane*, *Bdelloidea*, *Nematoda*, *Alona*, *Entomobryidae*, *Simuliidae*, *Metriocnemus*, *Polypedium* sp., *Stenochironomus*, *Rheotanytarsus*; **Group D**, *Oecetis*, *Phylloicus*, *Petrophila* sp.1, *Dryops*, *Hexatoma*; **Group E**, *Cricotopus* sp.2, *Nanocladius*; **Group F**, *Centropxyxis*, *Lesquereusia*; **Group G**, *Petrophila* sp.2, *Hydrophilus*. **Group H**, *Paratendipes*; **Group I**, *Diffugia*. **Group J**, *Leptonema*; **Group K**, *Pentaneura*; **Group L**, *Ablabesmyia*; **Group M**, *Cryptochironomus*; **Group N**, *Polypedium* gr. *fallax**; **Group O**, *Saetheria* sp.1; **Group P**, *Tribelos*; **Group Q**, *Amphipoda*; **Group R**, *Chydorus*. *Trivino-Strixino and Strixino (1994).

(Cohen *et al.* 1990). Detection of a link (interactions of predator and prey) was indicated in the body of the matrix by '1' determined on the basis of dietary analysis.

Species were categorized using the definitions of Briand and Cohen (1984) and Pimm *et al.* (1991). Top species have prey but no predators, intermediate species have both prey and predators, while basal species have predators and no prey. Organic matter, unicellular and filamentous algae, vascular hydrophytes and terrestrial insects were considered as basal species (Martinez 1991). Food web properties were

calculated for the six samples of each compartment (plankton, epiphyton and benthos). The number of species was determined, as well as the number of links, linkage density (number of species/number of links), proportion of top, intermediate and basal species, proportion of basal–intermediate, intermediate–intermediate, intermediate–top and basal–top links, following the definitions of Pimm *et al.* (1991). Cannibalistic links were removed to simplify the computer analysis (Thompson & Townsend 2000). Maximum food chain length was calculated as the number of links from a basal species to a top consumer

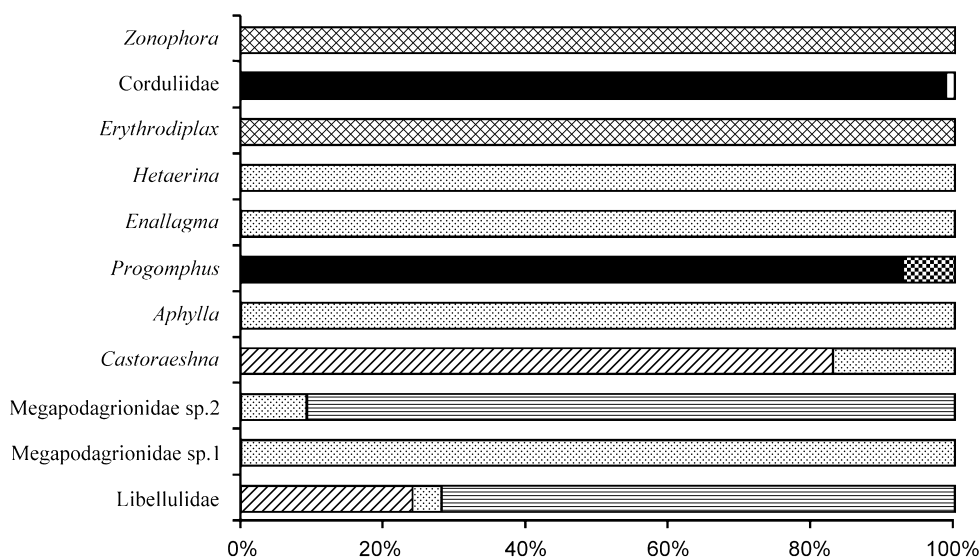


Fig. 2. Percentage of food items present in the diet of Odonata taxa sampled in the Potreirinho Creek: (▨) Coleoptera; (▩) Diptera – Chironomidae; (▧) Plecoptera; (■) Oligochaeta; (▤) Trichoptera; (▦) fragments of exoskeleton; (□) Crustacea – Copepoda.

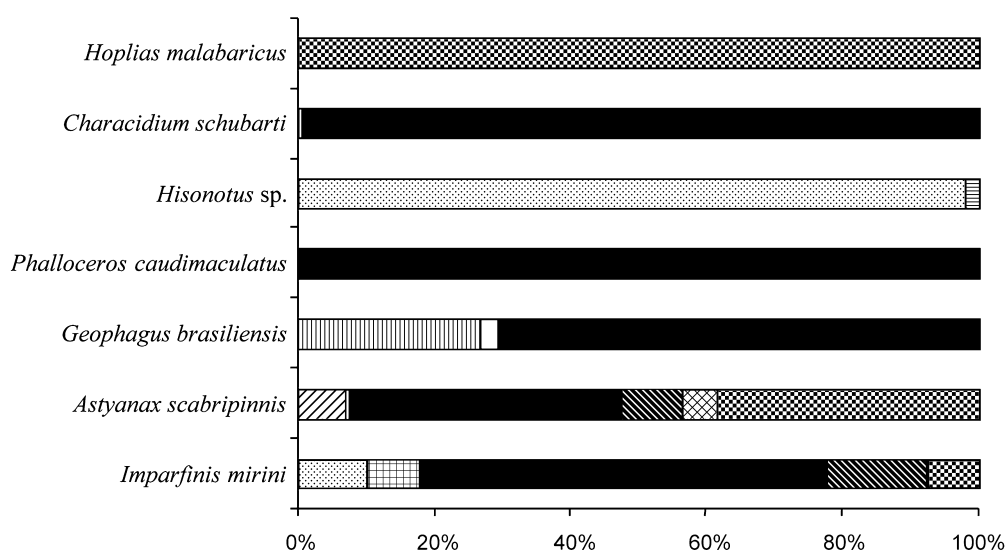


Fig. 3. Percentage (%) of food items present in the diet of fish species sampled in the Potreirinho Creek: (▨) organic matter; (▩) algae; (▧) nematoda; (▤) annelida; (▦) crustacea; (□) acarina; (■) aquatic insects; (▤) terrestrial insects; (▦) vascular plant; and (▦) fragments of exoskeleton.

