Independent and interactive effects of a top and an intermediate fish species on the food web structure of a tropical stream

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Abstract: Two fish species, one top predator (*Imparfinis mirini*) and one intermediate detritivorous species (*Hisonotus depressicauda*), were experimentally manipulated to evaluate their relative importance in structuring the periphytic community, as well as their effects on the other trophic levels. An enclosure experiment was conducted in the Potreirinho creek, a second order tributary of Paranapanema River, SE Brazil. Five treatments were used: enclosure of the predator species, enclosure of the detritivorous species, enclosure of both together, exclusion of all fish species (closed control cage), and cage open to all fish community (open control). Through direct and indirect effects, *I. mirini*, when alone, gave rise to a trophic cascade that resulted in a positive effect on algal resources. Through direct effects, *H. depressicauda*, when alone, reduced the amount of organic matter, resulting in a positive indirect effect on algae. In addition, when the two species were enclosed together, only the effects determined by the detritivorous species were present. The results indicate the important role of the intermediate detritivorous species in the maintenance of the composition and trophic structure of the analyzed community by reducing the effects caused by the top predator.

Introduction

Ecological communities are complex entities in which species affect each other via both direct and indirect interactions (Persson 1999). Many manipulative experiments have demonstrated that predators produce strong impacts on their prey (Power 1990, Flecker 1992, Konishi et al. 2001). When the effects of top predators are strong, they may propagate in food webs in many directions. Trophic cascades occur when carnivores greatly reduce their prey populations, and this influence has dramatic ecosystem manifestation one or even two links down the chain (Power 1990, Forrester et al. 1999, Persson 1999). However, ecosystem comparisons have shown differences in the strength of trophic cascades among ecosystem types (Shurin et al. 2002, Chase 2003). Trophic cascades caused by top predators were reported by some authors (Strong 1992, Polis and Strong 1996, Polis 1999) in systems with strong vertical trophic links between consumer and resource species. In stream food webs with great number of species, high complexity of links, great number of omnivorous species, and webs based on detritus there is an apparent lack of trophic cascades (Closs and Lake 1994, Schmid-Araya and Schmid 2000, Woodward and Hildrew

2001, 2002). However, some studies have shown that predators may also have prominent effects on resource-consumer interactions in detritus food chains (Nakano et al. 1999, Konishi et al. 2001).

Detritivorous fishes may also have an important role in the trophic structure of stream communities. Lamberti (1996) observed many examples of intermediate regulation of benthic webs. This author proposed that the influence of a dominant intermediate consumer may be extended horizontally (same trophic level) in the food web, or may be extended vertically to the top levels, resulting in an intermediate regulation. Flecker (1992) showed that the links between grazer fish and insects can be more important than the links between insectivorous fish and insects. According to this author, grazer fish changed the distribution and abundance of resources important for aquatic insects which resulted in a pressure higher than direct predation.

Although strong effects of top and intermediate species were observed in stream ecosystems (Power 1990, Flecker 1992, Konishi et al. 2001, Taylor et al. 2002, March and Pringle 2003, Ranvestel et al. 2004), few studies have addressed the independent or interactive effects of multiple consumers

(Wooton 1994, Trussell et al. 2006). Stelzer and Lamberti (1999) emphasized that evaluations of community structure based on manipulations of individual consumer species may be misleading when interaction modifications among consumers occur.

The manipulative experiment conducted in this work was used to verify the existence of trophic cascades in streams and to analyze the importance of a top and an intermediate species as regulators of the structure of this ecosystem. This experiment was realized in a second order stream, where previous results (Motta and Uieda 2005) showed the presence of a complex food web in the periphytic community. This food web presented a great number of species, a great number of links, a high trophic complexity and organic matter as the main basal resource. Two fish species were dominant in this stream, a top carnivorous species, *Imparfinis mirini* Haseman, 1911 (Heptapteridae family), and an intermediate detritivorous species, *Hisonotus depressicauda* (Ribeiro, 1918) (Loricariidae family). This experiment intends to answer two main issues: (1) can some of these two species of different trophic position regulate the food web structure of Potreirinho creek? and (2) if yes, how this regulation takes place?

Materials and methods

Study area

Potreirinho creek (23°03'S and 48°38'W) is a second order tributary of Paranapanema River, located in SE Brazil, State of São Paulo. The studied section is located at 850 m of altitude and presents sandy bottom (medium and fine sand) and low mean values of depth and width (0.22 m and 1.56 m, respectively). Low values of current speed (0.33 m/s) and discharge (0.09 m^3/s), high values of dissolved oxygen (9.06 mgO$_2$/l) and of percentage of saturation (103.8), and basic waters (pH 8.0) also characterize this stream. Riparian vegetation is present only at the left margin, although submerged vascular hydrophytes composed mainly of Poaceae are abundant in the entire channel.

