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Taxonomy, metrics or traits? Assessing macroinvertebrate community responses to daily flow peaking in a highly regulated Brazilian river system

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ABSTRACT

Damming disrupts lotic continuity, creating a lentic water body upstream of the dam and a lotic stretch downstream that is highly vulnerable to temporal fluctuations in flow and physiochemical quality depending on the operational regime of the dam. Thus, an essential part of any dam operation programme must take into account a typologically suitable environmental flow regime, in order to maintain downstream structure and function. We assessed the seasonal impact of daily flow peaking regimes on the taxonomic composition, metrics and traits of the macroinvertebrate community in the lotic section situated downstream of the Itutinga reservoir on the Rio Grande in the state of Minas Gerais in southeast Brazil. The flow manipulation experiments were carried out in both wet (January) and dry periods (July) of 2010. The samplings were carried out in two hydraulic situations (fixed flow and daily flow peaking). Benthic macroinvertebrates and sediment were collected in three habitat types (backwater, fluvial beach and running water). Water variables were measured only in the fluvial beach habitat. Both water column and sediment variables downstream were heavily influenced by the retention capacity of the reservoir rather than the daily flow peak value. The trait approach was more sensitive than abundance and metrics and could detect the effects of daily flow peaking. The benthic macroinvertebrate communities sampled downstream of the Itutinga reservoir were more influenced by the sediment composition at each of the three studied habitats, than by the tested daily flow peaking. However, given the short timescale of this study, it may be difficult to the influence of these two interrelated factors.

KEY WORDS ecosystem; dams; river regulation; assessment; bioindicators; macroinvertebrate traits; macroinvertebrate metrics; taxonomic composition

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INTRODUCTION

The past 50 years has witnessed a notable increase in the construction of hydroelectric dams in Brazil (Bortoleto, 2001). Damming severely disrupts lotic continuity (Barbosa *et al*., 1999), creating an artificial lentic water body upstream and a lotic stretch downstream that can be subject to considerable temporal fluctuations in flow and water parameters depending on the operational regime of the dam and reservoir (World Commission on Dams, 2000; Smokorowski *et al*., 2011). The operational regime of a given reservoir will result in alterations in the natural hydrologic regime of the lotic environment situated downstream (Poff *et al*., 1997), altering the frequency, magnitude and duration of extreme flows (Richter *et al*., 1996). This hydrological alteration influences the physical and chemical processes and properties in both water column variables and substrate composition, influencing energy dynamics and physical habitat availability (Bunn and Arthington, 2002; Suen and Eheart, 2006), which will be reflected in changes in the biological community structure, function (e.g. life cycles, connectivity and feed habits) and ecosystems integrity (Allan, 1995; Statzner *et al*., 1988; Bunn and Arthington, 2002; Bonada *et al*., 2008; Poff and Zimmerman, 2010;). Therefore, suitable management of downstream flows is one of the great challenges for the conservation and management of regulated rivers (Dudgeon *et al*., 2006; Acreman and Ferguson, 2010; Navarro-Llácer *et al*., 2010).

Ecological assessment methods are now a routine tool in aquatic resource management and planning, used to evaluate anthropogenic impacts on aquatic ecosystems (Li *et al*., 2010). The benthic macroinvertebrate community

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is a taxonomically and functionally diverse group commonly used in the ecological assessment of diverse anthropogenic impacts on aquatic ecosystems (Rosenberg and Resh, 1993; Bonada *et al*., 2008). Smokorowski *et al*. (2011) pointed out that constant changes in flow alter the wetted area, influencing the distribution of groups of benthic macroinvertebrates because of their specific adaptive characteristics to aspects of the flow regime. For example, organisms such as Odonata and Plecoptera have low mobility and are crawlers, so they commonly suffer from desiccation and predation in the littoral zone during low flow periods (Smokorowski *et al*., 2011) and are passively carried via drift during flow peaking (Wilcox *et al*., 2008). On the other hand, wormlike organisms such as Diptera, Trichoptera, Ephemeroptera and Coleoptera can burrow into the sediment in response to changes in flow resulting in their relatively common presence in regulated river segments (Smokorowski *et al*., 2011).

The use of biological and ecological attributes of benthic macroinvertebrates (traits) in ecological assessment is becoming increasingly popular (Feio and Dolédec, 2012). Traits aggregate both biological information (e.g. body size, aquatic stages, life cycle, dispersion, feed habits, food, reproduction, respiration or locomotion) and ecological information (e.g. transversal distribution, preferences for substrate type, current velocity, trophic status or saprobity) of the different macroinvertebrate taxonomic groups (Haybach *et al*., 2004), providing a 'functional community image' of the ecosystem, as described by Charvet *et al*. (2000). This information can be compared between different ecosystem types and eco-regions and are able to detect impacts caused by anthropogenic activities (e.g. dam building, deforestation and pollution) (Charvet *et al*., 2000; Haybach *et al*., 2004). Like metrics and indices, traits can be compared against reference conditions to assess the degree of change of an impacted system (e.g. Chessman *et al*., 2010; Varandas and Cortes, 2010; Ferreira *et al*., 2011; Brooks *et al*., 2011; Feio and Dolédec, 2012).

Many studies in temperate regions already consider both biological and ecological benthic macroinvertebrate traits to evaluate the impact of flow alterations in regulated rivers (Statzner *et al*., 1988; Cortes *et al*., 2002; Bunn and Arthington, 2002; Armitage, 2006; Dewson *et al*., 2007; Chessman *et al*., 2010; Brooks *et al*., 2011). However, in tropical regions, such as Brazil, there are virtually no studies on the response of macroinvertebrate traits to dam-mediated flow alterations. Dam operation regimes can be run-of-the-water or peaking, depending on the size and operating criteria (Smokorowski *et al*., 2011). Many dams that operate under a peaking regime need to increase daily power generation in direct relation to energy demands. Thus, dam operation based on peaking can result in constant increases and decreases in downstream flow concomitant with periods of high and low peaking of power generation (Pompeu and Vieira, 2002; Smokorowski *et al*., 2011).

This study assesses the response of benthic macroinvertebrate communities (taxonomic composition, metrics and traits) to simulations of daily full peaking operation, downstream of a dam situated in a high regulated river in the southeast of Brazil. We tested the following hypotheses in both wet and dry periods: (i) daily flow peaking would alter water column variables (e.g. temperature, dissolved oxygen, turbidity, pH and nutrients) and (ii) sediment composition (e.g. organic matter concentration and particle sizes), affecting the quality and quantity of available habitats that would (iii) influence the composition (taxonomy), structure, metrics and function (traits) of benthic macroinvertebrate communities. Finally, we hypothesized (iv) that a trait-based assessment approach would best express the impact of daily flow peaking because of its capacity to aggregate both biological and ecological characteristics of the communities.