(excluding feeding loops). Connectance is a measure of the system complexity or the degree to which the species in the web interact (Tavares-Cromar & Williams 1996). The connectance value was calculated as: $C = 2 \times L / (S(S - 1))$, where L is the total number of links in the web and S is the total number of species (Pimm *et al.* 1991).

Differences between compartments for all web parameters were statistically analysed by ANOVA (Systat 1997), considering six replicas of each compartment. The Tukey test was used to compare compartment pairs.

A pyramid of number was constructed for the stream community using the sum of unicellular and filamentous algae density as basal level.

RESULTS

Community analysis

A total of 112 consumers were identified in the Potrerinho Creek community, including 105 invertebrates and 7 fish species (Table 1). Among invertebrates, aquatic insects were the most diverse group representing 71.4% of the total taxon richness, followed by protozoans (11.5%) and rotifers (7.6%). Protozoans, rotifers and crustaceans presented the highest density values. The lowest density was observed for fishes (1 specimen m^{-3}). Taxon richness and total density (Table 1) showed consistent differences between planktonic, epiphytic and benthic samples analysed. The highest taxon richness was observed in the epiphyton, with aquatic insects being the most diverse group. Many insect orders with high taxon richness (Diptera, Odonata, Coleoptera and Hemiptera) occurred in this compartment but were rarely or never found in benthos and plankton. The benthic samples showed the highest density, determined mainly by protozoans and rotifers.

Dietary analysis

In Potrerinho Creek, the major resource categories exploited by invertebrates (Fig. 1a) were organic matter (34 taxa), aquatic animals (24 taxa), organic matter associated with algae (20 taxa) and vascular hydrophytes (5 taxa). The taxa that exploited those four resources occurred mainly in the epiphyton (Fig. 1b). In this compartment 67% of organic matter consumers (detritivores), 88.5% of invertebrate predators (Odonata, Coleoptera, Hemiptera), and 100% of vascular hydrophytes consumers (herbivores) were found.

Organic matter was present in the diet of almost all of the small groups, represented by 1–2 taxa each (groups E to R, Fig. 1a). Those detritivorous taxa were found mainly in the epiphytic and/or benthic compartments (Fig. 1b).

The detritivores were represented mostly by dipteran larvae (21 taxa), and the detritivores/herbivores by protozoans (7 taxa). Odonate nymphs (11 taxa) were the most diverse group of predators of aquatic animals, consuming mainly dipteran larvae (Fig. 2).

The fishes included 10 food items in their diet (Fig. 3), with aquatic insects being the major component for four fish species. *Astyanax scabripinnis* showed the broadest diet, with six food items recorded. Only *Hisonotus* sp. exploited organic matter and algae.

Fig. 4. Diagram of conglomerate Potrerinho Creek food web (T, terrestrial ecosystem; A, aquatic ecosystem). Taxa are represented by square. Taxa indicated without prey (?) are hemipterans for which no specific prey could be identified. Individual taxa and trophic species (st) are represented by a number inside a square: 1, unicellular algae; 2, filamentous algae; 3, organic matter; 4, vascular hydrophytes; 5, terrestrial insects; 6, *Arcella*; 7, *Diffugia*; 8, *Centropyxis*; 9, *Lesquereusia*; 10, *Nebela*; 11, *Quadrullella*; 12, *Heleopera*; 13, *Euglypha*; 14, *Trinema*; 15, *Cyphoderia*; 16, *Vorticella*; 17, Heliozoa; 18, *Keratella*; 19, *Euchlanis*; 20, *Lepadella*; 21, *Cephalodella*; 22, *Monommata*; 23, *Lecane*; 24, Bdelloidea; 25, *Ploesoma*; 26, Hydrozoa; 27, Nematoda; 28, Turbellaria; 29, Oligochaeta; 30, Hirudinea; 31, Acarina; 32, Ostracoda; 33, *Alona*; 34, *Chydorus*; 35, *Paracyclops*; 36, *Eucyclops*; 37, Amphipoda; 38, *Trichodactylus*; 39, Entomobryidae; 40, *Baetis*; 41, *Leptonema*; 42, *Oecetis*; 43, *Phylloicus*; 44, *Petrophila* sp.1; 45, *Petrophila* sp.2; 46, *Aphylla*; 47, *Progomphus*; 48, *Zonophora*; 49, *Castoraeschna*; 50, *Erythrodiplox*; 51, Libellulidae; 52, Megapodagrionidae sp.1; 53, Megapodagrionidae sp.2; 54, *Hetaerina*; 55, *Enallagma*; 56, Corduliidae; 57, *Tupiperla*; 58, *Paravelia*; 59, *Rhagovelia*; 60, Belostoma; 61, *Limnocois*; 62, *Ranatra*; 63, *Gyrinus*; 64, *Gyretes* (larvae); 65, *Gyretes* (adult); 66, *Megadytes* (larvae); 67, *Megadytes* (adult); 68, *Laccophilus*; 69, *Tropisternus*; 70, *Hydrophilus*; 71, *Heterelmis*; 72, *Hydrothassa*; 73, *Dryops*; 74, Brachycera; 75, *Hexatoma*; 76, Ceratopogonidae sp.1; 77, Ceratopogonidae sp.2; 78, Simuliidae; 79, *Pentaneura*; 80, *Ablabesmyia*; 81, *Labrundinia*; 82, *Procladius*; 83, *Cricotopus* sp.1; 84, *Corynoneura*; 85, *Thienemanniella*; 86, *Cricotopus* sp.2; 87, *Limnophyes*; 88, *Nanocladius*; 89, *Metriocnemus*; 90, *Parametriocnemus*; 91, Chironominae; 92, *Cryptochironomus*; 93, *Xestochironomus*; 94, *Polypedilum*; 95, *Polypedilum* (Tripodura)*; 96, *Polypedilum* gr. *Fallax**; 97, *Saetheria* sp.1; 98, *Saetheria* sp.2; 99, *Stenochironomus*; 100, *Tribelos*; 101, *Phaenopsectra*; 102, *Goeldichironomus*; 103, *Constempellina*; 104, *Paratendipes*; 105, *Rheotanytarsus*; 106, Tanytarsini Genus A*; 107, Tanytarsini Genus B*; 108, Tanytarsini Genus D*; 109, *Dixella*; 110, *Nimbocera paulensis*; 111, *Imparfinis mirini*; 112, *Hysonotus* sp.; 113, *Phallocerus caudimaculatus*; 114, *Geophagus brasiliensis*; 115, *Astyanax scabripinnis*; 116, *Characidium schubarti*; 117, *Hoplias malabaricus*. st1 = 63, 65, 66, 68, 71, 81, 90, 92, 94, 101, 102 and 108. st2 = 89 and 100. st3 = 72 and 74. st4 = 38, 62, 48, 50 and 64. st5 = 57, 58, 59 and 61. *Trivino-Strixino and Strixino (1994).