Experimental design

The experiment was conducted during the dry season, from July 17 to August 30, 1999. The manipulative experiment used the technique of enclosure and exclosure cages, one including a certain species in a known density and other excluding all fishes (Uieda 1999, Motta and Uieda 2002). The cages were built using wood (50 cm of length, 30 cm of width and 50 cm of height), closed by nylon net with 4 mm mesh (for details see Motta and Uieda 2002). The cages were fixed on the stream bottom using iron bars, which permitted to adjust the cages 20 cm above the bottom. Artificial plants were installed inside the cages to be used as artificial substratum.

A total of 7 fish species (*Characidium schubarti, Geophagus brasiliensis, Imparfinis mirini, Phalloceros caudimaculatus, Astyanax scabripinnis, Hoplias malabaricus* and *Hisonotus depressicauda*) were identified in the Potreirinho creek community (Motta and Uieda 2005). The fishes included ten food items in their diet (organic matter, algae, nematodes, annelids, crustaceans, acarids, aquatic insects, terrestrial insects, exoskeleton fragments, vascular plants), with aquatic insects being the major diet component for the first four fish species (Motta and Uieda 2005). *Astyanax scabripinnis* showed the broadest diet, consuming six food items, but mainly aquatic insects and fragments of exoskeleton. *Hoplias malabaricus* was exclusively carnivore (exoskeleton fragments). Only *Hisonotus depressicauda* exploited organic matter and algae. The two species used in the experiment, *I. mirini* and *H. depressicauda*, were the ones with the highest density in the stream and the ones that forage mainly in the vegetation, *I. mirini* by picking at relatively small preys from the vegetation and *H. depressicauda* by scraping at the surface of the vegetation.

Motta and Uieda (2005) investigated the structure and properties of Potreirinho creek food web, characterizing its planktonic, epiphytic and benthic compartments. The epiphytic food web was consistently more complex than the planktonic and benthic webs. The interface between aquatic plants and the open water environment is a particularly active zone for feeding interactions at all trophic levels, with fishes foraging mainly in the epiphytic subweb, where macrophytes offer prey refuge and trophic complexity (Motta and Uieda 2005). Based on these results, we intended now to analyze interactive vs. independent effects of the two most abundant fish species found in this stream and that forage on the epiphytic compartment. The use of plastic plants as substrate for the development of a periphytic matrix was tested before and showed to be adequate because it allows the uniformity of the sampled area and provided the establishment of a community similar to that of the natural substrate in a short time period (Motta and Uieda 2002).

Five treatments were established: (1) *Imparfinis mirini* enclosure (I), (2) *Hisonotus depressicauda* enclosure (H), (3) *I. mirini* and *H. depressicauda* enclosure (I + H), (4) exclusion of all fish species (closed control cage = CC), and (5) cage open to all fish community (open control = OC). The comparison between the two control cages allowed analyzing separately the effects of the experimental design (artifact due to retention of the flux by the net) and the effects of all community (free access of all species). One day before the installation of the experiment, the fishes were sampled using a seine and stocked in an aquarium. The standard length of the specimens of *I. mirini* used in the experiment varied from 31.6 to 44.4 cm, and of *H. depressicauda* from 33.6 to 36.4 cm. No effect of *I. mirini* predation on *H. depressicauda* was recorded during the experiment or in a previous work made in the same stream, analyzing the diet of the entire fish community (Motta and Uieda 2005). In the enclosures it was used one individual of each species per cage, what corresponds to the double of the natural density of both species (1 ind./m^3, defined by Motta and Uieda 2005).

Replicates of each treatment were distributed in three sections of the stream which were 10 m apart. At each section, one cage of each treatment was installed 1 m distant from one another. The five treatments were randomly distributed on each section, which was considered as a block for statistical analysis, except for the open control installed downstream each block. At this moment only one lateral side of the cage, with a branch of plastic plant attacked to the wood by the stem, was installed. After 28 days of colonization (time of exposition necessary to colonize the artificial substratum, determined by Motta and Uieda 2002), the cages were closed and the fishes were confined inside them.

The cages were monitored every two days when the external side of the net was carefully cleaned using a brush to avoid an excessive organic matter and sediment deposition. This clean was realized with the objective of minimize the flow reduction (Culp 1986). After 17 days of fish enclosure, the material inside the cages was collected. The superior side of the cage was opened and eighteen leaves of the artificial plant of each treatment were individually cut and carefully manipulated over a small sieve (250μm), in a way to keep the material deposited on the top and bottom of the leaves. Twelve leaves were individually separated and preserved in 4% formaldehyde for posterior community analysis in the laboratory. The leaves for sediment analysis (three) and total pigment analysis (three) were initially processed in the field, by washing (for sediment) or scraping (for pigments) the leaves over filters (AP 20). The fishes were fixed in 4% formaldehyde solution for posterior gut content analysis.