METHODS

Study design

The study was carried out with the direct collaboration of the Electric Company of Minas Gerais (CEMIG) and National Electric Energy Agency, through financial support and implementation of flow rates for the experiments.

The Rio Grande, located in the state of Minas Gerais, southeast Brazil (Figure 1), is a highly regulated system (12 hydroelectric power plants and dams installed along the river's length) with a length of 1300 km and a catchment area of 143 000 km^2 (Santos, 2010). The Itutinga reservoir is the second reservoir situated along the Rio Grande (upstream-downstream direction) and was chosen on the basis of the logistical criteria that would not detrimentally influence electric energy production of the CEMIG system. The Itutinga reservoir has both low height and reduced holding capacity, operating in run-of-the-river regime. Thus, the flow manipulation experiments were carried out in association with Camargos reservoir, situated approximately 2 km upstream of the Itutinga reservoir (Table I; Figure 1) and with about 70 times more holding capacity than the Itutinga reservoir (Table I).

The region's climate is humid subtropical (Köppen–Geiger classification: Cwb) with dry winters (April–September, mean 1410 ± 156 mm month^{-1}) and wet summers (October–March, mean 107 ± 12 mm month^{-1}) (Van Den Berg and Oliveira-Filho, 2000). The vegetation is typical of 'cerrado' (tropical savanna like) with predominating 'Campos' and 'Campos Cerrados' (Van Den Berg and Oliveira-Filho, 2000).

The samplings sites (habitats) are located about 5 km downstream of the Itutinga reservoir (44°39′W, 21°16′S; 850 m) (Figure 1).

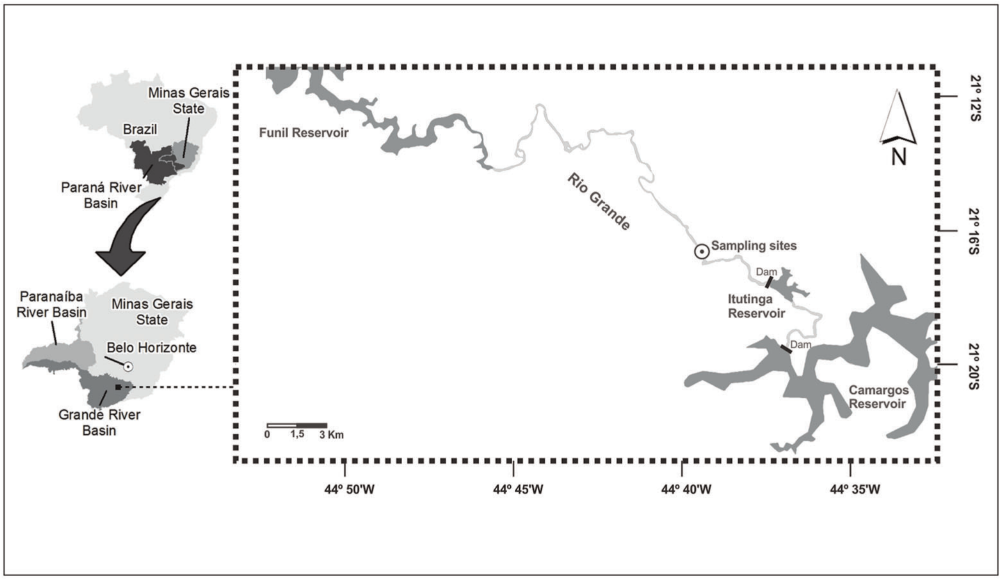

Figure 1. Map of the study area and the location of the habitats where the samples were collected downstream of the Itutinga reservoir, Rio Grande, southeast Brazil.

Table I. General characteristics of Itutinga and Camargos reservoirs situated on the Rio Grande, southeast Brazil.

General characteristics	Itutinga reservoir	Camargos reservoir
Start of operation	1955	1960
Flooded area (km^2)	2·03	50·46
Volume (hm^3)	11·4	792
Dam height (m)	23	36
Dam length (km)	550	608
Installed capacity (MW)	52	45
Generating units (turbines)	4	2

Experiments, samplings and data analysis

The flow manipulation experiments were carried out in January (wet period) and July (dry period) of 2010. In order to evaluate the effect of full peaking operation regimes on macroinvertebrate communities, we imposed two distinct hydraulic situations, namely the 'fixed flow' (reference) and 'daily flow peaks'. The historical average flow between 1931 and 1953 was analysed prior to dam construction to determine the 'fixed flow' in both wet and dry periods. The 'daily flow peaks' applied in this study were based on the full peaking operations applied by the management requirements for energy production.

Sampling was carried out in both wet and dry periods. Prior to each sampling period, flow from the Itutinga dam was stabilized for 30 consecutive days, on the basis of the higher values of long-term average flow values for each period (fixed flow: 327 m^3 s^{-1} in the wet period, January and 108 m^3 s^{-1} in the dry period, July). Following the 30-day stabilized flow period, samples of water, sediment and benthic macroinvertebrates were collected for 6 consecutive days. After the 36th day, the full peaking flow regime simulation was started (daily flow peaking between 5:00 and 10:00 pm), and water, sediment and benthic macroinvertebrate collections were carried out for another 6 consecutive days. The daily flow fluctuation was between 380 and 480 m^3 s^{-1} for the wet period in January and between 110 and 170 m^3 s^{-1} for the dry period in July (Figure 2). Sampling was carried out in three different habitat types, namely, backwaters (BW), fluvial beaches (FB) and running waters (RN) (Table II).

Characterization of physical and chemical variables

Water column. Water temperature (°C), electrical conductivity (µs cm^{-1}), pH, turbidity, total dissolved solids (TDS) (µg l^{-1}) and water redox potential (mV) were measured daily (a total of 12 days) in the water column in the FB habitat only (preliminary studies showed no significant difference in these parameters between all three habitats) in both hydraulic situations during both the wet and dry period, using an electronic multi-parameter probe (YSI - model: 6600, Yellow Springs, Ohio, USA) (total of 24 water samples). Water samples were taken for laboratorial analyses of dissolved oxygen (mg l^{-1}), total alkalinity (µEq/l of CO_2), total phosphorous (mg l^{-1}) and total nitrogen (mg l^{-1}) (APHA, 2008).