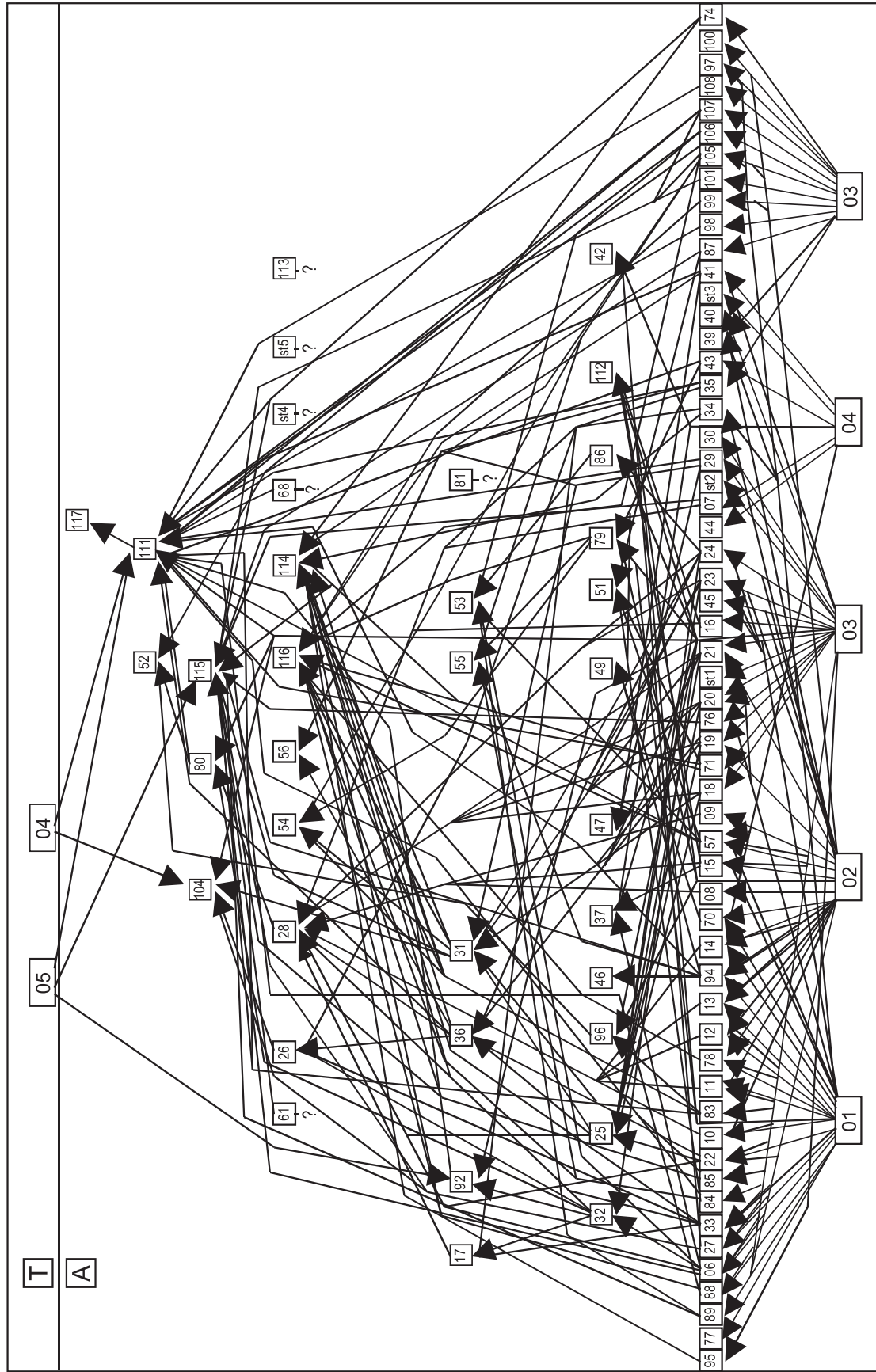


Table 2. Invertebrates consumed by fishes and their presence X (or absence –) in planktonic, epiphytic and benthic samples (fish food web number described in Fig. 4 legend)