In the laboratory, the method used to determine the dry mass and ash-free dry mass of sediment was: dry the filter (at $60^{o}C$ for 24 h), weigh (dry mass), ash in a muffle furnace (1h at $550^{o}C$), and reweigh (ash-free dry mass). The periphyton scraped from the artificial leaves was extracted in acetone for total pigment analysis (Golterman et al. 1978).

The invertebrates were separated from the leaves for qualitative and quantitative analysis by washing and scraping the leaves in the formaldehyde. The macrofauna was sorted by sucrose flotation (Havens et al. 1996), identified, and counted. After that, subsamples of the remaining material were examined in Sedg Wick-Rafter chambers to determine the microfauna and microflora density.

Food web analysis

The food web of each treatment was constructed with the diet data determined for all animals sampled. Diet of macroinvertebrates and fishes was determined through the analysis of gut contents, using an occurrence method (Hyslop 1980) and a biovolume method (Esteves and Galetti 1995). The diet of microinvertebrates was determined through the literature. For details of diet determination, see Motta and Uieda (2004a,b, 2005).

To compose the diagram of these food webs, we used the same methodology of Cohen et al. (1990), with the species grouped in trophic species (taxa with the exact same get of

predator and prey). This procedure causes no lost of information because it was not used in the food web parameters calculation but only to simplify the illustration. We compiled the food web using a matrix of predation with the identified taxa as row and column headings in a binary matrix (Cohen et al. 1990). Detection of a link (interaction of predator and prey), determined on the basis of dietary analysis, was indicated in the body of the matrix by "1".

Species were categorized utilizing the definitions of Briand and Cohen (1984) and Pimm et al. (1991). Top species have prey but not predators, intermediate species have both prey and predators, while basal species have predators and no prey. Organic matter, unicellular and filamentous algae were considered as basal species (Martinez 1991). Food web properties were calculated for the three replicates of each treatment. Number of species, 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 were determined following the definitions of Pimm et al. (1991). Cannibalistic links were removed to simplify the computer analysis (Thompson and Townsend 2000). Maximum food chain length was calculated as the number of links from basal species to a top consumer (excluding feeding loops). Connectance, defined as a measure of the system complexity or the degree to which the species in the web interact (Tavares-Cromar and Williams 1996), 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).

Statistical analysis

We analyzed the experiment as a randomized complete block design, with blocks representing different sections of the stream (Flecker 1992). Analysis of variance assumes that all data present normal distribution and homogeneous variances (Sokal and Rohlf 1995). Thus, the data on taxon density was transformed as log $(x + 1)$ because the variances were not homogeneous (Hartley test; Sokal and Rohlf 1995). Differences between treatments (ANOVA) were analyzed for: algae and invertebrate density, total density and species richness, density and species richness per trophic level, dry weight and ash-free dry weight of sediment, total pigments and web parameters. The sequential Bonferroni correction was used to determine if the difference found between two treatments is due to the treatment or if the difference is simply due to random chance. For ANOVA, we used the software SYSTAT 7.0 (Systat 1997). The blocks were tested but did not present significant differences.

To verify a possible association between organic matter and algae we used a linear correlation analysis, which uses the Pearson correlation coefficient (r). From the data on composition and density of invertebrates, we performed a single linkage cluster analysis using Euclidean distance (Krebs 1999).

Results

Effects of the treatments on the periphytic community

The basal resources and animal taxa presented in the periphytic community of *Imparfinis mirini* enclosure treatment (Table A1, see Appendix) showed a high number of significant differences, when compared the enclosure to the closed and open control. A significant higher amount of organic matter was observed in the closed control and in the *I. mirini* enclosure, when compared to the open control (Table A1). The algae density (total, unicellular and filamentous) was significantly greater where *I. mirini* was present (open control and enclosure). Although the density of many invertebrate taxa differed at *I. mirini* treatment, only three dipterans larvae (*Beardius*, *Harnischia* and *Kiefferulus*) showed significantly greater densities at *I. mirini* enclosure (Table A1).

In the *H. depressicauda* enclosure, only four variables showed significant differences when compared to closed and open controls (Table A1). A significant decrease in the total and unicellular algae density was observed in the closed control and *H. depressicauda* enclosure, when compared to the open control. The *H. depressicauda* enclosure also affected significantly two genera of invertebrates, *Lecane* (Rotifera) and *Cricotopus* (Diptera).

In the treatment with the two species enclosed together, a significantly higher amount of organic matter was observed than in the open control treatment (Table A1). The effect of this treatment upon the algae was similar to the one found at *H. depressicauda* enclosure. In addition, the presence of both species resulted in an increase of *Cricotopus* density and a decrease of *Djalmabatista* density (dipterans larvae).

Effects of the treatments on the food web parameters

When analyzed the 21 food web parameters (Table A2), the treatments of *I. mirini* enclosure showed a greater number of significant differences. In the *I. mirini* presence most of the analyzed parameters increased, except for the proportion of basal-top links that decreased. Otherwise, the *H. depressicauda* presence displayed only two significant effects on food web parameters: a reduction in the proportion of top species and an increase in the prey/predator ratio (Table A2).