Sediment. Sediment and macroinvertebrate samples were collected daily using a Petersen dredge (0·0375 m^2) during the two 6-day sampling cycles (fixed flow and daily fluctuation) in each habitat type for both hydraulic situations during both the wet and dry periods (a total of 72 sediment samples). The granulometric composition of substrate (%) was determined using a screening method (Suguio, 1973), modified by Callisto and Esteves (1996). Organic concentrations (%) were

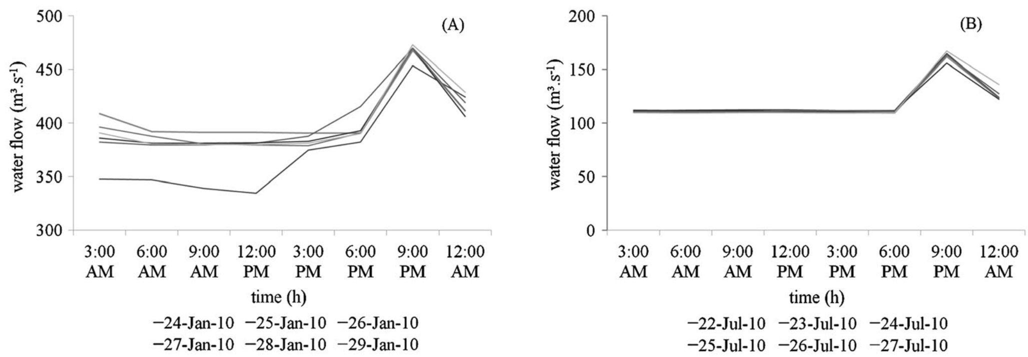

Figure 2. Scheme of the 6 days of experiment, simulating daily flow peaking (between 5:00 and 10:00 pm) in both seasons: wet (A), ranging from 380 to 480 $m^3 s^{-1}$ and dry (B), ranging from 110 to 170 $m^3 s^{-1}$), downstream of the Itutinga reservoir, Rio Grande, southeast Brazil (2010).

Table II. General characteristics of the three habitat types (BW, backwaters; FB, fluvial beaches and RN, running waters) sampled downstream of the Itutinga reservoir, Rio Grande, southeast Brazil.

General characteristics	BW	FB	RN
Depth (m)	1	1	1
Width (m)	50	50	50
Flow ($m^3 s^{-1}$)	0	0	0·48
Predominant habitat type	Pools	Beach	Riffles
Predominant substrate particle size	<0·50 mm	0·50–1·00 mm	>1·00 mm
Aquatic macrophytes	Absent	Absent	Present
Organic matter (%)	1·62	0·52	0·70

determined using the gravimetric ash-free dry weight method. Aliquots ($0{\cdot}3 \pm 0{\cdot}1$ g) were ashed (550 °C for 4 h) and weighed; the difference between the initial weight of sample and weight after ashing gave the percentage of content of organic sediment samples.

Benthic macroinvetebrates

Benthic macroinvertebrates samples were collected for 6 consecutive days using a Petersen dredge. Four replicates (four dredges) were collected from each habitat type, in both hydraulic situations (fixed flow and daily flow peaking) in wet and dry periods giving a total of 288 benthic macroinvertebrate samples. The samples were washed through 1·0, 0·5 and 0·25 mm sieves and preserved in 70% alcohol. Material was identified to family level using specialized literature (Pérez, 1988; Merritt and Cummins, 1998; Mugnai *et al*., 2010) and deposited in the reference collection of the Instituto de Ciências Biológicas of the Universidade Federal de Minas Gerais.

Data analysis

Physical and chemical variables. Prior to statistical analyses, we confirmed normality and homogeneity of variance of water column and sediment data by using the Kolmogorov–Smirnov test and Levene's test respectively. The samples of each water column variable were standardized (the values of each sample within each water column variable was divided by the total values of samples within each water column variable); sediment granulometry composition and organic matter concentrations were expressed as percentage.

We tested for differences for water parameters between both hydraulic situations in wet and dry periods by using the *t*-test (significance level: $p < 0{\cdot}05$). For the substrate variables, we tested for differences between both hydraulic situations, in each habitat type, in wet and dry periods by using a one-way analysis of variance (ANOVA) and Tukey's honestly significant difference post hoc test (significance level: $p < 0{\cdot}05$) to determine where the detected significant differences resided in the data set.

Benthic macroinvertebrate communities. To characterize and compare the benthic macroinvertebrate communities in each habitat and hydraulic situation, we calculated family level richness (S), Shannon–Wiener diversity index (H′) and density (ind m^{-2}). To compare the effect of both hydraulic situations (fixed flow and daily flow peaking) and the substrate composition (habitat types) on macroinvertebrate community structure and function, we >derived three data sets, namely, taxonomic composition (family level identification and relative abundance log $(x+1)$ transformed), structure and composition metrics (standardized) and biological and ecological traits (percentage of individuals).

Metrics were calculated using the ASTERICS software, version 3.3.1 (AQEM Assesment System, Essen, Germany, http://www.aqem.de) developed as part of the EU funded assessment system for the ecological quality of streams and rivers throughout Europe using benthic macroinvertebrates (AQEM) project (Hering *et al*., 2004). Because many of the AQEM metrics such as biotic indices, or tolerance descriptors, could not be directly extrapolated from European river systems to tropical rivers, we selected a subset of 59 generic metrics describing macroinvertebrate composition and structure. Redundant metrics were removed using the Spearman rank correlation (highly correlated variables based on a threshold value of $r \geq 0{\cdot}6$ or $r \leq -0{\cdot}6$). A subset of 23 non-redundant metrics was tested for hydraulic situation (fixed flow vs daily flow peaking) and habitat sensibility by using the Kruskal–Wallis non-parametric variance analysis (significance level: $p < 0{\cdot}05$). Similarity percentages (SIMPER) analysis was used to detect the contribution of each selected metric to the degree of dissimilarity between the two hydraulic situations (fixed flow and daily flow peaking) and substrate composition (habitats).