Invertebrates used as food by fishes	Food web number	Occurrence of invertebrate prey			Fish predator (food web number)
		Plankton	Epiphyton	Benthos	
<i>Arcella</i>	6	X	–	X	115
<i>Difflugia</i>	7	X	X	X	115
<i>Cyphoderia</i>	15	X	X	X	112
<i>Vorticella</i>	16	–	X	–	112
Nematoda	27	X	X	X	115
Oligochaeta	29	–	X	X	111
Acarina	31	–	X	X	114, 115 and 116
<i>Alona</i>	33	X	X	–	114
<i>Chydorus</i>	34	X	–	–	114
<i>Paracyclops</i>	35	–	X	X	111
<i>Eucyclops</i>	36	X	X	–	111 and 114
<i>Leptonema</i>	41	–	X	–	111 and 116
<i>Phylloicus</i>	43	–	X	–	111
<i>Tupiperla</i>	57	–	X	–	111 and 116
<i>Limnocois</i>	61	–	X	–	115
<i>Laccophilus</i>	68	–	X	–	111
<i>Heterelmis</i> (larvae)	71	–	X	X	111, 114, 115 and 116
<i>Brachycera</i>	74	–	X	–	111, 114 and 115
<i>Hexatoma</i>	75	–	X	–	115
Simuliidae	78	–	X	X	116
<i>Pentaneura</i>	79	–	X	X	116
<i>Ablabesmyia</i>	80	–	X	X	111
<i>Cricotopus</i> sp. 1	83	–	X	X	111, 115 and 116
<i>Corynoneura</i>	84	–	X	–	111 and 116
<i>Thienemaniella</i> sp. 3	85	–	X	–	111, 115 and 116
<i>Limnophyes</i>	87	–	X	–	114 and 115
<i>Nanocladius</i>	88	–	X	X	111, 114 and 116
<i>Metriocnemus</i>	89	–	X	–	115
<i>Cryptochironomus</i>	92	–	–	X	111
<i>Polypedilum</i>	94	–	X	X	111 and 115
<i>Polypedilum</i> (Tripodura)	95	–	X	X	114
<i>Saetheria</i> sp. 2	98	–	–	X	111
<i>Stenochironomus</i>	99	–	X	–	116
<i>Phaenopsectra</i>	101	–	X	–	115
<i>Rheotanytarsus</i>	105	–	X	X	111, 114, 115 and 116
Tanytarsini Genus B	107	–	X	X	111 and 115
Tanytarsini Genus D	108	–	X	–	111

Food web structure

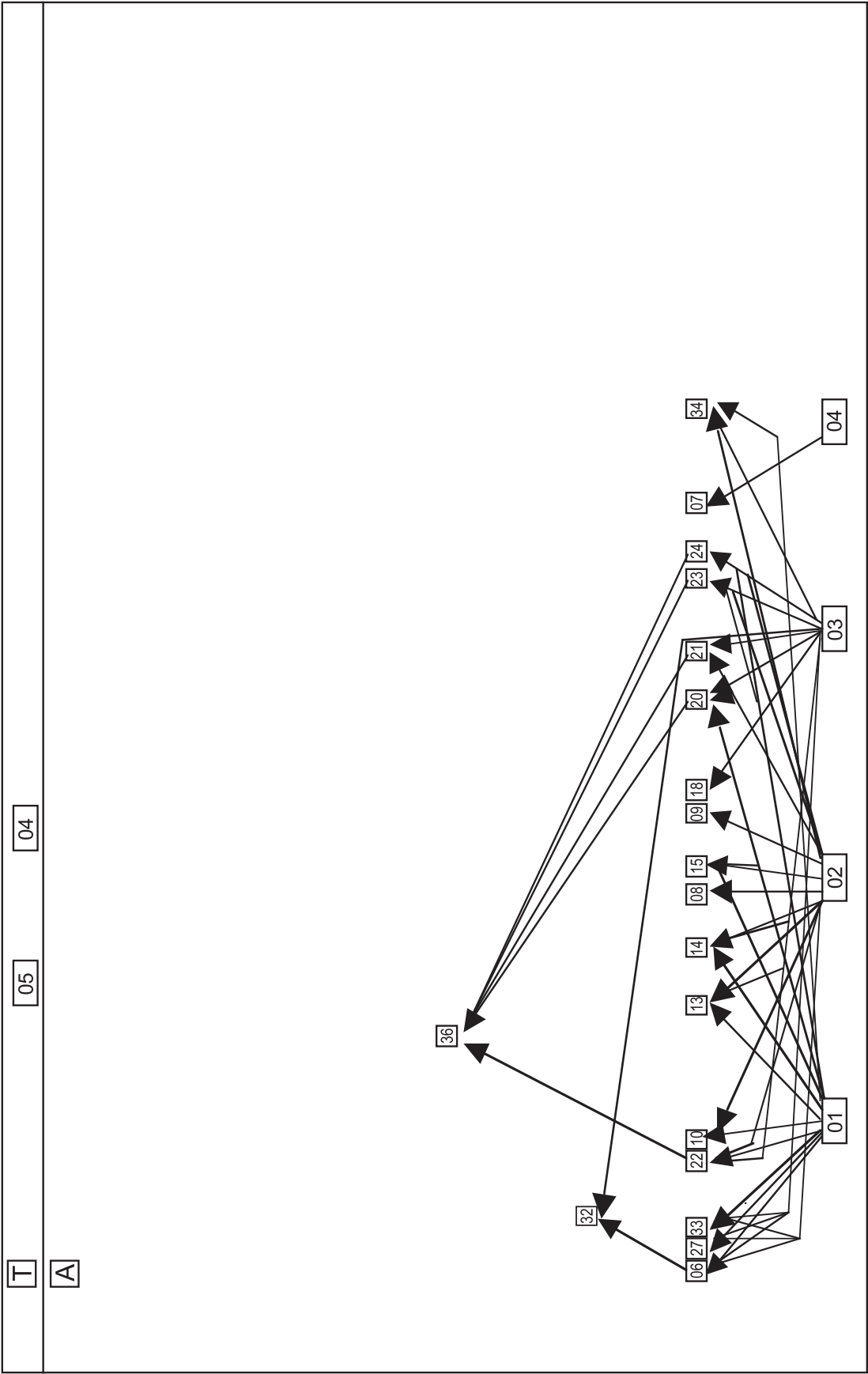
The food web of Potrerinho Creek (Fig. 4) showed a high degree of trophic complexity and seven trophic levels. The diagram shows five basal resources (numbers 1–5; Fig. 4), plus all organisms sampled in the three compartments (plankton, epiphyton and benthos), and the fishes. The fish species played an important role in connections between different compartments (Table 2), consuming items present in all three compartments, although with a predominance of epiphytic invertebrates.

