

Trophic organization and food web structure of southeastern Brazilian streams: a review.

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ABSTRACT: Trophic organization and food web structure of southeastern Brazilian streams: a review.

The present study reviews some trophic patterns of southeastern Brazilian streams. The food resources availability, the relationship between production and importation, the establishment of feeding guilds, and the patterns of trophic structure of fish and macroinvertebrate communities, with a particular emphasis on food webs, are discussed. In the four food webs used as examples, the following aspects were emphasized: (1) the importance of allochthonous material input to the aquatic system, (2) the importance of detritus and algae as a link between the detritus and the grazing chain, (3) the spatial and temporal variation in the trophic structure, and (4) the high degree of omnivory.

Key-words: trophic structure, stream, macroinvertebrates, fish, food web.

RESUMO: Organização trófica e estrutura de tramas alimentares de riachos no sudeste do Brasil: uma revisão.

O presente estudo revisa algumas características dos padrões tróficos observados em riachos do sudeste do Brasil. Os recursos disponíveis, as relações entre produção e importação, o estabelecimento de guildas alimentares e os padrões da estrutura trófica de comunidades de peixes e macroinvertebrados, com ênfase particular em tramas alimentares, são alguns dos pontos discutidos. Nas quatro tramas alimentares usadas como exemplo foi enfatizado: (1) a importância da entrada de material alóctone para o sistema aquático, (2) a importância dos detritos e algas como uma ligação entre a cadeia de detritos e de pastagem, (3) a existência de variação espacial e temporal na estrutura trófica e (4) o alto grau de onivoria.

Palavras-chave: estrutura trófica, riachos, macroinvertebrados, peixes, trama alimentar.

Introduction

The understanding of the trophic structure and organization of an ecosystem depends on the knowledge of food resources availability, diet and interaction mechanisms among the species during the utilization of these resources.

For temperate river ecosystems, Allan (1995) points out the trophic complexity caused mainly by the polyphagy, which leads to a considerable overlap of species diet. For tropical rivers, the available information on the trophic complexity is not much. Although Brazil has a considerable hydrographic network, few studies of faunistic surveys on the aquatic invertebrates have been done, mainly due to the difficulty of immature taxonomic identification (Oliveira & Froehlich, 1997). This difficulty causes the scarcity of studies on the diet of these invertebrates and much of the information is inferred from temperate environments.

The level of systematic knowledge on Brazilian stream ichthyofauna is

characterized by a great heterogeneity among the various taxonomic groups, some very well studied and others less studied (Buckup, 1999). The available information on the diet of Brazilian stream fishes is also very restricted, when compared to the amount of existing studies on the same theme in rivers and dams (Arcifa et al., 1988; Carvalho et al., 1998). This is significant if we consider the abundant surface of streams in the country and, particularly, the speed of disturbance and destruction of many areas (Esteves & Aranha, 1999).

Information about trophic organization and food web structure of southeastern Brazilian streams also are scarce. Many aspects of trophic organization and food web structure and functioning can reveal fundamental properties of stream ecosystem, leading to the understanding of relationships and predicting dynamics.

Thus, in the present study we intend review some trophic patterns of stream communities in southeastern Brazil. The resources availability, the trophic structure

and organization of macroinvertebrate and fish communities, and the food web patterns are some of the points discussed.

Food Resources

The categories of food resources in stream ecosystems are: (1) organic detritus; (2) periphyton; (3) living animal tissue, and (4) living plant tissue.

Organic detritus is composed by all kinds of biogenic matter in different periods of microbial decomposition (Darnell, 1964). Detritus comprises a mixture of animal and vegetal matter of allochthonous and autochthonous origin. An important source of allochthonous organic matter assimilated by animals is derived from leaf litter input from riparian vegetation. Leaf litter breakdown is a continuous process where large particles of organic matter are incorporated into fungal and consumer biomass, and reduced to fine particulate organic matter (FPOM) and dissolved organic matter (DOM) by biotic and abiotic processes (Graça et al., 2001). Despite the allochthonous or autochthonous origin of detritus, several authors reported organic matter as the main food resource of stream communities (Hildrew et al., 1985; Closs & Lake, 1994; Schmid-Araya et al., 2002). This trophic pattern also has been observed for streams studied in Brazil, being particulate organic matter the main item of the diet of most aquatic insects (Baptista et al., 1998; Henriques-Oliveira et al., 2003; Roque et al., 2003; Motta & Uieda, 2004; Motta & Uieda, 2005).

Although periphyton is composed mostly of algae, many authors (Wetzel, 1983; Cole, 1994; Allan, 1995) emphasize its structural complexity and the association of algae with a diversity of heterotrophic organisms and organic matter. This association forms a matrix or biofilm that can re-cover any surface of the stream, and can be used as a direct food source by many taxa (Cummins & Klug, 1979; Allan, 1995; Winterbourn, 1995; Motta & Uieda, 2004; Motta & Uieda, 2005).

Live vascular plants, represented by aerial, submersed or floating species, are more common in plain streams or flooded areas. In headwaters, where it is more shaded and the current velocity is higher, we can find bryophytes adhered to the rocky substrate. In general, the macrophytes are considered as a food resource of little significance, eaten by a limited number of

invertebrates. The thick cellulose walls, the high amount of lignin (Allan, 1995), and the presence of defensive components (Newman, 1991) are considered as possible causes for the low herbivory on macrophytes, hence, constituting a barrier against their ingestion and digestion. Despite those defensive characteristics, in some situations macrophytes can be an important food resource for stream fishes, as reported by Vilella et al. (2002) for a fish community of an Atlantic forest river in southern Brazil. Although aquatic macrophytes enter the aquatic food web mostly as detritus (fine and coarse particulate organic matter) than as living vegetal tissue (Pomeroy, 1980), some studies developed in temperate streams have shown that herbivory loss was significantly high (Jacobsen & Sand-Jensen, 1995).

Animal preys can be ingested wholly, in pieces or even just have their body liquids taken. Because of the great diversity of the stream fauna, it can be easily understood why the potential risk of predation is so great, with all organisms being potential prey to others in some period of their lives.

Trophic guilds

The understanding of the trophic structure of an ecosystem depends on the diet of species, although there are some problems in defining what they consume. One problem is the high polyphagy of most species observed in the aquatic ecosystem (Vadas, 1990; Havens et al., 1996; Merritt & Cummins, 1996a) that can complicate the species classification within trophic levels. Another problem is the difficulty to distinguish the items of the gut content, which may lead to generalizations, like using the broad category of herbivore-detritivore (Allan, 1995), or even omnivore (Merritt & Cummins, 1996a). Thus, the trophic levels are not always clear-cut for the species and their resolution is clearly coarse (Hooper et al., 2002).

A solution to this problem in the river ecosystem, presented initially for macroinvertebrates of temperate regions (e.g. Merritt & Cummins, 1996b), is the classification of the species based on how food is obtained, rather than on the type of food ingested. Thus, the species that consume a resource by a similar mode are considered as members of the same guild.