The food web diagrams constructed for each treatment show that the inclusion of *I. mirini* caused the greatest alterations on food web structure (Figs. A1, A2 and A3 In Appendix). Only in the inclusion of this fish species we observed modifications at all levels of the food web.

Despite not observing significant statistical differences between treatments in the total density and in the densities separately for levels 1, 2 and 3, we observed a trend of higher density of organisms in the *I. mirini* enclosure at the three levels (Fig. 1). At *I. mirini* enclosure food web (Fig. A1), the density of many organic matter consumer taxa present in trophic level 1 increased significantly (st3 representing the tro-

phic species comprised by Ciliophora, *Baetis*, Leptophlebiidae, *Heterelmis*, *Djalmabatista*, *Phaenopsectra* and Tanytarsini Genera D; number 59 representing *Harnischia* and number 60 representing *Kiefferulus*). In trophic level 2, *Beardius* (number 56), a consumer of filamentous algae and organic matter, increased significantly in density. The increase in the density of trophic level 3 was due to the appearing of *Hetaerina* (44), an Odonata top predator.

Otherwise, the treatments differed in relation to the values of total species richness and of the richness at trophic level 1. When compared the treatments, a significant higher species richness value was observed in the closed control and in the *I. mirini* enclosure, for the total richness (F = 9.447; P = 0.031) and for the richness at trophic level 1 (F = 8.215; P = 0.038).

By analyzing the diet of *I. mirini*, it is possible to observe its predatory effect (Fig. 2). The food of greatest occurrence in its diet was Diptera, mainly *Reotanytarsus* larvae (Fig. 3
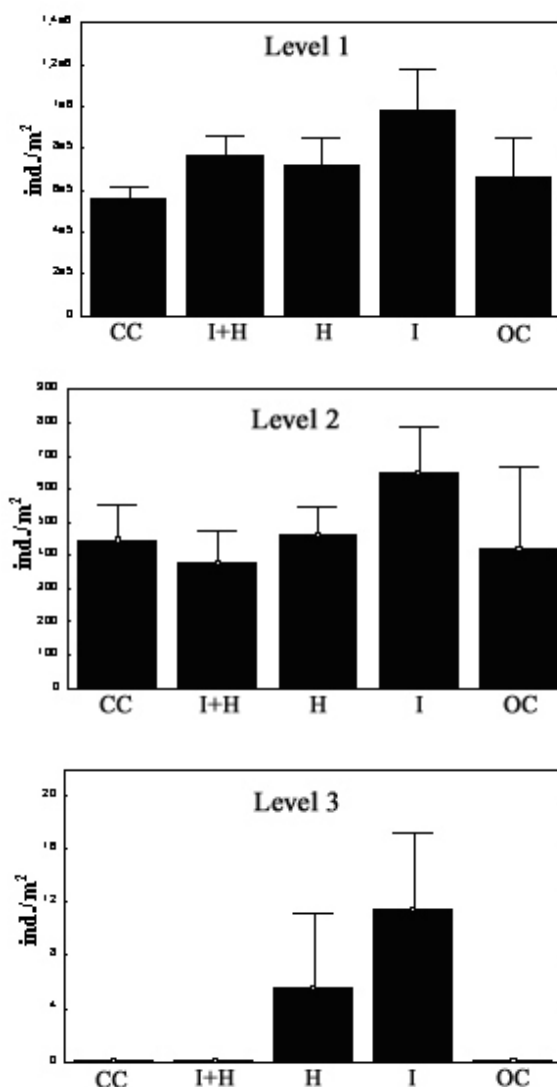

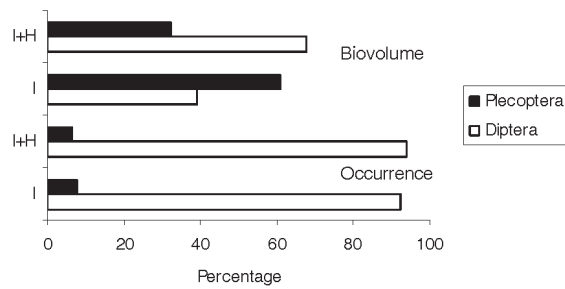**Figure 1**. Mean density obtained for each trophic level in the different treatments.