Biological and ecological traits were selected on the basis of Usseglio-Polatera *et al.* (2000b). Five of 22 ecological traits, related with these characteristics, were discarded because the data was derived from a relatively small study area, without marked altitudinal, longitudinal and temperature gradients. Each trait was divided into modalities (trait categories), following the 'fuzzy coding' approach described in Feio and Dolédec (2012); Tachet *et al.* (1994); Usseglio-Polatera *et al.* (2000b). This method involves the assignment of an affinity score of each taxon to each category for a given trait. The original affinity scores matrix of Usseglio-Polatera *et al.* (2000b) is based on genus and species taxonomic level data; we adapted the original database affinity scores for family level identification by averaging the affinity scores of genera belonging to the same family. An affinity score ranging from 0 to 3 was allocated to each taxon for each trait category in the following way: 0, no affinity of taxon to a given category; 1, a weak affinity to a given trait category; 2, a substantial affinity to a given trait category and 3, a high affinity to a given trait category. Missing information on invertebrate traits or modalities was taken from available literature, summarized in Varandas and Cortes (2010). Traits for which no information was available were scored 0 (zero). For more details about the fuzzy coding procedure, see also Tachet *et al.* (1994); Usseglio-Polatera and Biesel (1994). Subsequent analyses were based on the assumption that this adapted family-level identification affinities matrix approach could be applied in different geographic regions.

Traits were coded for 32 of the 37 identified taxa, representing 86% of the individuals sampled. The taxa-trait fuzzy matrix was multiplied by the number of individuals in the respective family at each site and subsequently transformed in a site-trait array of the number of taxa. Redundant modalities were removed using the Spearman rank correlation (threshold value of $r \geq 0{\cdot}6$ or $r \leq -0{\cdot}6$) and by observing draftsman plots of variables. Non-redundant traits ($n = 37$) were tested for hydraulic situation (fixed flow vs daily flow peaking) and substrate composition (habitat type) by using the Kruskal–Wallis non-parametrical variance analysis (significance level: $p < 0{\cdot}05$). SIMPER analysis was used to detect the contribution of each selected trait to the dissimilarity of hydraulic situations (fixed flow and daily peaking) and substrate composition (habitats).

A permutational multivariate analysis of variance (PERMANOVA) based on a Bray–Curtis similarity matrix was used to test for differences in benthic community response (taxonomic composition, metrics and traits) in wet and dry periods for (i) hydraulic situation (two fixed factors, hydraulic situation and habitats; one random factor, days) and (ii) habitats [two fixed factors were habitats and days; sampling units (dredges) were the random factor].

Distance-based linear models (DISTLM) were derived for each biological data set to assess and compare the links between (i) water column variables and (ii) sediment and benthic macroinvertebrates structure and function, as a result of the difference in the total number of water column samples ($n = 24$) and sediment samples ($n = 72$). To evaluate overall links between sediment variables and benthic macroinvertebrates communities, we based DISTLM analyses on grouped data by calculating mean values of the four dredges collected in each habitat type per day (288 samples ÷ 4 dredges (per habitat) = 72 samples). We applied the same approach to DISTLM analyses between water column variables and benthic macroinvertebrates communities, by calculating the mean value of the four dredges collected in each day and grouped (average) the data from three habitats (288 samples ÷ 4 dredges = 72 samples ÷ 3 habitats = 24 samples).

Distance-based linear models predictors were environmental variables, which were fitted individually or together in three different matrices data sets (taxonomic composition, metrics and traits). The corrected Akaike Information Criterion (AICc) was used to establish the selection criteria, on the basis of the step-wise selection procedure, to evaluate the 'best' model (for taxonomic composition, metrics or traits) that explains benthic macroinvertebrates distribution patterns and their responses to natural and anthropogenic pressures (Anderson *et al.*, 2008). AICc (Sugiura, 1978; Hurvich, 1989) is a derivation of AIC that is used when the number of samples (N) is small in relation to the number of predictor variables (Burnham *et al.*, 2010). AIC is a likelihood-based measure of a model's goodness of fit and the lowest number of environmental parameters necessary to optimize the global AIC by significantly increasing the amount of explained variation in a given model (Akaike, 1974). For visual interpretation of the models in multidimensional space, we used distance-based redundancy analysis (dbRDA) to generate ordination plots to illustrate associations between environmental variables and biological data.

All analyses were carried out using PRIMER 6 software (PRIMER-E Ltd) (Clarke and Gorley, 2006) PERMANOVA + for PRIMER software (Anderson *et al.*, 2008) or STATISTICA 8.0 software PRIMER-E Ltd (StatSoft, 2007).

RESULTS

Physical and chemical descriptors

T-test results revealed significant differences between the water column parameters turbidity, TDS and phosphorous for fixed flow and daily flow peaking during the wet period only (Table III). Highly significant differences were found between habitat sediment parameters in both the wet (ANOVA one-way: $F_{16,\ 52} = 3{\cdot}54$; $p = 0{\cdot}0002$) and the dry periods (ANOVA one-way: $F_{16,52} = 5{\cdot}36$; $p = 0{\cdot}000002$) (Table IV). However, no significant differences were found between fixed flow and daily flow peaking, independent of habitat or seasonal period.

Benthic macroinvertebrates

A total of 15 462 benthic macroinvertebrates were collected and identified from 37 taxa, comprising Arthropods (33 taxa), Annelids (2 taxa), Molluscs (1 taxon) and Nematodes (1 taxon) (Appendix). Higher levels of richness and Shannon–Wiener diversity occurred during the wet period (Table V), but higher density values occurred during the dry period (Table V). The Chironomidae was the dominant macroinvertebrate family in the three habitats for both hydraulic situations and two seasonal periods (Appendices 1 and 2). Higher diversity values, including a higher proportion of rheophilic taxa (e.g. Hydropsychidae, Hydroptilidae and Simuliidae) occurred in the RN habitat (Appendices 1 and 2 as well as Table V).

The metrics selection procedures revealed six metrics that were sensitive to the different hydraulic situations. Five metrics were selected for the wet period (22% contribution to the total dissimilarity) and one selected for the dry period (3·38% contribution to the total dissimilarity). The same procedure carried out to select metrics sensitive to habitat level effects (i.e. substrate) identified 13 metrics. Six metrics were selected for the wet period (30% contribution to total dissimilarity) and 11 metrics selected for the dry period (45% contribution to total dissimilarity).

Table III. Physical and chemical variables of water column (mean ± SD) sampled under influence of both hydraulic situations, fixed flow and daily flow peaking in both the periods, wet period (January) and dry period (July). In each line within each seasonal period, the means followed by the same letter are not significantly different from each other by Tukey's test, significance level of 0·05).