In order to examine the food web structure at a smaller spatial scale, the data were also analysed separ-

ately for each of the three compartments (Figs 5–7). Among compartments, the food webs showed considerable variation in structure. The epiphytic food subweb (Fig. 6) was consistently more complex than planktonic (Fig. 5) and benthic (Fig. 7) subwebs.

A summary of descriptive statistics for the compartmentalized food webs emphasized the spatial difference in structure (Tables 3,4). The number of species, number of links and maximum food chain length were significantly higher in the epiphytic

Fig. 5. Planktonic compartment food web in Potrerinho Creek (see Fig. 4 legend for component description).



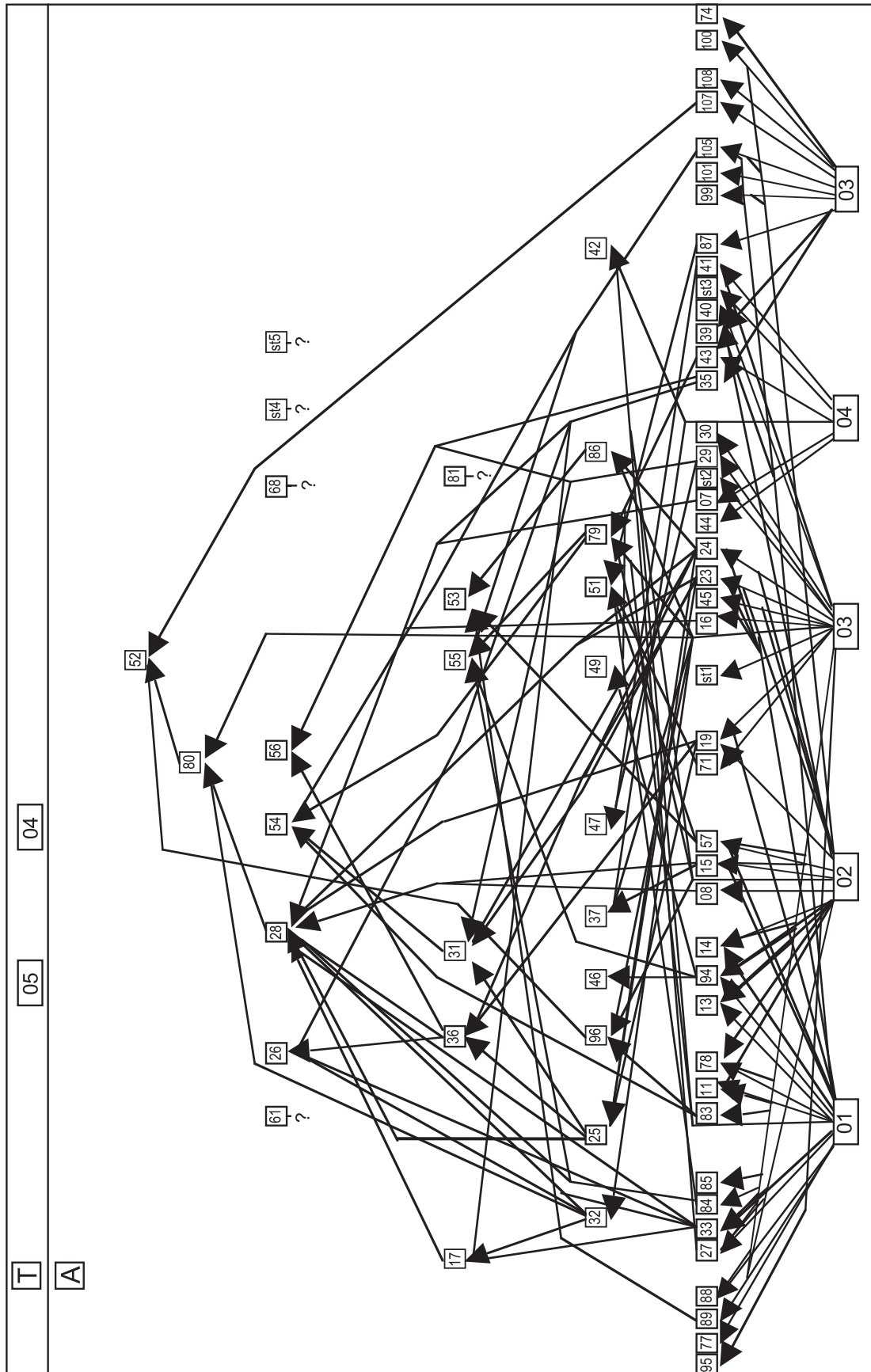


Table 3. Food web statistics analysed separately for the three compartments and for the conglomerate web of Potreirinho Creek, with data on compartments presented for each sample and for the summarized web

Compartments	Number of species	Number of links	Linkage density	Connectance	Maximum food chain length
Plankton					
Sample 1	18	39	2.2	0.255	2
Sample 2	20	44	2.2	0.232	2
Sample 3	19	40	2.1	0.246	2
Sample 4	17	32	1.9	0.235	2
Sample 5	20	42	2.1	0.221	2
Sample 6	19	40	2.1	0.234	2
Summary	22	55	2.5	0.238	2
Epiphyton					
Sample 1	73	140	1.9	0.053	4
Sample 2	71	136	1.9	0.055	4
Sample 3	68	140	2.1	0.061	6
Sample 4	69	124	1.8	0.053	3
Sample 5	80	150	1.8	0.047	4
Sample 6	63	101	1.6	0.052	3
Summary	92	199	2.2	0.048	6
Benthos					
Sample 1	21	43	2.0	0.205	2
Sample 2	19	33	1.7	0.193	2
Sample 3	17	33	1.9	0.243	3
Sample 4	22	36	1.6	0.156	3
Sample 5	20	37	1.9	0.195	3
Sample 6	27	48	1.8	0.137	3
Summary	39	75	1.9	0.101	3
Conglomerate food web	117	345	3.0	0.05	7

compartment than in the other two (Tables 3,4). Also, the connectance was significantly lower in the epiphyton. The significant differences of most food web parameters (Table 4) were determined by an increase in the number of trophic species, represented mainly by intermediate species.