Trophic guilds could be defined as a group that subsist utilizing the same group of resources or with similar niche characteristics and dimensions that are comparable inside a community (e.g. Callisto & Esteves, 1998). Because trophic guilds may be defined independently from the component species, they become very useful when the functional organization of different communities are being compared, mainly when they are not composed of common species. Thus, the definition of trophic guilds should be a priority for a better understanding on how diversity affects ecosystem functioning, particularly primary production, secondary production, and ecosystem level resource use (Hooper et al., 2002).

The division of macroinvertebrates in guilds based on the morphological-behavioral mechanisms, referred as functional feeding groups (Cummins, 1973; Merritt & Cummins, 1996b), separates the organisms according to the method used to capture food, so members of different guilds might be consuming the same food. However, functional feeding groups are not of easy application in tropical (Winterbourn, 1995), or even in temperate streams (Mihuc & Mihuc, 1995).

The adoption in tropical streams of the categories proposed for temperate streams should be done with caution (Callisto & Esteves, 1998; Cheshire et al., 2005). The transfer of information on functional feeding groups between regions (temperate vs. tropical) is not appropriated for taxa with broad geographic distribution. Motta (1996), when analyzing the gut contents of aquatic insects collected in a stream in southeastern Brazil, found divergence with the data cited in the literature of temperate region for the same taxa. It is also important to recognize that most aquatic insects are not restricted to a functional feeding group, like chironomid larvae (Nessimian & Carvalho, 1998; Nessimian et al., 1999; Henriques-Oliveira et al., 2003), or more specifically shredder insects (Mihuc & Mihuc, 1995).

Recently, Rosi-Marshall & Wallace (2002) studying streams in a temperate region also observed divergences between functional feeding group and food resource, with taxa classified as shredders consuming resource other than leaf tissue. These authors showed the importance of gut content analysis in determining trophic status and resource utilization in the studied

community rather than the classification on functional feeding groups based only on morphologic-behavioral mechanisms.

Clearly, this discussion shows the difficulties to assign species within trophic groups for a better understanding of trophic structure of stream ecosystems. Not only macroinvertebrates but also fishes represent an important component of streams and should be included for a comprehensive analysis of the trophic structure. In studies realized in southeastern Brazilian streams, we are classifying invertebrates and fishes into trophic groups based on the same basic categories of food resources (Uieda et al., 1997; Motta & Uieda, 2004). In this classification we are using the periphyton feeder category for insects and fishes which feed on the mixture of algae, organic matter, and microbiota adhering to the surface of substrates. The periphyton feeder group takes into account not only the morphologic-behavioral mechanism of food intake but also the type of food ingested. This category also identifies an important trophic pathway of stream communities.

For the analysis of stream trophic structure, it is possible to use the classification of macroinvertebrates and fishes into five trophic groups. (1) Detritivores feeding on coarse and fine particulate organic matter, (2) herbivores feeding on living vascular plant tissues and/or algae, (3) carnivores preying animals, (4) periphyton feeders consuming both algae and particulate organic matter associated with a microbiota, and (5) omnivores utilizing resources from two or more of the above mentioned trophic groups.

Trophic organization

Macroinvertebrates

The relative importance of biotic and abiotic factors on the structure and functioning of the river ecosystem communities is historically divided into two opposite views (Reice 1994 apud Baptista et al., 1998). One of them views the communities as structured by biotic interactions according to environmental variations in spatial and temporal scale, thus forming strongly structured and independent communities. In the opposite view, the biota of the rivers is a gathering of opportunist species, which survive and increase their population while the conditions are favorable in between

catastrophic flood periods and dry periods. A more moderating and comprehensive concept, the River Continuum Concept (RCC) was proposed by Vannote et al. (1980), which stated that the communities can be placed in between these two extremes, being organized and limited by deterministic processes and stochastic factors. In the RCC model the communities present predictable structural and functional organization patterns, which vary according to the relative position throughout the longitudinal river profile (Vannote et al., 1980).

Although the RCC has been developed based on data of non-disturbed temperate rivers ecosystem and mainly for the macroinvertebrates community, a comparative analysis with ecosystems of other regions may facilitate the definition of trophic structure patterns of stream communities. In general this model shows: (1) the importance of litter input which influences the density of shredder insects; (2) the increase of scrapers in the sections where primary production is favored by light and nutrients; (3) the link between the abundance of collectors and the quantity of FPOM as a result of the litter decomposition and the importation from upstream sections, and (4) the constant relative abundance of predators.

In Brazil, studies developed in disturbed and non-disturbed streams tried to analyze the RCC predictions. In a pristine Atlantic Forest stream, located in the state of Rio de Janeiro, the structural and functional organization of an aquatic insect community, analyzed through a longitudinal gradient, corroborated in great part the RCC predictions (Baptista et al., 1998). However, Callisto & Esteves (1998), when analyzing the functional categories of benthic macroinvertebrates in four lotic ecosystems under the influence of bauxite mining in Central Amazon, found different results from the RCC model predictions and showed the limitation of this model for disturbed environments.

A number of investigations have tested the river continuum concept in tropical streams and observed that some functional groups, mainly shredders, did not conform to the predictions. Some studies in the tropics pointed out a lack of shredder species (Walker, 1987; Rosemond et al., 1998; Dobson et al., 2002), other an occurrence in low density and richness (Kikuchi, 1996). The functional differences

between tropical and temperate streams may be one explanation for the differences on shredders occurrence (Dobson et al., 2002). This could be due to the enhanced microbial activity replacing shredder activity at high temperatures. Alternatively, it could be a result of low palatability of detritus input from dominant riparian trees at tropical regions. Another reason could be methodological: the determination of functional feeding groups may be incorrect or focussing not in potentially shredding taxa. Shredders guild may be occupied by others taxa than insects, such as crabs. Otherwise, some studies developed in Brazilian (Baptista et al., 1998) and Australian streams (Cheshire et al., 2005) found a high percentage of shredders, and emphasized their importance as components of the invertebrate assemblages in terms of biomass and species richness.

Fishes

The classification of stream fish species diet based only on the type of ingested food, as it is done in the majority of works that analyze ichthyofauna trophic structure, can also result in categories of little use in studies of resource partitioning among the species. If information on how (feeding strategies), where (spatial distribution) and when (temporal distribution) the food is obtained is added to this feeding classification, it will be easier to interpret the relationships among species. Reviews of trophic patterns (Esteves & Aranha, 1999) and feeding behavior patterns of tropical stream fishes (Sabino, 1999) constitute important contributions to the understanding of the trophic structure of Brazilian streams.

Some consistent trophic structure patterns can be extracted from the information compiled in the two studies cited above:

a) a predominance of omnivores, a generalized trophic group, which may be explained by a flexibility of stream fishes in consuming diversified items when the preferred item is in a short supply;

b) a predominance of aquatic insects on fish diet, represented mainly by Chironomidae larvae (Diptera), probably related to the great abundance of this resource in streams;

c) a spatial and temporal variation in the diet of many species, according to

alterations in the food availability, caused by alterations in the abiotic (physical, chemical and basin characteristics) and biotic conditions (species interaction);

d) an importance of terrestrial resources for stream fish communities, since they constitute the main way that organic matter enters the system;

e) an importance of algae, found in association with microorganisms and organic matter in a periphytic matrix, scraped from substrates by grazer fishes;

f) a high food overlap among species, that use spatial, temporal and behavioral differences in the exploitation of food resource as mechanisms to reduce this overlap;

g) changes in the feeding niche breadth of the species caused by alterations in the resource availability.