	Wet period		Dry period	
Abiotic variables	Fixed flow	Daily fluctuations	Fixed flow	Daily fluctuations
Water temperature (°C)	25·24 ± 0·18[a]	25·03 ± 0·21[a]	18·00 ± 0·13[a]	18·05 ± 0·15[a]
pH	7·23 ± 0·24[a]	7·14 ± 0·13[a]	7·39 ± 0·26[a]	7·37 ± 0·09[a]
Electrical conductivity ($\mu S\ cm^{-1}$)	13·33 ± 0·52[a]	13·00 ± 0·71[a]	14·83 ± 2·04[a]	16·00 ± 0·63[a]
Total dissolved solids ($\mu g\ l^{-1}$)	9·00 ± 0[a]	8·20 ± 0·45[b]	10·00 ± 1·67[a]	10·17 ± 0·41[a]
Turbidity (NTU)	48·95 ± 6·47[a]	59·62 ± 6·89[b]	2·04 ± 0·13[a]	2·03 ± 0·16[a]
Water redox (mV)	275·67 ± 55·51[a]	225·75 ± 59·4[a]	277·67 ± 48·12[a]	256·80 ± 69·03[a]
Dissolved oxygen ($mg\ l^{-1}$)	7·60 ± 0·32[a]	7·35 ± 0·66[a]	9·02 ± 0·26[a]	8·77 ± 0·15 [a]
Total nitrogen ($\mu g\ l^{-1}$)	0·07 ± 0·01[a]	0·07 ± 0·02[a]	0·05 ± 0·01[a]	0·05 ± 0·01[a]
Total phosphorus ($mg\ l^{-1}$)	51·33 ± 22·8[a]	29·16 ± 1·99[b]	28·90 ± 0·98[a]	31·35 ± 7·40[a]
Dissolved oxygen saturation (%)	91·98 ± 3·90[a]	88·95 ± 7·95[a]	95·17 ± 2·64[a]	92·67 ± 1·51[a]
Total alkalinity ($\mu Eq\ l^{-1}$ of CO_2)	45·35 ± 23·21[a]	46·02 ± 2·52[a]	121·90 ± 7·42[a]	117·52 ± 19·75[a]
Total carbon dioxide (%)	51·56 ± 27·14[a]	53·78 ± 4·38[a]	136·42 ± 11·90[a]	130·38 ± 23·92[a]

Table IV. Percentage of organic matter and sediment fractions (mean ± SD) sampled in the three fluvial habitats (BW, backwaters; FB, fluvial beaches and RN, running waters) in both the periods, wet period (January) and dry period (July). In each line within each seasonal period, the means followed by the same letter are not significantly different from each other by Tukey's test, significance level of 0·05).

Sediment variables (%)		Dry period			Wet period		
		BW	FB	RN	BW	FB	RN
Organic matter	OM	1·0 ± 0·8[a]	0·5 ± 0·2[a]	0·8 ± 0·5[a]	1·8 ± 1·8[a]	0·6 ± 0·4[a]	0·9 ± 0·5[a]
Pebbles	P	0	0	3·9 ± 9·6 [a]	0	3·8 ± 7·3 [a]	1·1 ± 1·8[a]
Gravel	G	0	6·8 ± 8·2[b]	24·5 ± 29·3[b]	2·8 ± 6·5[a]	8·4 ± 10[a]	31·2 ± 21·7[b]
Very coarse sand	VCS	0·1 ± 0·1[a]	2·4 ± 2·5[b]	7·3 ± 7·9[b]	4 ± 9·4[a]	2·9 ± 2·9[a]	10·7 ± 8·3[a, b]
Coarse sand	CS	0·7 ± 0·7[a]	5·4 ± 5·4[b]	7·6 ± 7[b]	2·3 ± 4·3[a]	5·9 ± 5·1[a]	7·7 ± 6·6[b]
Medium sand	MS	12·2 ± 8·7[a]	13·7 ± 9·1[a]	15·9 ± 13·1[a]	11·6 ± 8·7[a]	17·1 ± 10·3[b]	11·5 ± 8·2[a, b]
Fine sand	FS	38·3 ± 13·1[a]	37·8 ± 13·9[a]	17 ± 13·2[b]	32·7 ± 14·1[a]	35·2 ± 12·5[a]	15·5 ± 11·8[a, b]
Very fine sand	VFS	45·0 ± 16·7[a]	33·5 ± 16·2[a, b]	23·2 ± 20·2[b]	41·1 ± 23·7[a]	26·3 ± 13[b]	21·6 ± 19·7[c]
Silt plus clay	S	3·8 ± 5·8[a]	0·5 ± 0·3[a]	0·8 ± 1·0 [a]	5·5 ± 6·2[a]	0·3 ± 0·2[a, b]	0·8 ± 0·9[b]

Table V. Basic metrics of benthic macroinvertebrates communities (mean ± SD) sampled during fixed flow and daily flow peaking in wet period (January) and dry period (July) in the three fluvial habitats (BW, backwaters; FB, fluvial beaches and RN, running waters).

	BW	FB	RN	BW	FB	RN
Basic metrics	Fixed flow			Daily fluctuations		
Wet period						
Richness (S)	17	20	14	19	22	17
Diversity (H′)	1·06	0·94	1·69	1·03	0·90	1·71
Density (ind m^{-2})	6625	8250	11 350	8488	8075	13 838
Dry period						
Richness (S)	16	10	18	18	8	17
Diversity (H′)	0·28	0·24	0·62	0·44	0·25	0·69
Density (ind m^{-2})	23 100	20 675	25 100	21 663	27 788	18 325

Table VI. Traits selected from specific pressures (percentage of individual), daily flow peaking and substrate composition, with the percentage of contribution of each category for the total data set in the similarity percentage analysis, two periods, wet period (January) and dry period (July), downstream of the Itutinga reservoir (2010).