Figure 2. Frequency of occurrence and biovolume of prey taxa ingested by *I. mirini* in two treatments, I and (I+H).
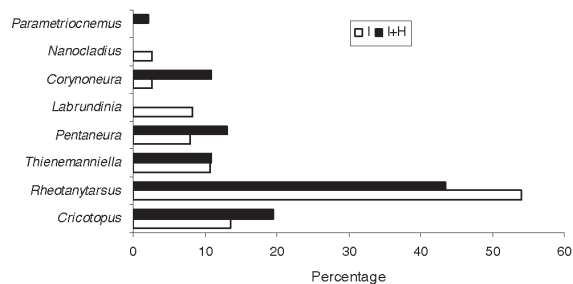

Figure 3. Frequency of occurrence of dipterans larvae ingested by *I. mirini* in two treatments, I and (I+H).
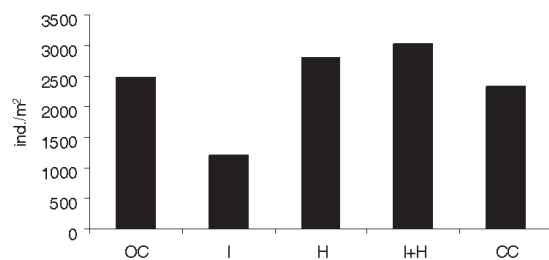

Figure 4. Mean density of *Rheotanytarsus* (Diptera) sampled in five treatments.

Figure 5. Mean density of macroinvertebrates consumers of organic matter (black bars) and organic matter plus algae (white bars) in five treatments.
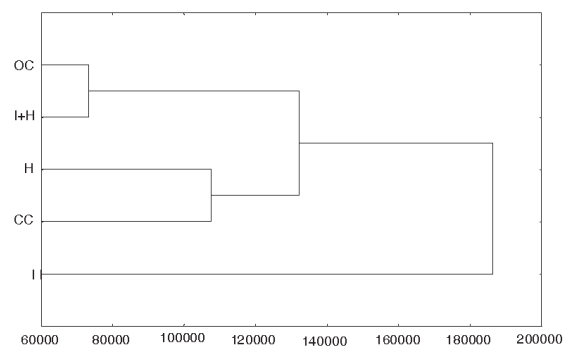
Figure 6. Linkage cluster analysis (Euclidean distance) performed with invertebrates density found in the five treatments.
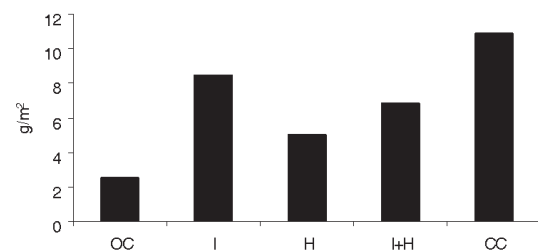
Figure 7. Organic matter dry mass sampled in the five treatments.
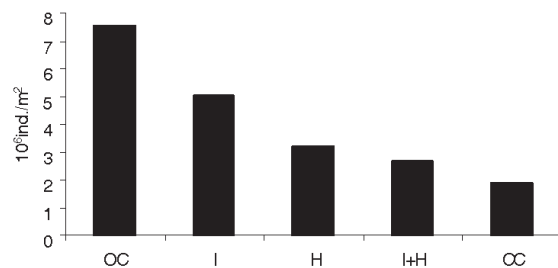
Figure 8. Algal mean density in the five treatments.

and species 68 at Fig. A1) whereas the most representative in the biovolume analysis was Plecoptera (Fig. 2). The Plecoptera genera *Tupiperla* was found in the guts of *I. mirini*, but it was not found at *I. mirini* enclosure (Fig. A1). At the manipulative experiment, *I. mirini* reduced the density of *Rheotanytarsus* only when enclosed alone (Fig. 4). Also at this treatment the mean density of macroinvertebrates consumers of organic matter was greater than the density of macroinvertebrates consumers of organic matter and algae (Fig. 5).