In most of the patterns listed above the importance and integration of the abiotic and biotic factors structuring the stream fish communities is evident. A relatively new approach in Brazil, but well developed in temperate regions, is the use of experimental manipulation to analyze how ecological processes affect the structure and trophic organization of stream communities (e.g. Uieda, 1999). Contrasting with descriptive methods, the experimental manipulation can supply data on cause-effect relationships among the manipulated variables (Peckarsky & Penton, 1990). Esteves & Aranha (1999) stress the development of manipulative studies as a new perspective for studies on trophic ecology of stream fishes in Brazil.

Flecker & Feifarek (1994), analyzing the structure of invertebrate assemblages in two Andean streams, suggested that physical disturbance can exert a major influence on the structure of neotropical streams. During the dry season, however, biotic interactions are most likely to replace disturbance in controlling community patterns of distribution and abundance (Flecker & Feifarek, 1994). Preliminary data from an experimental manipulative study developed on a Brazilian stream, in which macroconsumers (mainly fishes) were excluded from delimited areas of the stream substrate (V.S. Uieda, personal communication), reinforced this pattern. This experiment has shown seasonal differences in the action of abiotic and biotic factors in structuring basal resources (organic matter and algae) of this system. In the period of

greater rainfall, the rain had an important action in the substrate homogenization by washing away sediments and associated algae. However, in prolonged nearly zero pluviosity periods, the macrofauna exerted an important and expressive effect on the sediment deposition and on the development of algae, through a direct action, utilizing this resource as food, or indirect action which consisted in the predation of other detritivore/herbivore species.

Thus, although we can already define various trophic structuring patterns of stream fish communities in Brazil, a better understanding of determinant factors of this structure is still necessary, in order to allow the formulation of hypotheses about the functioning of these systems.

Food web structure

The interaction among species from a trophic point of view, that is, food web structure and organization, is important to understand the natural community functioning. Food web is defined as a net of interactions among a group of organisms, populations or aggregates of trophic units that can be studied under three points of view (Winemiller & Polis, 1996). (1) Descriptive webs that show the presence and absence of food links among the species of the community. (2) Bioenergetic webs that quantify the energy and matter transportation through predation. (3) Functional webs that identify the food links that play the most influence on the community structure and dynamics.

Some preliminary hypotheses about the effects of network structure upon river food web structure and dynamics was presented by Power & Dietrich (2002) and Woodward & Hildrew (2002). As stressed by those authors, how longitudinal gradients in productivity, disturbance regimes and habitat structure down rivers affect food web structure and dynamics are some important points to be explored and to answer questions of food web responses to some of the network properties of river drainages. Some points reinforced by those authors will be here exemplified by us for Brazilian streams, like: (1) the relationship between food chain length and habitat size, (2) the importance of terrestrial plant detritus and algae as basal energy resources of river food webs, (3) how downstream

changes in habitat size affect functional groups and food webs.

A fundamental aspect of any food web is the source of primary production that supports consumer populations. The autotrophic or heterotrophic condition of stream ecosystems, which is determined through an estimation of the primary productivity, varies according to the characteristics of these systems. As one moves from headwaters to downstream, more sunlight hits the streambed and stream temperature and algal productivity increase (Power & Dietrich, 2002). Thus, the type of vegetation cover, substrate, topography, and rainfall can determine conditions of autotrophy or heterotrophy. Small streams in heavily forested areas have low autochthonous primary productivity because of light limitation, the main factor that affects the primary productivity in tropical streams (Necchi & Branco, 1992; Oliveira & Calijuri, 1996; Motta, 1996).

In two adjacent areas of a 3rd order stream in southeastern Brazil, one with forested margins and other only with shrubby vegetation, the influence of the riparian forest over the autotrophic or heterotrophic condition was evident (Henry et al., 1994; Uieda & Kikuchi, 1995; Uieda et al., 1997; Afonso et al., 2000). The removal and impoverishment of the riparian forest determined a decrease in the input of coarse organic matter, an increase in the light incidence, and a major development of periphytic algae and macrophytes in this stream (Henry et al., 1994; Afonso et al., 2000). Despite the fact that daily and annual vegetation biomass imported exceeded 20 fold the animal biomass (Uieda & Kikuchi, 1995), the latter, represented by terrestrial insects, constitute an important food resource to the ichthyofauna of this environment (Uieda et al., 1997). Although the primary productivity was not estimated in this stream, an increase in the availability of periphytic algae in the area with lesser shading can be deduced through the food consumed by the fishes collected there. The species that fed on periphyton were found predominantly in the area with lesser vegetation cover (Uieda et al., 1997). Thus the modification in the availability of food resources, in this case determined by anthropic effects, may consequently determine alterations in the food web structure. The link between streams and their adjacent

riparian zone involves flows of materials and movement of organisms, represented by terrestrial invertebrates that fall into streams and feed fish, and the reciprocal flow of adult aquatic insects that emerge and feed riparian consumers, like birds and spiders (Baxter et al., 2005). Any disturbance on these fluxes can cause effects at individual, population, community, and ecosystem levels (Baxter et al., 2005).

Studies focusing on stream food webs constitute a new approach in Brazil. Four descriptive food web examples developed in Brazilian streams, although few, allow the observation of certain patterns that can be tested in future studies. Data of the first three food web examples will be shown here in more details because they were not published (Potreirinho stream) or published in less accessible literature (Uberaba region published in a regional journal, Atalho stream presented in a master Thesis). The fourth food web example (Motta & Uieda, 2005) is among the largest, most complete documented stream food web studies in southeast Brazil.

The food web diagram of a stream located in Itatinga region (São Paulo State) shows how a modification on the ecotone area, according to the definition of Henry (2003), can affect food web structure (V. S. Uieda and P. Buzzatto, unpublished; Fig. 1). Two stretches of Potreirinho stream were studied (Tab. 1), a headwater section surrounded by a gallery forest and a downstream section surrounded mainly by herbaceous vegetation. Clearly, the headwater section presented a small number of feeding linkages while the downstream section presented a high number of species and trophic interactions (Fig. 1). This high food web structure complexity observed may be attributed to two factors. First, the partial removal of riparian vegetation downstream resulted in an increase of light incidence and possibly on the autochthonous primary productivity. However, this habitat modification probably had little effect on allochthonous resource availability, with vegetal material and terrestrial insects being important food items for fishes in this section. Apparently the higher food resource availability at the downstream section can support a higher species richness and trophic complexity in the food web structure than the headwater section. Roque et al. (2003), in a food web of a stream with forested margins (São Paulo

State), also observed a relation of a high trophic complexity and species richness with great food resources availability. Second, the two sections showed differences in the structural complexity of

habitat. The great environmental heterogeneity of downstream area may be attributed to the development of marginal vegetation (Henry et al., 1994; Uieda & Kikuchi, 1995).