	Trait Category	Code	Hydraulic situation		Substrate composition	
Biological Traits			Wet	Dry	Wet	Dry
Maximal body size	>2–4 cm	>2–4	—	—	3·34	—
Life duration	≤1 year	≤1y	—	—	—	14·72
	≥1 year	≥1y	16·85	14·72	16·85	—
Reproductive cycles	>1	>1	—	—	—	6·16
Aquatic stages	Egg	Egg	—	7·62	8·17	7·62
	Larva	Larv	3·43	—	3·43	—
Reproduction types	Clutches, in vegetation	Clveg	—	—	—	2·31
Dispersion	Aquatic passive	Aqpass	3·69	—	3·69	—
	Aerial active	Aeact	6·73	—	6·73	—
Resistance forms	Eggs, statoblasts	Egst	—	5	—	5
	Housings against desiccation	Desic	—	—	0·55	—
	Diapause or dormancy	Diap	7·85	—	7·85	7·85
	None	None	—	8·04	—	8·04
Respiration	Tegument	Teg	—		—	9·23
	Plastron	Plast	—	—	1·73	—
	Spiracle	Spir	—	—	4	—
Locomotion and substrate relation	Flier	Flier	—	—	0·72	—
	Surface swimmer	Suswin	—	—	—	0·58
	Full water swimmer	Fuswin	—	3·11	6·01	3·11
	Crawler	Craw	6·09	—	6·09	—
Food	Living macrophytes	Limacrop	4·78	—	4·78	4·78
	Living microinvertebrates	Limicroin	—	2·05	—	—
	Living macroinvertebrates	Limacroin	2·59	2·59	3	3
Feeding habits	Absorber	Absor	1·57	—	1·59	1·59
	Scraper	Scrap	7·3	—	—	3·86
	Filter-feeder	Filfeed	—	4·97	—	—
	Piercer	Pierc	—	—	—	0·48
	Predator	Pred	—	—	—	1·83
Ecological Traits						
Transversal distribution	River channel	Chann	—	—	—	3·9
Substrate	Flags/boulders/cobbles/pebbles	Boulder	—	—	—	2·5
	Sand	Sand	—	—	—	1·03
Current velocity	Null	Null	—	—	—	2·98
Trophic status	Mesotrophic	Meso	—	—	3·76	2·82
Saprobity	A-mesosaprobic	Amesosap	—	—	2·25	1·54
pH	>5	pH > 5	—	—	5·77	3·79
Total contribution to dissimilarity (%)			60·88	48·10	90·31	98·72

The traits selection procedures identified a total of 16 traits modalities sensitive to the different hydraulic situations; 10 were selected for the wet period (61% of contribution to the total dissimilarity), and eight were selected for the dry period (48% of contribution to the total dissimilarity) (Table VI). For habitat level effects, a total of 26 traits were selected, 19 traits for the wet period (95% of contribution to the total dissimilarity) and 23 traits for the dry period (90% of contribution to the total dissimilarity) (Table VI).

The permutational multivariate analysis of variance results comparing two hydraulic situations showed significant differences only in dry period, and the different types of biological data presented different levels of significance (p-values). Metrics and traits showed a better response to hydraulic situation (fixed factor) than the taxonomic composition data (Table VII).

Significant differences were also observed in benthic macroinvertebrates in relation with habitat types. There were significant differences in taxonomically based abundance between habitats in the wet and dry seasons and the fixed and daily peaking flow regimes (Table VIII). Significant differences were found between habitats for metrics for both wet and dry periods but only during the

Table VII. Permutational multivariate analysis of variance results (Pseudo-F e p) of macroinvertebrate taxonomic composition (abundance), metrics and traits for fixed flow and daily flow peaking in both the periods, wet period (January) and dry period (July), in the three fluvial habitats (BW, backwaters; FB, fluvial beaches and RN, running waters).

	Abundance		Metrics		Traits	
	F	*p*	*F*	*p*	*F*	*p*
Wet period						
Hydraulic situation	0·91	0·455[a]	3·46	0·088[a]	3·96	0·058[a]
Habitats	2·81	0·004**	3·73	0·010**	3·49	0·028*
Days	2·46	0·000****	1·55	0·077[a]	2·3	0·003**
Dry period						
Hydraulic situation	2·19	0·060[a]	6·25	0·044*	5·64	0·035*
Habitats	2·81	0·004**	1·7	0·209[a]	5·69	0·008**
Days	2·94	0·000***	3·3	0·004**	2·59	0·005**

[a] $P > 0{\cdot}05$; *$P \leq 0{\cdot}05$; **$P \leq 0{\cdot}01$; ***$P \leq 0{\cdot}001$; ****$P \leq 0{\cdot}0001$.

Table VIII. Permutational multivariate analysis of variance results (Pseudo-F e p) of the three macroinvertebrate data sets (abundance, metrics and traits) for the three habitat types (BW, backwaters; FB, fluvial beaches and RN, running waters) sampled in fixed flow and daily flow peaking for the wet period (January) and dry period (July).

	Abundance		Metrics		Traits	
	F	*p*	*F*	*p*	*F*	*p*
Wet period, fixed flow						
Habitats	2·88	0·008**	3·65	0·05*	2·27	0·114[a]
Days	2·08	0·003**	0·35	0·948	2·96	0·001***
Dredges	0·9	0·580[a]	1·61	0·180[a]	2·02	0·050[a]
Wet period, daily flow peaking						
Habitats	2·29	0·029*	1·84	0·144[a]	5·12	0·005**
Days	2·67	0·000***	2·38	0·020**	2·2	0·009**
Dredges	1·44	0·103[a]	0·91	0·517[a]	1·01	0·433[a]
Dry period, fixed flow						
Habitats	7·18	0·006**	4·21	0·020*	4·26	0·023*
Days	1·09	0·386[a]	0·61	0·804[a]	1·11	0·371[a]
Dredges	1·89	0·052[a]	1·68	0·283[a]	1·95	0·324[a]
Dry period, daily flow peaking						
Habitats	3·28	0·027*	2·59	0·095	7·48	0·001***
Days	3·68	0·000***	3·84	0·000****	2·33	0·011*
Dredges	1·11	0·341[a]	2·65	0·099[a]	1·11	0·38[a]

[a] $P > 0{\cdot}05$; *$P \leq 0{\cdot}05$; **$P \leq 0{\cdot}01$; ***$P \leq 0{\cdot}001$; ****$P \leq 0{\cdot}0001$.

fixed flow regime (Table VIII). Significant differences were detected in macroinvertebrate traits between habitats for daily fluctuations during the wet period and both fixed and daily flow peaking situations during the dry period (Table VIII).

Distance-based linear models, AICc results and dbRDA ordination plots revealed distinct associations between different benthic macroinvertebrate data sets and water column variables (Table IX). Taxonomic composition data and metrics do not present any strong links with water column variables. However, there was a strong association between both the biological (e.g. aquatic stages, food, respiration, dispersion, resistance forms, feeding habits, life cycle, locomotion and substrate relation) and ecological macroinvertebrate traits (pH preference and transversal distribution), with pH ($p = 0{\cdot}002$), turbidity ($p = 0{\cdot}090$) and total dissolved solids ($p = 0{\cdot}018$) (best solution, AIC: 51·48; $R^2 = 0{\cdot}45$; Figure 3). The first axis of the dbRDA plot described 34·1% of total variation (Figure 3) revealing that TDS had more influence on macroinvertebrate structure and function during the dry period, whereas turbidity had more influence during the wet period.