The food web obtained with the enclosure of *H. depressicauda* presented just small differences when compared to the control treatments. We detected alterations in the base of the web, with a reduction on algae density (Fig. A2), and at trophic level 1, with an increase in *Cricotopus* density (spe-
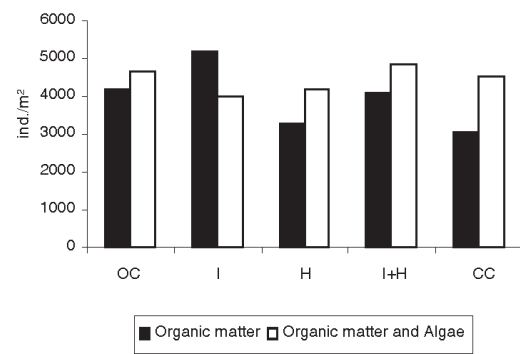
Figure 9. Food webs (left) and trophic cascade diagrams (right): A – Example of a typical trophic cascade, B – Trophic cascade found at *I. mirini* enclosure treatment. Bold arrows indicate the effect of trophic cascade; + and – symbols indicate an increase or reduction in density, respectively; OM- organic matter; A- algae.
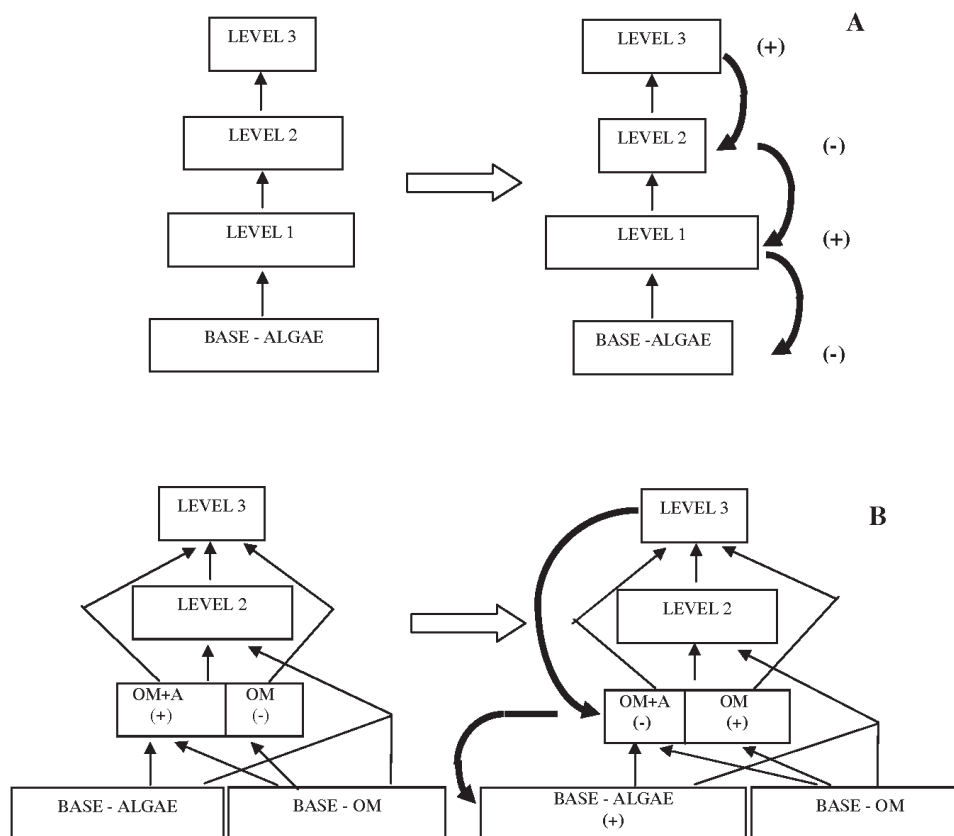
cies 57), an organic matter consumer. In addition, two Odonata species (44 and 45) appeared at this treatment (Fig. A2).

The treatment including I. mirini and H. depressicauda (Fig. A3) showed effects similar to the ones presented at the treatment with *H. depressicauda* enclosed alone (Fig. A2). Otherwise, the direct effects of the predation of *I. mirini* were little at this inclusion treatment. The stonefly *Tupiperla* (number 41) was found colonizing the artificial substratum (Fig. A3) and the density of *Rheotanytarsus* was not reduced (Fig. 4), compared to the treatment with *I. mirini* alone.

The dendrogram based on the invertebrate community composition found in each treatment showed three distinct groups (Fig. 6). The enclosure of *I. mirini* and *H. depressicauda* together presented a small distance from the open control, whereas the enclosure with only *H. depressicauda* was closer to the closed control (exclusion of all fish species). The *I. mirini* enclosure was the most distant treatment.

The analyses of the density of the basal resources of the food web, organic matter (Figure 7) and algae (Figure 8) showed a picture different from the above. The low density of organic matter differentiated the open control from the other treatments (Fig. 7), with an opposite relationship for algae density (Fig. 8). The correlation between the deposition

of organic matter and the development of algae was significantly negative (r = -0.4323, p<0.05).

Discussion

Effects of Imparfinis mirini in the absence of Hisonotus depressicauda

A negative or predatory direct effect of the experimental manipulation of *I. mirini* alone could be inferred from the diet analysis. Its effect on *Reotanytarsus* and *Tupiperla*, the most important food items ingested by *I. mirini*, reduced half the density of the first and was so strong on the plecopterous *Tupiperla* that it was not found colonizing the artificial substrate, but only in the predator gut content. The lack of statically significant differences on *Reotanytarsus* and *Tupiperla* density, when compared the enclosure and controls, may have been related to the relatively small sample size (three replicates per treatment) and to a spatial heterogeneity of the invertebrate community.

This predatory effect can be related to the positive indirect effect on *Harnischia* and *Kiefferullus* (Diptera), insects of the same trophic level of *Rheotanytarsus* and *Tupiperla*, suggesting a reduction on space and/or resource competition.

Although several studies have showed weak effects of predation in streams (Culp 1986, Thorp 1986), our results are more consistent with others that have showed that fish can have strong effects on their preys (Gilliam et al. 1989, Power 1990, McPeek 1998, Flecker and Townsend 1994), altering the food web structure through various trophic levels.