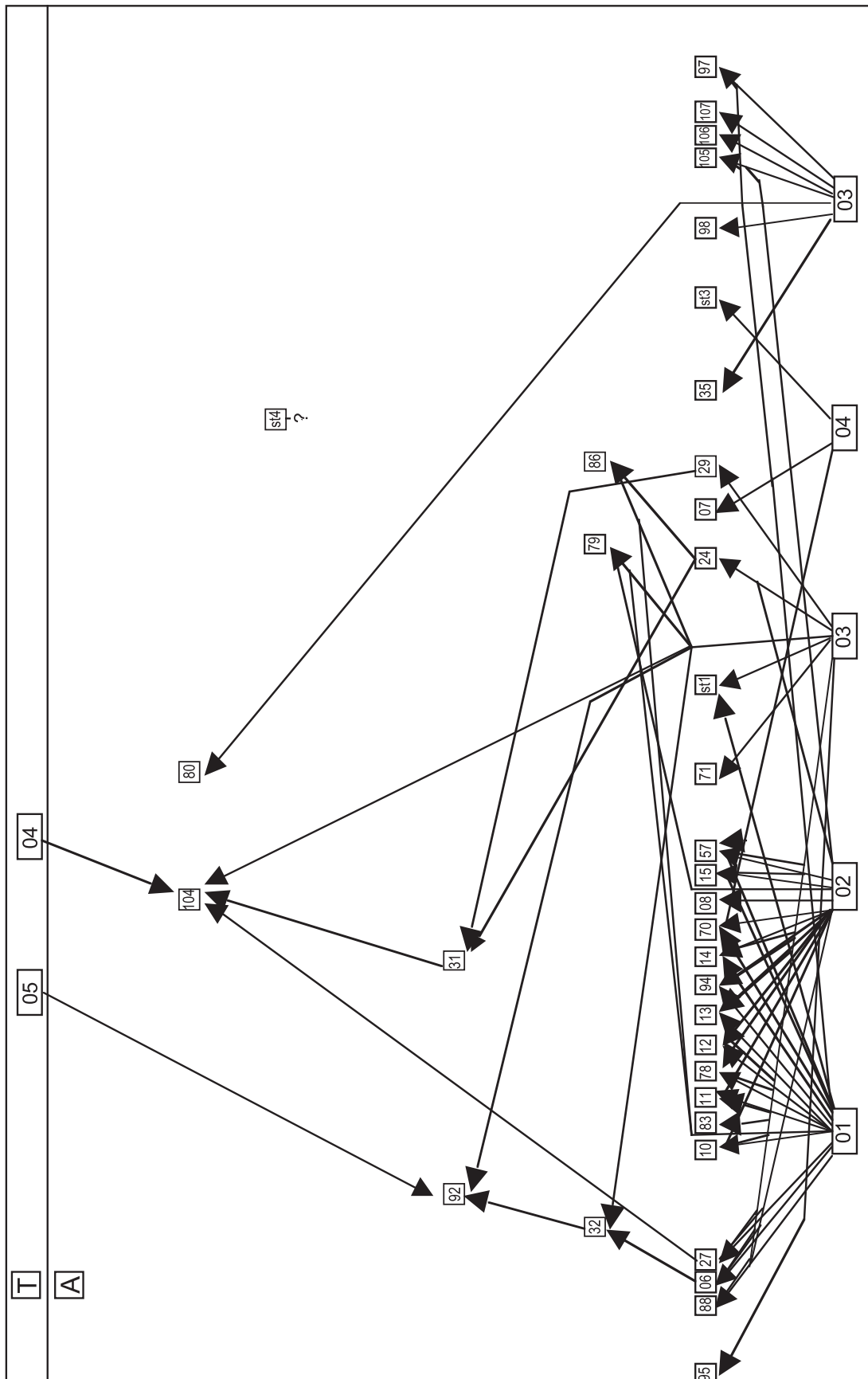
The pyramid of numbers showed a drastic reduction in the density of individuals at higher trophic levels (Fig. 8). The density decreased from 5.7×10^9 ind. m^{-3} at the base to less than 1 ind. m^{-3} at trophic level seven. More taxonomic units were found at the first and fourth trophic levels (Table 5). The greatest number of trophic levels (six) was exploited by arthropods, followed by fishes (five trophic levels). Only arthropods and fishes were found at higher trophic levels, with the fish *Hoplias malabaricus* (Bloch, 1794) the only top predator at trophic level 7.

In the Potreirinho Creek web, the basal resources were used by taxa not only from the first trophic level, but also taxa up to trophic level six (Fig. 9). Omnivory was the predominant feeding habit among species at higher trophic levels (100% of taxa from trophic levels 4–6).

DISCUSSION

The Potreirinho Creek food web, with 117 identified taxa, is among the largest, most complete stream webs documented. Although it is important to increase the accuracy of food-web studies, it is not always feasible to describe all the trophic components in exhaustive detail. The Potreirinho Creek food web presented a good taxonomic resolution of all levels, except the base. Many food web studies are criticized because of the taxonomic and trophic aggregations used, especially at the base. Moreover, as emphasized by Yodzis and Winemiller (1999), it may never be possible to resolve all trophic units of a food web at the level of biological species. Even if full resolution at species level was possible within a food web, some degree of aggregation would be desirable. Fully resolved food webs would be too complex to work for many purposes (Yodzis & Winemiller 1999). It is necessary to define what kind and what degree of aggregations are acceptable for a given analysis. In Potreirinho Creek, the objective was to study the food web structure comparing the planktonic, epiphytic and benthic compartments.

Fig. 6. Epiphytic compartment food web in Potreirinho Creek (see Fig. 4 legend for component description).**Fig. 7.** Benthic compartment food web in Potreirinho Creek (see Fig. 4 legend for component description).