Distance-based linear models, AICc results and dbRDA ordination plots for benthic macroinvertebrates data and sediment variables indicated that the best variables fitting the abundance data (best solution, AICc: 511·75; $R^2 = 0{\cdot}09$)

Table IX. Results of the corrected Akaike Information Criterion and the *F* and *p* from the distance-based linear models analyses for the three sets of macroinvertebrate data (abundance, metrics and traits) in both the wet period (January) and dry period (July).

Sediment variables (%)	Abundance			Metrics			Traits		
	AICc	*F*	*p*	AICc	*F*	*p*	AICc	*F*	*p*
Gravel	513·1	3·478	0·004**	457·6	6·452	0·008**	224·6	4·241	0·016***
Medium sand	—	—	—	449·4	3·369	0·048*	220·4	4·051	0·010***
Very fine sand	511·7	3·512	0·004**	450·6	9·336	0·001****	222·4	4·335	0·008***
Silt plus clay	—	—	—	448·55	2·96	0·059[a]	—	—	—

[a] $P > 0{\cdot}05$; *$P \leq 0{\cdot}05$; **$P \leq 0{\cdot}01$; ***= $P \leq 0{\cdot}001$; ****= $P \leq 0{\cdot}0001$

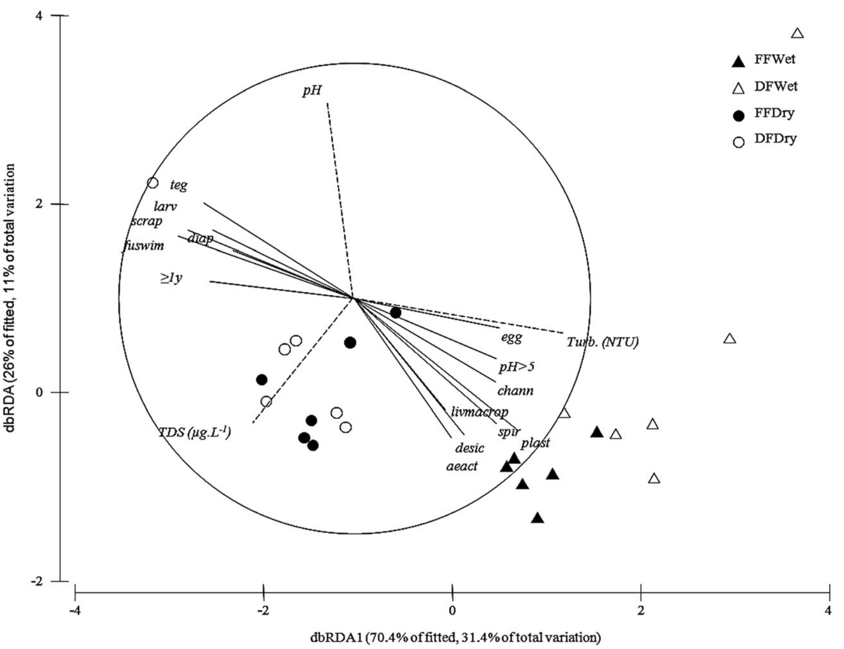

Figure 3. Distance-based redundancy analysis ordination of first and second fitted axes relating water column variables with selected macroinvertebrate traits downstream of the Itutinga reservoir. The length and direction of the vector projections for the water column variables, previously selected by the distance-based linear models, represent the strength and direction of the relationships. Full descriptions of the abbreviations attributed to the traits are given in Table III. The acronyms mean the following: TDS, total dissolved solids and turb, turbidity. The other acronyms in the figure are the combination of the follow acronyms related with hydraulic situation (FF, fixed flow and DF, daily fluctuations) and seasonal period (wet, wet period and dry, dry period) (e.g. FFWet, sampled in under fixed flow situation in the wet period).

were gravel and very fine sand. Gravel, very coarse, medium sand and very fine sand substrates (best solution, AICc: 448·55; $R^2 = 0{\cdot}26$) provided the best fit for explaining changes in metrics. The sediment variables best describing the macroinvertebrate trait model (best solution, AICc: 220·42; $R^2 = 0{\cdot}15$) were gravel, medium and very fine sand fractions (Table IX). The lowest AICc value of the trait model indicates that this is the best model for assessing the effect of daily flow peaking on facets of the benthic macroinvertebrates community. The dbRDA ordination plot (Figure 4) clearly shows how gravel, medium sand and very fine sand were significantly related with both biological (life cycle, feeding habits and reproduction) and ecological traits (transversal distribution, trophic status, saprobity and pH). The percentage of total variation along axis one was lower than the dbRDA for water column variables (14·1%). There was no clear seasonal difference in substrate composition or between fixed and peaking hydraulic situations. Gravel is more closely associated with RN, whereas very fine sand and medium sand were related with BW and FB habitat types.

DISCUSSION

Dams disrupt downstream natural lotic flow regimes (Poff *et al*., 1997) as a result of the operational flow regimes (Pompeu and Vieira, 2002) that differ greatly from natural flow regime of unregulated river systems they were built on (World Commission on Dams, 2000; Cortes *et al*., 2002; Maroneze *et al*., 2011). Reservoirs formed upstream of dams retain organic and inorganic particles derived from the upstream section of the drainage system (Barbosa *et al*., 1999), altering important physicochemical and biological processes downstream. These alterations disrupt the continuity and natural river processes, such as the flow of nutrients and energy (Vannote *et al*., 1980). As a result, stretches of rivers situated downstream of dams are highly dependent on the physicochemical characteristics of the reservoir situated upstream.

Our first hypothesis that the daily flow peaking can alter the water column variables was not supported by our results because most water column parameters did not differ significantly between the tested hydraulic regimes (Table III), although there was a significant increase in turbidity, TDS and total phosphorous during the daily fluctuation phase of the wet period. This is probably because of the expansion flow onto the adjacent floodplain, resulting in increased input of allochthonous organic material and sediments (Poff *et al*., 1997). Despite detection of significant changes in these values (Tukey's honestly significant difference post hoc test), values for turbidity, TDS and total phosphorous were considered low, according to the established limits defined by CONAMA (National Council of Environment), resolution number 357/2005 (Brasil, 2005).