The trophic cascade observed in the Potreirinho Creek (Fig. 9.B) does not support the traditional trophic cascade model (Fig. 9.A) that was defined as an indirect mutualism between non-adjacent trophic levels in a simple food chain (Menge 1995). In the Potreirinho creek, the top predator *I. mirini* determined a trophic cascade through positive indirect effects on basic resources (algae) without modifying the total density of trophic level 1. When the composition of this trophic level is analyzed, it is possible to see the effect of the top predator. It reduced the density of macroinvertebrate consumers of organic matter and algae (*Rheotanytarsus*, *Tupiperla* and others), whereas dipteran consumers of organic matter, which were not preyed on, were favored and increased their density. Persson (1999) emphasized the importance of considering the horizontal heterogeneity and the compensatory species response in food web studies, patterns found in *I. mirini* enclosure. This omnivorous predator (fish feeding on different trophic levels) caused an effect on the base and on the first trophic level, but not on the level immediately below it, showing that this food web also presented a vertical heterogeneity.

Other impacts of predators on primary producers may occur through indirect effects, specifically by modifying behavior (Werner and Peacor 2003). Cascading effects arising from changes in prey diet or habitat selection in response to an increase of predation risk represent examples of trait-mediated indirect effects (Trussell et al. 2004). Changes in prey behavior in response to predator risk, although not analyzed in this study, need to be considered as a potential effect on the trophic cascade. Multitrophic interactions produce a richer variety of diversity-functioning relationships than the monotonic changes predicted for single trophic levels (Duffy et al. 2007).

Omnivory of top predator (vertical heterogeneity), horizontal heterogeneity of trophic level 1 and species compensatory responses of different trophic guilds can be responsible for Potreirinho creek food web not corresponding to the traditional trophic cascade model. Similar explanation for the absence of cascading effect was given by Nyström et al. (1996) and Pace (1998) working in temperate pond and lake, respectively.

The direct effect caused by the top predator *I. mirini*, through the reduction in the density of its preys, propagated throughout the entire web, and raised its complexity as a whole by a significant increase in almost all parameters of the web. The effects of *I. mirini* propagated through various trophic levels (vertical effect) and inside trophic level 1 (horizontal effect), increasing the total richness. However, we observed that the entrance and exit of species came to a balance, which kept constant the linkage density. A decline in the con-

nectance is expected when there is a concomitant exchange on the number of trophic species and trophic linkage in the way to maintain the food web stability (Pimm et al. 1991, Schmid-Araya et al 2002). This situation was found at our top predator enclosure, although the connectance decline was not significant. Thus, we can conclude that the strong effects of the predator were not enough to destabilize the food web. Sprules and Bowerman (1988) suggested that omnivores can enhance community stability by effectively shortening the links between top species and those lower in the web, such as observed for the omnivore top predator studied in the Potreirinho creek.

Effects of Hisonotus depressicauda in the absence of Imparfinis mirini

A series of studies on stream communities (Flecker 1992, Pringle et al. 1993, Pringle and Blake 1994, Flecker 1996) have shown that fishes and invertebrates that were alga and organic matter consumers may generate a strong trophic effect on basal resources. In Potreirinho creek web, the intermediate species *H. depressicauda* directly and negatively affected (vertical effect) the amount of organic matter. Otherwise, the experimentation artifact of cages contributing to a high deposition of organic matter inside the treatments (Peckarsky and Penton 1990) may be the cause of the smaller efficiency of *H. depressicauda* in consuming organic matter (not significant although its enclosure reduced by half the amount of organic matter when compared to the closed control).

Despite the fact that *H. depressicauda* also feeds on algae, it did not reduce the density of this resource when compared to the closed control. This was probably due to the small amount of algae (2%) in the biovolume analysis of this species diet. The reduction in the amount of organic matter caused by *H. depressicauda* may have led to a weak positive indirect effect of this fish on the algae density. A negative correlation between algae density and amount of organic matter was observed.

The physical disturbance of sediment by fishes may be an important mechanism affecting the resource availability and consequently influencing invertebrate abundance (Flecker 1996). But in our study *H. depressicauda* did not deeply modify the density of most invertebrates, causing only a positive indirect effect on *Cricotopus* (Diptera). This detritivorous larva increased in density exactly on treatments where carnivorous invertebrates (Odonata in *H. depressicauda* enclosure) or its fish predator (at *I. mirini* enclosure) are present, maybe in response to an increase in the deposition of organic matter inside the cages.

In the Potreirinho creek, *H. depressicauda* reduced the amount of organic matter (direct effect) through foraging activity and precipitated an increase on alga density (indirect effect), which probably affects the insect community and consequently the food web structure. The small proportion of top species in the *H. depressicauda* treatment alone is related to the occurrence of two Odonata top predators at level 3,

Table 1. Results of interactive and independent effects obtained by the manipulative experiment conducted at Potreirinho creek. Values similar (=), smaller (<) or higher (>), when compared to the treatments for each analysed community parameter.