Thus, aggregation of basal level components was not a problem, because the three compartments were described with the same level of resolution. Moreover, the growth form of the algae (unicellular and filamentous algae) was more informative than the biological species level for the analysis of this basal resource. In Potreirinho Creek, although most consumers exploited unicellular and filamentous algae, two dipteran larvae (*Cricotopus* sp2 and *Nanocladius*) exploited only filamentous algae. Steinman (1996) described the apparent rejection of filamentous algae by grazers and the apparent selectivity by protist herbivores for unicellular diatoms. According to this author, the removal of the algae is related more to morphological constraints of feeding apparatus of grazers than to discrimination of algal taxa (Steinman 1996).

Havens *et al.* (1996) emphasized the need for studies that included all trophic levels in analyses of food

webs. However, most stream food webs have been constructed with emphasis only upon macro-invertebrates (Closs & Lake 1994; Tavares-Cromar & Williams 1996; Corigliano & Malpassi 1998; Thompson & Townsend 1999). Recently, two studies demonstrated the importance of meiofauna in the structure of a stream food web (Schmid-Araya & Schmid 2000; Schmid-Araya *et al.* 2002a). The inclusion of meiofauna resulted in an increase of web complexity, and consequently caused modifications in the food web patterns. In the food web of Potreirinho Creek, the meiofauna, represented by rotifers, crustaceans, annelids, and early instars of insect larvae, were present at high density showing the importance of this group as a food resource for higher trophic levels. Schmid-Araya and Schmid (2000) suggested that feeding on meiofauna enhances the survival and growth of predatory and omnivorous macrofaunal taxa because of their nutritional value as

Table 4. Results of ANOVA test on food web properties used for compartments comparison (followed by TUKEY multiple comparisons)[†]

Source of variation	F	P	Plankton	Comparisons between food webs			
				Benthos	Epiphyton		
Number of trophic species	342.1	0.000	b	=	b	<	a
Number of trophic linkage	120.4	0.000	b	=	b	<	a
Linkage Density	6.5	0.094	–		–		–
Connectance	103.9	0.000	a	>	b	>	c
Proportion of basal species	66.2	0.000	a	=	a	>	b
Proportion of intermediate species	11.4	0.000	b	=	b	<	a
Proportion of top species	4.1	0.03	a	=	ab	=	b
Proportion of B–T links	33.4	0.001	b	<	a	>	c
Proportion of I–T links	73.2	0.000	b	>	c	<	a
Proportion of I–I links	10.5	0.014	b	=	b	<	a
Proportion of I–B links	17.4	0.001	a	>	b	<	a
Maximum food chain length	12.7	0.000	b	=	b	<	a

[†]TUKEY comparisons are included only for statistics in which there were significant overall alterations between spatial webs based on ANOVA. Different letters indicates treatments significantly different. B, basal; I, intermediate; T, top.

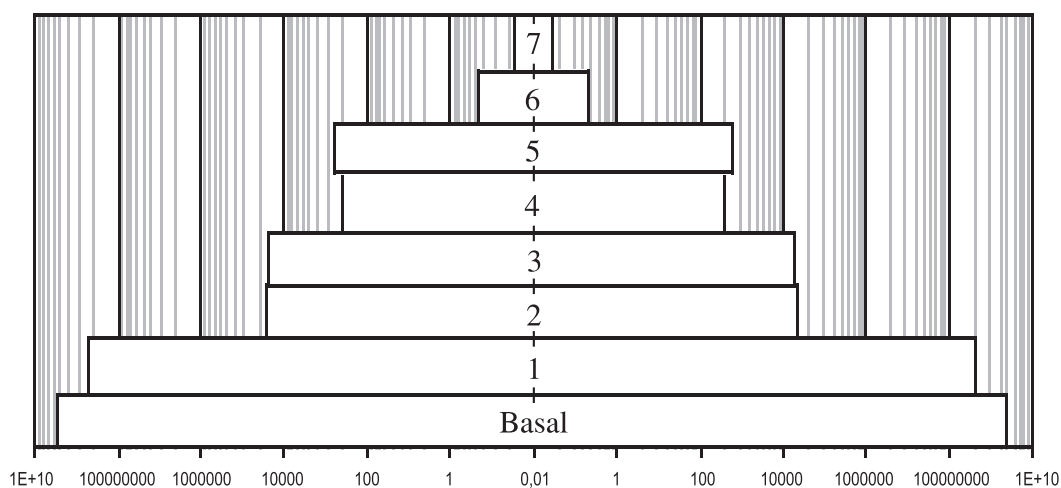


Fig. 8. Pyramid of number obtained in the Potreirinho Creek.

food and because their body size makes them available to early instar larvae.

In the Potreirinho Creek food web, a high percentage (59%) of consumers exploited organic matter. The importance of organic matter as basal food resource has been found in various streams of temperate and tropical regions (Hildrew *et al.* 1985; Closs & Lake 1994; Tavares-Cromar & Williams 1996; Schmid-Araya *et al.* 2002a). Species-rich and detritus-based systems may be responsible for the high degree of omnivory observed (Hall & Raffaelli 1991), because a detritus base is generally associated with a low productivity of these systems (Briand 1985). Thus, the high number of omnivores observed in the Potreirinho Creek food web may be due to the greater amount of energy available at lower trophic levels. A high species richness, a detritus-based system and a high degree of omnivores apparently characterizes stream food webs in temperate and tropical regions. These characteristics may also be responsible for the rarity of strong, top-down trophic cascades observed in streams (Closs &

Lake 1994). In these ecosystems, the impact of top predators such as fish tend to dissipate along the food web (Strong 1992) due to the high degree of omnivory, substitution of species, and compensation among species for the functions of others (Menge *et al.* 1994).

The pyramid of number derived from the Potreirinho Creek food web also showed peculiarity in its structure. The pattern of reduction in density of individuals at higher trophic levels, was not evident when comparing adjacent trophic levels (basal and first trophic levels, second and third trophic levels, and so on). This result may be explained by the size similarity between organisms of adjacent trophic levels. Another explanation for this density similarity is the observed high degree of omnivory. This means that one level can support another above it of the same density because their components are exerting a predation pressure both on the adjacent level and on lower levels.