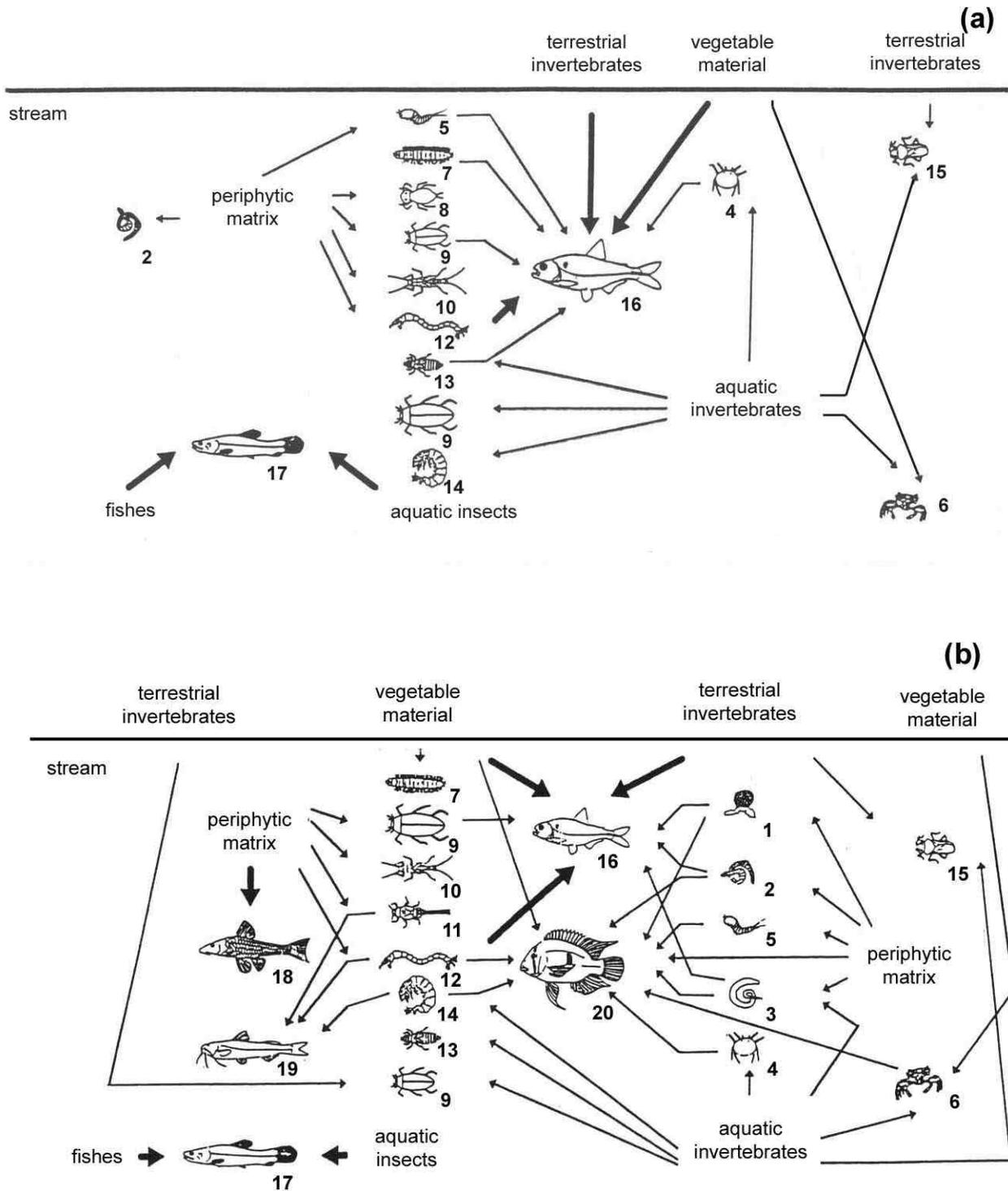


Figure 1: Diagrammatic representation of the food web of two sections of Potrerinho stream, at the headwater (a) and downstream (b) stretches. Large arrows indicate de main items of fish diet (V. S. Uieda & P. Buzzato; unpublished). Numbers discriminated in the Appendix.

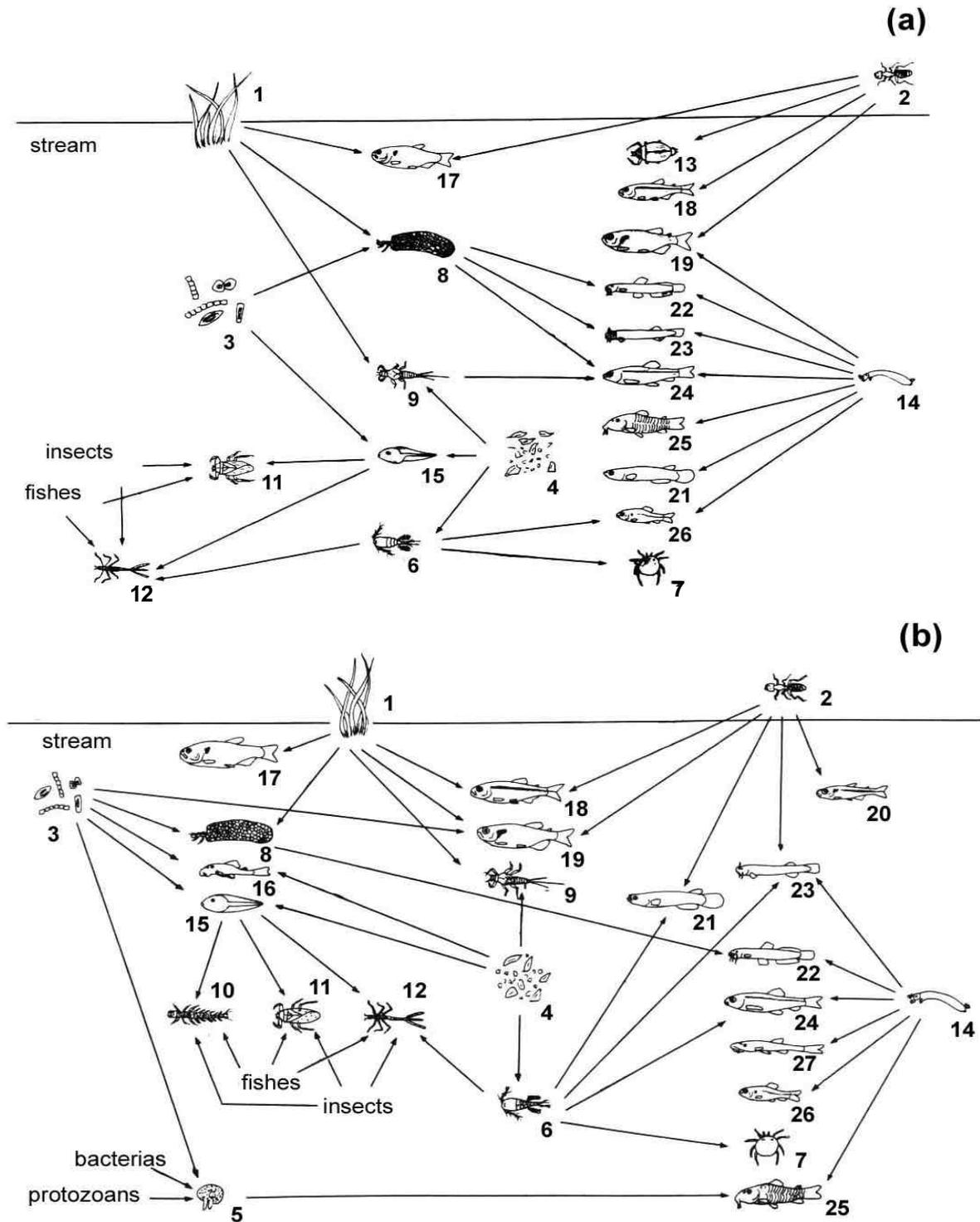
Table 1: Main characteristics of the three Brazilian streams used for food web comparisons (* adapted from Bain & Stevenson, 1999).