COMMUNITY PARAMETERS	TREATMENTS				
	OC	CC	I	H	I+H
Organic matter dry mass	<	>	OC< I =CC	OC≤ H ≤CC	OC<I+H=CC
Algae density	>	<	OC< I >CC	OC>H≥CC	OC>I+H≥CC
Trophic level density	=	=	OC≤ I ≥ CC	OC= H= CC	OC=I+H=CC
Invertebrates density	≠	≠	OC≠ I ≠CC	OC≠ H ≈CC	OC≈I+H≠CC
EFFECTS OF *I. mirini*		CC	I	H	I+H
Negative direct– Predation upon algivorous and detritivorous preys.		-	yes	-	no
Positive indirect– Increase of Diptera detritivorous density.		-	yes	-	no
Positive indirect– Increase of algae density.		-	yes	-	no
EFFECTS OF *H. depressicauda*					
Negative direct– Reduction of organic matter dry mass.		-	-	yes	yes
Positive indirect– Increase of algae density.		-	-	yes	yes

which determined the great prey/predator ratio that was observed.

Effects of the interaction of a top species and an intermediate species on the periphytic community

The fishes of Potreirinho creek were important regulators of the web base resources because the amount of organic matter was greater and algal density was smaller in the exclusion of fishes (closed control) than in the open control (Table 1). However, this regulation did not occur through modifications in the density of invertebrates in each trophic level, but through alterations in the community composition. The increase in organic matter in the closed control probably did not result in an increase in the density of invertebrates because organic matter may not be a limiting resource for these animals in the Potreirinho creek. In environments with food webs based on detritus, the fishes can cause modifications in the community composition and may alter the base of the web, without necessarily modifying the density of the trophic levels. Both manipulated fish species probably interact in the maintenance of the trophic structure of the periphythic community in this stream.

The effects of *I. mirini* predation occurred only in the absence of *H. depressicauda* (Table 1). Reduction in the density of the two main preys of the top predator (*Rheotanytarsus* and *Tupiperla*) was not observed when the two fish species were enclosed together. Since the predation effect did not occur in this last situation, no indirect positive effect on algae was observed either. Two mechanisms may be responsible for the fact that *H. depressicauda* inhibits the effects of *I. mirini* predation, consequently inhibiting the indirect posi-

tive effect on algae. One mechanism may be related to the presence of microhabitats that can be used as refuge to preys, affecting the foraging efficiency by fishes (Power 1990). *H. depressicauda* may be in some way modifying the habitat structure, making *Rheotanytarsus* and *Tupiperla* less vulnerable to predation by *I. mirini*. Another mechanism may be related to behavioral interactions. *H. depressicauda* may reduce the foraging area of *I. mirini* through space limitation. These two mechanisms represent interaction modification in that *H. depressicauda* affects the relations between *I. mirini* and its preys, without directly affecting the abundance of both.

On the other hand, *I. mirini* seems to not interfere in the effects caused by *H. depressicauda* which were similar to the ones when this species was alone (Table 1). However, some effect of the presence of *I. mirini* might occur or else the treatments of combined inclusion of *I. mirini* and *H. depressicauda* would not have differed from *H. depressicauda* alone.

Thus, *I. mirini* and *H. depressicauda* presented independent and interactive effects. From the interactive effects that were observed in the present study, the effect of *H. depressicauda* is of great importance in structuring the community of Potreirinho creek. In the absence of *H. depressicauda*, the majority of the food web parameters differed from the open control treatment (Table 1). Thus, intermediate detritivorous species may have an important role in the maintenance of the trophic structure and community composition in streams by reducing the effects of top predators. Clearly, evaluations of community structure based on manipulation of only individual consumer species may be misleading when interaction modifications occur among consumers

(Stelzer and Lamberti 1999), such as observed in the Potreirinho creek.

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Appendix: Figures and tables

Figure 1. Diagram of *Imparfinis mirini* enclosure food web, compared with closed and open controls. Basal resources, individual taxa and trophic species (st) are represented by a number inside a square. Different square size indicates the interval of mean density obtained for each species. The density was not determined only for organic matter (number 3) and vascular plants (number 4). Taxa indicated without prey are hemipterans for which no specific prey could be identified. The resource inside double line square had its density significantly higher then the resource inside bold line square. Gray square represents taxon that occurred only in one treatment. Bold lines indicate resources preferentially ingested by the fish species.

Figure 2. Diagram of *Hisonotus depressicauda* enclosure food web, compared with closed and open controls (see Figure 1 legend for components description).

Figure 3. Diagram of *Imparfinis mirini* plus *Hisonotus depressicauda* enclosure food web, compared with closed and open controls (see Figure 1 legend for components description).

Table 1. Results of the ANOVA followed by Bonferroni multiple comparisons used to analyze the effect of fish enclosures upon the basal resources and animal community density of Potreirinho creek.

Table 2. Results of the ANOVA followed by Bonferroni multiple comparisons used to analyze the effect of fish enclosures upon the food web parameters of Potreirinho creek.

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