In Potreirinho Creek, the greatest trophic complexity was found in the epiphytic subweb, compared to the planktonic and benthic subwebs. This demonstrated substantial spatial variation in the structure of food webs within a single type of habitat when considered as a small spatial scale. In Potreirinho Creek, greater species richness and trophic complexity were observed in the epiphytic subweb and these may be associated with the physical structure of substratum. The aquatic macrophytes probably provide a substratum more stable and structurally complex than the sediment. In the benthic substratum the presence of small inorganic particles (sand grains) tend to make it more unstable and abrasive. Although a greater density of micro and meiofauna was observed in the benthic compartment, this subweb did not contain large invertebrate predators. This may be associated with the refuges provided by interstitial spaces in sand that should reduce foraging efficiency of large invertebrate predators. In contrast, in the epiphytic subweb, the additional species were mainly large invertebrate predators that utilize the more structurally complex

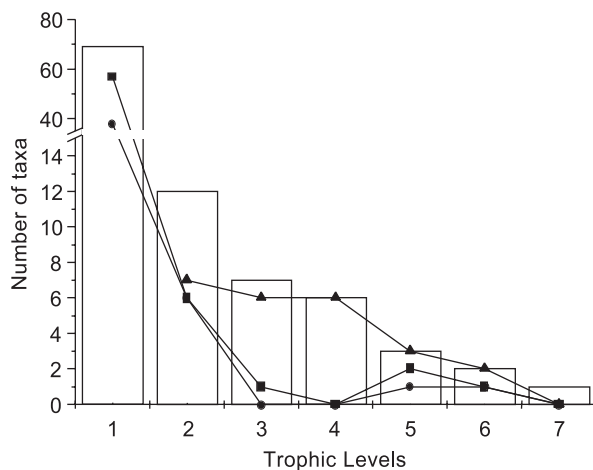


Fig. 9. Number of taxa, number of consumers of basal resources (organic matter and algae), and omnivores obtained by trophic level, in the Potreirinho Creek.

Table 5. Mean density (ind. m⁻³) of taxonomic units of each trophic level in the Potreirinho Creek

Taxonomic unit	Basal	Trophic levels						
		1	2	3	4	5	6	7
UA	5.7×10^9	—	—	—	—	—	—	—
FA	5.5×10^7	—	—	—	—	—	—	—
Protozoa	—	1.0×10^9	—	33 190	—	—	—	—
Hydrozoa	—	—	—	—	36	—	—	—
Rotifera	—	1.4×10^7	33 190	—	—	—	—	—
Turbellaria	—	—	—	—	36	—	—	—
Nematoda	—	2.0×10^5	—	—	—	—	—	—
Annelida	—	5.4×10^4	—	—	—	—	—	—
Arthropoda	—	5.2×10^4	20 726	10 694	541	1354	0.17	—
Chordata	—	—	0.30	—	0.21	0.20	0.28	0.06
Total	5.7×10^9	1.0×10^9	53 916.30	43 884	613.21	1354.20	0.45	0.06

FA, filamentous algae; UA, unicellular algae.

macrophytes as substrate for foraging and refuge from fish predators. The analysis of resource exploration by invertebrates belonging to each compartment showed that a greater number of detritivore species was found in the epiphytic subweb. This suggests that organic matter is more available in the epiphytic subweb and/or foraging efficiency of micro and meiofauna is greater in vascular hydrophytes.

The greater richness of species in the epiphytic subweb resulted in modifications of all web parameters. The high proportion of intermediate species in the epiphytic subweb, determining an increase of intermediate-intermediate links and a reduction of basal-top links, may be explained not only by the increase in species richness but also by a reduction of species without a predator, as found by Closs and Lake (1994).

The increase of the epiphytic food web diversity also resulted in longer food chain length. This food web characteristic increases with number of species as a function of the increase of links between large top predators and intermediate meiofauna present at high levels (Warren 1989). We suggest that the greater species richness and trophic complexity obtained in the epiphytic subweb might be due to the higher degree of habitat complexity supported by the macrophyte substrate.

Controversy persists about connectance values, possibly due to the variability in documenting links (Hall & Raffaelli 1993). Schmid-Araya *et al.* (2002b) analysed three possible and related explanations for the pattern of declining connectance with increasing richness. These may be applied to the Potrerinho food web. First, a preponderance of non-predatory species (herbivores/detritivores) will not increase the maximum number of links per species (Closs & Lake 1994), as non-predators by definition can consume only basal species (Schmid-Araya *et al.* 2002b). Second, the high body size difference between meio and macrofauna could also decrease encounter rate, and thus the number of realized food web links. Third, low connectance in stream communities can be attributed to a more frequent and intense physical disturbance regime and to spatial heterogeneity found in streams, limiting the realized links between species by reducing the encounter rates between them.

Despite differences observed in the structure of the three subwebs, they are highly connected by trophic interactions. Such connections decompartmentalize webs and increase complexity (Polis 1991). The conglomerate food web of Potrerinho Creek showed this complexity and can be differentiated by the effective participation of fishes in all subwebs. The high degree of fish omnivory associated with their movements at different spatial scales suggests that these animals have a significant role in the food web dynamic

of Potrerinho Creek. The role of fishes as a link between different compartments has also been demonstrated for other aquatic habitats (Winemiller 1990; Winemiller & Jepsen 1998; Schindler & Scheuerell 2002).

The interface between aquatic plants and the open water environment is a particularly active zone for feeding interactions at all trophic levels (Winemiller & Jepsen 1998). This may be applied to Potrerinho Creek, with fishes foraging mainly in the epiphytic subweb, where macrophytes offer prey refuge and trophic complexity. This interface role of macrophytes and the interconnections which result from fish foraging, diluted the compartmentalization of the Potrerinho food web. Winemiller and Jepsen (1998) also found a lack of habitat compartmentalization in their food web, and used three explanations for that: (i) macrophytes are used as prey refuge; (ii) edge habitats with more structural complexity are used as foraging regions; and (iii) there is frequent movement between habitats by either predators and prey. The same explanation can be applied to the Potrerinho Creek food web.

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