	characteristics	headwater section	downstream section
Potreirinho stream (São Paulo State)	coordinates	23°03'S, 48°38'W	
	riparian vegetation	present	only at left margin
	submerged marginal vegetation	absent	present and abundant
	habitat type *	sheet	straight scour
	substrate *	continuous basalt smooth bedrock	gravel, sand, silt
	stream reach type *	bedrock, cascade, step pool	symmetrical cross section channel
	width (m)	1.0	1.6
	depth (m)	0.3-0.6	0.2-0.6
	distance between the sections (m)	500	
	characteristics	headwater section	downstream section
Rio Claro stream (Minas Gerais State)	coordinates	19°40'S, 47°34'W	19°33'S, 47°41'W
	riparian vegetation	absent	absent
	submerged marginal vegetation	present and abundant	present
	habitat type *	riffle	straight scour
	substrate *	cobble, pebble, totally submerged	cobble, pebble, sand, silt
	stream reach type *	pool-riffle	pool-riffle and edgewater
	width (m)	1.3-4.3	7.5-19.0
	depth (m)	0.4-1.0	0.2-1.3
	distance between the sections (m)	8000	
	characteristics	dry season	wet season
Atalho stream (São Paulo State)	coordinates	23°02'S, 48°34'W	
	riparian vegetation	absent	
	submerged marginal vegetation	present	present and abundant
	habitat type *	straight scour	
	substrate *	sand, silt, macrophytes	
	stream reach type *	symmetrical cross section channel	
	width (m)	0.7	1.0
	depth (m)	0.3	0.4
	discharge (m ³ /s)	0.04	0.08

This same pattern was observed again in another study developed in two sections of a stream located in Uberaba region, Minas Gerais State (Uieda et al., 1987). A higher trophic complexity at the downstream section was observed when compared to the headwater section (Fig. 2). Although the riparian vegetation was absent from both

sections, the downstream section had a high environmental heterogeneity, characterized by a more variable substrate and stream reach types (Tab. 1). The increase in volume and structural complexity is an important downstream characteristic related to the increase in the availability of prey refuges from predators (Power & Dietrich, 2002).

Figure 2: Diagrammatic representation of the food web of two sections of Rio Claro stream, at the headwater (a) and downstream (b) stretches (modified from Uieda, et al., 1987). Numbers discriminated in the Appendix.



An increase on food web complexity as a function of a great environmental heterogeneity was also observed in a study developed by Motta (1996) in one section of Atalho stream, at two seasons, utilizing a higher species taxonomic resolution. The

high complexity of the rainy season food web (Fig. 3) is visible through the increase in the number of trophic levels (7 and 6, in the rainy and dry period respectively), number of species (75 and 68), and number of trophic linkages (236 and 173).

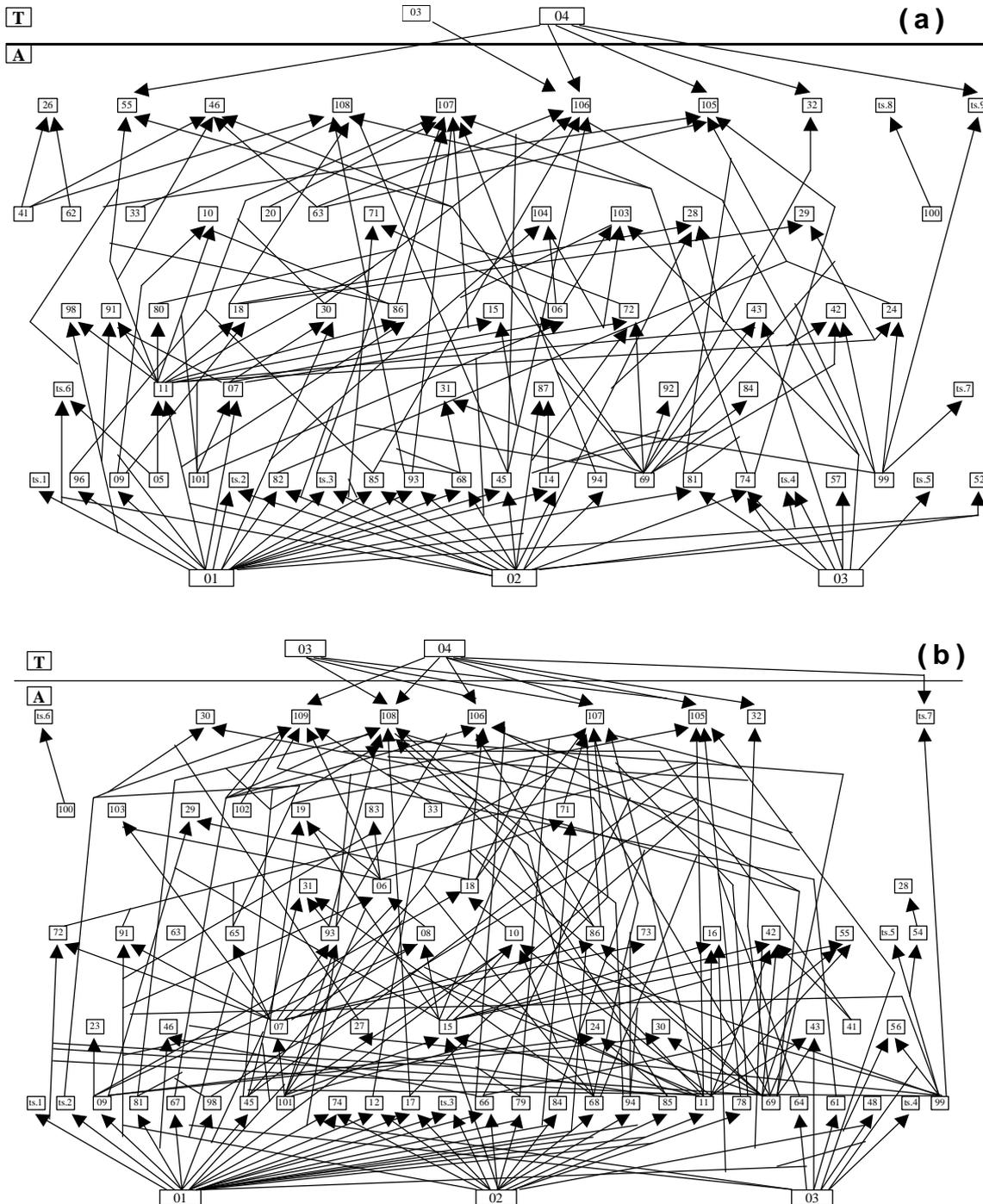


Figure 3: Diagrammatic representation of the food web of Atalho stream (T = terrestrial and A = aquatic compartments), during the dry (a) and rainy (b) seasons (extracted from Motta, 1996). Taxa numbers discriminated in the Appendix. The trophic species (ts) corresponded to different group of taxa in each season. At dry season: **ts.1**= 58, 70, 97; **ts.2**=34, 35, 83, 90, 95; **ts.3**= 12, 13, 66; **ts.4**= 56, 64; **ts.5**= 47, 61; **ts.6**= 76, 88; **ts.7**= 25, 51; **ts.8**= 37, 38, 39, 40; **ts.9**= 49, 50. At rainy season: **ts.1**= 21, 22, 59, 58, 77, 75, 96; **ts.2**= 70, 74; **ts.3**= 34, 35, 44, 80, 89, 97; **ts.4**= 47, 60; **ts.5**= 25, 51, 52, 53; **ts.6**= 36, 37, 38; **ts.7**= 49, 50.

The expansion of the stream, in area and volume, in response to flooding at rainy period (Tab. 1) probably increases the environmental heterogeneity and provides an immediate input of allochthonous detritus and invertebrates that influence resource availability. Some authors working in southeastern Brazilian streams observed a high allochthonous importation during the rainy period and attributed this to the rainfall (Necchi & Branco, 1992; Oliveira & Calijuri, 1996) that also influences the velocity of the current and the amount of suspended material in the water. This period apparently can also support the addition of fish species with large biomass, like the catfish *Rhamdia* sp. found only during the rainy period (species number 109, Fig. 3b). Motta (1996), analyzing the quantity of autochthonous carbon production compared to the allochthonous carbon at Atalho stream, found a high value of importation at the rainy period (0.113 and 0.002 gC/m²/day imported and produced, respectively) and a high value of production at the dry period (0.083 and 0.165 gC/m²/day imported and produced, respectively). These results show that the relative importance of the importation and production of carbon is dynamic, with a seasonal balance that can influence the food web structure.

The habitat complexity influence upon the food web structure was also demonstrated by Motta & Uieda (2005) in a second-order stream located in southeast Brazil (São Paulo State). The structure and properties of this food web were analyzed in a small spatial scale, characterizing its planktonic, epiphytic and benthic compartments. The epiphytic compartment showed consistently a more complex food web than the other two compartments probably due to the higher degree of habitat complexity supported by macrophyte substrate (Motta & Uieda, 2005).

For the Brazilian food web examples presented above, some general patterns can be observed. (1) The incorporation of allochthonous material in the structure of the communities reinforces the linkage between the terrestrial and the aquatic environments. (2) The basic resources of the chain, detritus and algae, represent an important food source to invertebrates and vertebrates and a link between detritus and grazing chains. (3) A spatial and temporal variation in the trophic structure of stream ecosystems can be related to an alteration

in the structural complexity of the environment. (4) A high degree of omnivory is supported by a great diversity of invertebrates and by a solid food chain base. Similar patterns were also observed in tropical Australian streams (Cheshire et al., 2005).

Despite presenting a series of problems, like the species taxonomic resolution, the diet definition for microscopic organisms and the snapshot view of the system structure, these studies represent an important contribution and a starting point for the development of this recent line of research in Brazilian streams.

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References

- Afonso, A.A.O., Henry, R. & Rodella, R.C.S.M. 2000. Allochthonous matter input in two different stretches of a headstream (Itatinga, São Paulo, Brazil). *Braz. Arch. Biol. Technol.*, 43:335-343.
- Allan, J.D. 1995. *Stream ecology: structure and function of running waters*. Chapman & Hall, London. 388p.
- Arcifa, M.S., Froehlich, O. & Northcote, T.G. 1988. Distribution and feeding ecology of fishes in a tropical Brazilian Reservoir. *Soc. Cienc. Nat. La Salle*, 68:39-57.
- Bain, M.B. & Stevenson, N.J. 1999. *Aquatic habitat assessment: common methods*. American Fisheries Society, Bethesda. 216p.
- Baptista, D.F., Buss, D.F., Dorvilé, L.F.M. & Nessimian, J.L. 1998. O conceito de continuidade de rios é válido para rios de Mata Atlântica no Sudeste do Brasil? In: Nessimian, J.L. & Carvalho, E. (eds.) *Ecologia de insetos aquáticos*. Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro. p.209-222.
- Baxter, C.V., Fausch, K.D. & Saunders, W.C. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biol.*, 50:201-220.
- Buckup, P.A. 1999. Sistemática e biogeografia de peixes de riachos. In: Caramaschi, E.P.R. & Peres-Neto, P.R. (eds.)

- Ecologia de peixes de riachos. Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro. p.91-138.
- Callisto, M. & Esteves, F.A. 1998. Categorização funcional dos macroinvertebrados bentônicos em quatro ecossistemas lóticos sob influência das atividades de uma mineração de bauxita na Amazônia Central (Brasil). In: Nessimian, J.L. & Carvalho, E. (eds.) Ecologia de insetos aquáticos. Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro. p.223-234.
- Carvalho, E.D., Fujihara, C.Y. & Henry, R. 1998. A study of the ichthyofauna of the Jurumirim Reservoir (Parapanema River, São Paulo State, Brazil): fish production and dominant species at three sites. *Verh. Int. Verein. Limnol.*, 26:2199-2202.
- Cheshire, K., Boyero, L. & Pearson, R.G. 2005. Food webs in tropical Australian streams: shredders are not scarce. *Freshwater Biol.*, 50:748-769.
- Closs, G.P. & Lake, P.S. 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. *Ecol. Monogr.*, 64:1-21.
- Cole, G.A. 1994. *Textbook of Limnology*. Waveland Press, Illinois. 283p.
- Cummins, K.W. 1973. Trophic relations of aquatic insects. *Annu. Rev. Entomol.*, 18:183-206.
- Cummins, K.W. & Klug, M.J. 1979. Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Syst.*, 10:147-172.
- Darnell, R.M. 1964. Organic detritus in relation to secondary production in aquatic communities. *Verh. Int. Verein. Limnol.*, 15:462-470.
- Dobson, M., Magana, A., Mathooko, J.M. & Ndegwa, F.K. 2002. Detritivores in Kenyan highland streams: more evidence for the paucity of shredders in the tropics? *Freshwater Biol.*, 47:909-919.
- Esteves, K.E. & Aranha, J.M.R. 1999. Ecologia trófica de peixes de riachos. In: Caramaschi, E.P.R. & Peres-Neto, P.R. (eds.) Ecologia de peixes de riachos. Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro. p.157-182.
- Flecker, A.S. & Feifarek, B. 1994. Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. *Freshwater Biol.*, 31:131-142.
- Graça, M.A.S., Ferreira, R.C.F. & Coimbra, C.N. 2001. Litter processing along a stream gradient: the role of invertebrates and decomposers. *J. North Am. Benthol. Soc.*, 20:408-420.
- Havens, K.E., Bull, L.A., Warren, G.L., Crisman, T.L., Philips, E.J. & Smith, J.P. 1996. Food web structure in a subtropical lake ecosystem. *Oikos*, 75:20-32.
- Henriques-Oliveira, A.L., Nessimian, J.L. & Dorville, L.F.M. 2003. Feeding habits of Chironomid Larvae (Insecta: Diptera) from a stream in the Floresta da Tijuca, Rio de Janeiro, Brazil. *Braz. J. Biol.*, 63:269-281.
- Henry, R. 2003. Ecótonos nas interfaces dos ecossistemas aquáticos. Rima, São Paulo. 349p.
- Henry, R., Uieda, V.S., Afonso, A.A. & Kikuchi, R.M. 1994. Input of allochthonous matter and structure of fauna in a Brazilian headstream. *Verh. Int. Verein. Limnol.*, 25:1866-1870.
- Hildrew, A.G., Townsend, C.R. & Hasham, A. 1985. The predatory Chironomidae of an iron-rich stream: feeding ecology and food web structure. *Ecol. Monogr.*, 10:403-415.
- Hooper, D.U., Solan, M., Symstad, A.J., Díaz, S., Gessner, M.O., Buchmann, N., Degrande, V., Grime, P., Hulot, F.D., Mermillod-Blondin, F., Roy, J., Spehn, E.M. & Van Peer, L. 2002. Species diversity, functional diversity and ecosystem functioning. In: Loreau, M., Naeem, S. & Inchausti, P. (eds.) Biodiversity and ecosystem functioning: syntheses and perspectives. Oxford University Press, Oxford. p.195-208.
- Jacobsen, D. & Sand-Jensen, K. 1995. Variability of invertebrate herbivory on the submerged macrophyte *Potamogeton perfoliatus*. *Freshwater Biol.*, 34:357-365.
- Kikuchi, R.M. 1996. Composição e distribuição das comunidades animais em um curso de água corrente (Córrego Itaúna, Itatinga-SP). Botucatu, UNESP, 134p (Master Thesis).
- Merritt, R.W. & Cummins, K.W. 1996a. Trophic relations of macroinvertebrates. In: Hauer, F.R. & Lamberti, G.A. (eds.) *Methods in stream ecology*. Academic Press, San Diego. p.453-473.
- Merritt, R.W. & Cummins, K.W. 1996b. An introduction to the aquatic insects of North America. 3th ed. Kendall/Hunt, Dubuque. 861p.

- Mihuc, T.B. & Mihuc, J.R. 1995. Trophic ecology of five shredders in a Rocky Mountain stream. *J. Freshwater Ecol.*, 10:209-216.
- Motta, R.L. 1996. Trama alimentar das comunidades animais em um curso de água corrente (Ribeirão do Atalho, Itatinga – SP). Botucatu, UNESP, 154p (Master Thesis).
- Motta, R.L. & Uieda, V.S. 2004. Diet and trophic groups of an aquatic insect community in a tropical stream. *Braz. J. Biol.*, 64:809-817.
- Motta, R.L. & Uieda, V.S. 2005. Food web structure in a tropical stream ecosystem. *Aust. Ecol.*, 30:58-73.
- Necchi Jr., O. & Branco, L.H.Z. 1992. Preliminary evaluation of primary production in a stream of São Paulo State, Southeastern Brazil. *Rev. Bras. Biol.*, 52:319-324.
- Nessimian, J.L. & Carvalho, A.L. 1998. Ecologia de insetos aquáticos. Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro. 309p.
- Nessimian, J.L., Sanverino, A.M. & Oliveira, A. 1999. Relações tróficas de larvas de Chironomidae (Diptera) e sua importância na rede alimentar em um brejo de dunas no Estado do Rio de Janeiro. *Rev. Bras. Entomol.*, 43:47-53.
- Newman, R. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. *J. North Am. Benthol. Soc.*, 10:89-114.
- Oliveira, M.D. & Calijuri, M.C. 1996. Estimate of the rate of primary production in two lotic systems, based on hourly change of dissolved oxygen – Itaqueri and Lobo Rivers (São Paulo State). *An. Acad. Bras. Cienc.*, 68:103-111.
- Oliveira, L.G. & Froehlich, C.G. 1997. Diversity and community structure of aquatic insects (Ephemeroptera, Plecoptera and Trichoptera) in a southeastern Brazilian mountain stream. *Acta Limnol. Bras.*, 9:139-148.
- Peckarsky, B.L. & Penton, M.A. 1990. Effects of enclosures on stream microhabitat and invertebrate community structure. *J. North Am. Benthol. Soc.*, 9:249-261.
- Pomeroy, L.R. 1980. Detritus and its role as a food source. In: Barnes, R.S.K. & Mann, K.H. (eds.) *Fundamentals of aquatic ecosystems*. Blackwell Scientific Publications, Oxford. p.84-102.
- Power, M.E. & Dietrich, W.E. 2002. Food webs in river networks. *Ecol. Res.*, 17:451-471.
- Roque, F.O., Pepinelli, M., Fragoso, E.N., Ferreira, W.A., Barillari, P.R., Yoshinaga, M.Y., Trivinho-Strixino, S., Verani, N.F. & Lima, M.I.S. 2003. Ecologia de macroinvertebrados, peixes e vegetação ripária de um córrego de primeira ordem em região de Cerrado do Estado de São Paulo (São Carlos, SP). In: Henry, R. (ed.) *Ecótonos nas interfaces dos ecossistemas aquáticos*. Rima, São Carlos. p.313-335.
- Rosemond, A.D., Pringle, D.M. & Ramirez, A. 1998. Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. *Freshwater Biol.*, 39:359-373.
- Rossi-Marshall, E.J. & Wallace, B. 2002. Invertebrate food webs along a stream resource gradient. *Freshwater Biol.*, 47:129-141.
- Sabino, J. 1999. Comportamento de peixes em riachos: métodos de estudo para uma abordagem naturalística. In: Caramaschi, E.P.R. & Peres-Neto, P.R. (eds.) *Ecologia de peixes de riachos*. Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro. p.183-208.
- Schmid-Araya, J.M., Hildrew, A.G., Robertson, P.E. & Winterbottom, J. 2002. The importance of meiofauna in food webs: evidence from acid stream. *Ecology*, 83:1271-1285.
- Uieda, V.S. 1999. Experimentos de manipulação de organismos aquáticos em riachos. In: Pompêo, M.L.M. (ed.) *Perspectivas da limnologia no Brasil*. União, São Luis. p.169-179.
- Uieda, V.S. & Kikuchi, R.M. 1995. Entrada de material alóctone (detritos vegetais e invertebrados terrestres) num pequeno curso de água corrente na Cuesta de Botucatu, São Paulo. *Acta Limnol. Bras.*, 7:105-114.
- Uieda, V.S., Buzzato, P. & Kikuchi, R.M. 1997. Partilha de recursos alimentares em peixes em um riacho de serra do Sudeste do Brasil. *An. Acad. Bras. Cienc.*, 69:243-252.
- Uieda, V.S., Uieda, W., Carneiro, A.B.C., Silveira, S.A., Melo, M.L.S. & Dornelas, R.H. 1987. Rede alimentar em duas comunidades de um riacho de água doce. In: *Anais do Seminário de Ciências da FIUBE*. FIUBE, Uberaba, p.97-113.

- Vadas Jr., R.L. 1990. The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America. *Environ. Biol. Fishes*, 27:285-302.
- Vannote, R.L., Minshall, G.W., Cummins, K.W.L., Sedell, J.R. & Cushing, C.E. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.*, 37:130-137.
- Vilella, F.S., Becker, F.G. & Hartz, S.M. 2002. Diet of *Astyanax* species (Teleostei, Characidae) in an Atlantic Forest River in Southern Brazil. *Braz. Arch. Biol. Technol.*, 45:223-232.
- Walker, I. 1987. The biology of streams as part of Amazonian forest ecology. *Experientia*, 43:279-287.
- Wetzel, R.G. 1983. *Periphyton of freshwater ecosystems*. Dr. W. Junk Publishers, The Hague. 346p.
- Winemiller, K.O. & Polis, G.A. 1996. *Food webs: integration of patterns & dynamics*. Chapman & Hall, New York. 472p.
- Winterbourn, M.J. 1995. River and stream of New Zealand. In: Cushing, C.E., Cummins, K.W. & Minshall, G.W. (eds.) *River and stream ecosystems*. Elsevier, Amsterdam. p.695-716.
- Woodward, G. & Hildrew, A.G. 2002. Food web structure in riverine landscapes. *Freshwater Biol.*, 47:777-798.

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Appendix

List of basic resources and taxa found in the food web diagrams.

Fig. 1 - Potreirinho stream (V. S. Uieda & P. Buzzato; unpublished)

1	Protozoa - Testacida	11	Ephemeroptera immature
2	Annelida	12	Diptera immature
3	Nematoda	13	Odonata immature
4	Hidracarina	14	Trichoptera immature
5	Microcrustaceans	15	Hemiptera immature and adult
6	Crustaceans - Decapoda	16	<i>Astyanax scabripinnis</i>
7	Lepidoptera immature	17	<i>Hoplias malabaricus</i>
8	Collembola	18	<i>Hisonotus</i> sp.
9	Coleoptera adult	19	<i>Imparfinis mirini</i>
10	Plecoptera immature	20	<i>Geophagus brasiliensis</i>

Fig. 2 - Rio Claro stream (Uieda et al., 1987)

1	Vascular hydrophytes	15	Tadpole
2	Terrestrial invertebrates	16	<i>Hypostomus ancistroides</i>
3	Algae	17	<i>Hasemania melanura</i>
4	Organic matter	18	<i>Astyanax scabripinnis</i>
5	Protozoa - Testacida	19	<i>Hyphessobrycon anisitsi</i>
6	Microcrustaceans	20	<i>Bryconamericus stramineus</i>
7	Hidracarina	21	<i>Rivulus urophthalmus</i>
8	Trichoptera immature	22	<i>Heptapterus</i> sp.
9	Ephemeroptera immature	23	<i>Trichomycterus</i> sp.
10	Megaloptera immature	24	<i>Jobertina</i> sp.
11	Hemiptera immature and adult	25	<i>Aspidoras</i> sp.
12	Odonata immature	26	<i>Phoxinopsis</i> sp.
13	Coleoptera adult	27	Hypoptopomatinae
14	Diptera immature		

Fig. 3 - Atalho stream (Motta, 1996)

1	Organic matter	56	<i>Megadytes</i>
2	Algae	57	<i>Berosus</i>
3	Vascular hydrophytes	58	<i>Tropisternus</i>

Fig. 3 - Atalho stream (Motta, 1996)

4	Terrestrial invertebrates	59	Heterelmis
5	Protozoa	60	Hydrothassa
6	Testacida	61	Lixus
7	Rotatoria	62	Diptera
8	Nematoda	63	Pupa de Diptera
9	Oligochaeta	64	Tipulidae
10	Hirudinea	65	Psychoda
11	Cladocera	66	Ceratopogonidae
12	Alona	67	Forcipomyiidae
13	Acroperus	68	Simulium
14	Ostracoda	69	Chironomidae
15	Copepoda	70	Djalmabatista
16	Cyclopoida	71	Ablabesmyia
17	Harpacticoida	72	Larsia
18	Acarina	73	Pentaneura
19	Entomobryidae	74	Cricotopus
20	Ephemeroptera	75	Corynoneura
21	Leptophlebiidae	76	Thienemanniella sp. 3
22	Paraleptophlebia	77	Chaetocladius
23	Phyllogomphoides	78	Eukiefferiella
24	Progomphus	79	Limnophyes
25	Zonophora	80	Nanocladius
26	Castoraeschna	81	Orthocladius
27	Corduliidae	82	Polypedilum sp. 2
28	Neocordulia	83	Chironomus
29	Dasythemis	84	Cryptochironomus
30	Erythrodiplax	85	Polypedilum sp. 1
31	Hetaerina	86	Polypedilum sp. 2
32	Enallagma	87	Saetheria
33	Plecoptera	88	Stenochironomus
34	Gripopterix	89	Tribelos
35	Paragripopterix	90	Pseudochironomini
36	Paravelia	91	Phanopsectra
37	Rhagovelia	92	Beardius
38	Limnocois	93	Rheotanytarsus
39	Pelocoris	94	Tanytarsus
40	Graptocorixa	95	Dixella
41	Trichoptera	96	Empididae
42	Leptonema	97	Chelifera
43	Smicridea	98	Hemerodromia
44	Neotrichia	99	Aquatic insects fragments
45	Oxyethira	100	Living animals
46	Marilia	101	Microinvertebrates
47	Parapoynx	102	Scales

Fig. 3 - Atalho stream (Motta, 1996)

48	Petrophila	103	Hyla albopunctata
49	Gyrinus.	104	Hyla prasina
50	Gyretes (adults)	105	Astyanax scabripinnis < 30mm
51	Gyretes (larvae)	106	Astyanax scabripinnis >31mm
52	Agabus	107	Characidium schubarti < 40mm
53	Celina	108	Characidium schubarti > 41mm
54	Cybister	109	Rhamdia sp.
55	Laccophilus		