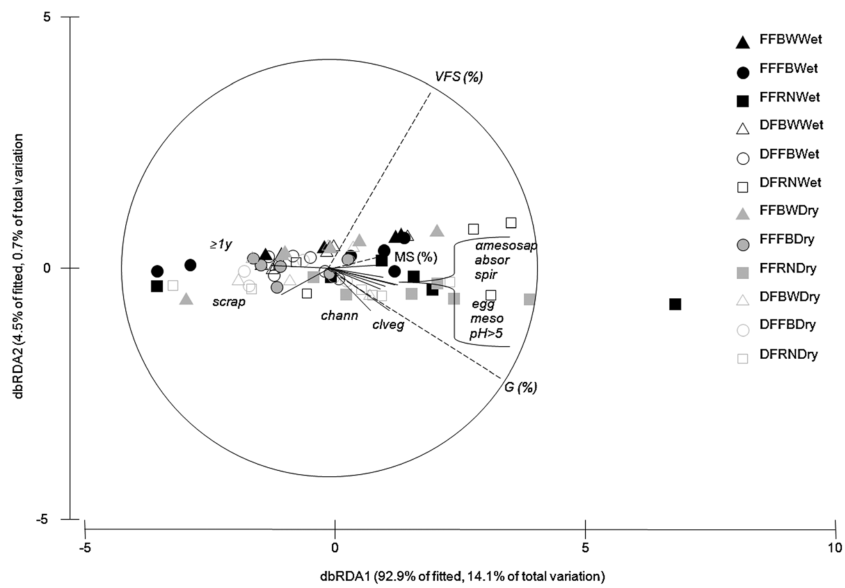

Figure 4. Distance-based redundancy analysis ordination of first and second fitted axes relating sediment composition with biological and ecological invertebrates traits set downstream of the Itutinga reservoir, Rio Grande, southeast Brazil in 2010. Vectors projections are given for the water column variables selected by the distance-based linear models routine. The length and direction of the vector projections for the water column variables selected by the distance-based linear models routine represent the strength and direction of the relationship. Full descriptions of the abbreviations attributed to the traits are given in Table III. The acronyms mean the following: G, gravel; MS, medium sand and VFS, very fine sand. The other acronyms in the figure are the combination of the following acronyms related with hydraulic situation (FF = fixed flow and DF = daily fluctuations), fluvial habitat type (BW, backwater; FB, fluvial beach and RN, running water) and seasonal period (wet, wet period and dry, dry period) (e.g. FFBWWet, sampled in under fixed flow situation in the backwater habitat type in the wet period).

We detected significant differences in the substrate composition between habitat type, although they were apparently unaffected by the daily flow peaking regime tested in this study. The size and complexity of habitat substrate were related with specific hydraulic conditions in each habitat type. For example, RN habitats, i.e. riffles, are more complex in terms of habitat diversity (Brooks *et al.*, 2005), with diverse particle sizes. The size and complexity of substrate decreased in habitats with high hydraulic dissipation of energy, such as the fluvial beach habitat, and the smallest particle sizes were found in the BW habitat. The organic matter content of the substrates was low in the three habitats studied because of the retention of fine and coarse organic matter by the reservoir situated upstream of the study area, affecting river continuum dynamics (Vannote *et al.*, 1980; Barbosa *et al.*, 1999).

Our second hypothesis was that alterations in water column variables and sediment composition due to daily flow peaking would result in changes in different facets of the benthic macroinvertebrates community. The lack of observed significant differences in the benthic macroinvertebrate taxonomic composition data between fixed flow and daily fluctuations indicates that this type of data is unsuitable for detecting alterations in dam-mediated flow regimes, as observed by Cortes *et al.* (2002) and Almeida *et al.* (2009). Benthic macroinvertebrate traits and, to a lesser extent, metrics better reflected changes in flow regime (e.g. Dolédec and Statzner, 2008; Tomanova *et al.*, 2008; Brooks *et al.*, 2011), particularly in the dry period. In the dry periods, the rainfall levels are low with less flow variations. Thus, the susceptibility of the macroinvertebrate communities increased under the effect of daily fluctuations, which was better detected using biological and ecological macroinvertebrate traits. The lower AICc from DISTLM analysis (Table IX) and higher percentage dissimilarity between flow regimes from the SIMPER analysis (Table VI) support the applicability of traits as a tool for evaluating the effect of regulation on river systems. This supports the findings of several studies that have evaluated the use of traits to detect and predict different types of natural and anthropogenic impacts on freshwater ecosystems (Charvet *et al.*, 2000; Usseglio-Polatera *et al.*, 2000a; Haybach *et al.*, 2004; Statzner *et al.*, 2008; Feio and Dolédec, 2012, Dolédec and Statzner, 2008; Tomanova *et al.*, 2008; Brooks *et al.*, 2011). The findings of many of these studies suggest that a trait-based approach results in a more robust data set that is less susceptible to the influence of seasonal and geographic patterns.

Alterations in the downstream benthic macroinvertebrate communities caused by daily flow peaking regimes result from the interplay of environmental, ecological and biological factors on the basis of physical and chemical parameters of the water body, geomorphological characteristics of the river basin, connectivity (lateral and longitudinal), physical characteristics of habitats (pools, FB and rifles) and microhabitats (predominant substrates) (Ligeiro *et al.*, 2010), interspecific and intraspecific competition and the type of anthropogenic impacts around. The homogenization of available habitats and the constant alterations in flow (seasonal, daily or hourly) and in some water column parameters simplify the aquatic ecosystems, altering the communities structure and function, favouring the dominance of groups like dipterans (e.g. Chironomidae), trichopterans (e.g. Hydropsychidae) and ephemeropterans (e.g. Leptohyphidae), with life history strategies and evolutionary adaptations for natural flow alterations (Ogbeibu and Oribhabor, 2002; Silva-Santos *et al.*, 2004), and hindering the survival of groups like Odonata and Plecoptera, which suffer more influence of the variation in water level (Smokorowski *et al.*, 2011).

CONCLUSIONS

The results of this study indicate that the structure and function of the macroinvertebrate community downstream of the Itutinga reservoir are influenced predominantly by substrate type and, to a lesser extent, by water column variables. The predominance of biological traits such as respiration, life cycle, locomotion and feeding habits are generally correlated with substrate composition, in particular, the levels of organic particulate matter. The daily flow peaking hydraulic regimes tested by the experiment at the Itutinga reservoir do not appear to be sufficiently different from the fixed flow regime to provoke detectable changes in the water column variables substrate composition and consequent influences on macroinvertebrate structure and function. Further similar studies in other dams covering a range of operation regimes would provide more information about the influence of daily flow peaking on the hydraulic habitats and macroinvertebrates downstream dams, and the macroinvertebrate trait responses proved to be a good tool.

On the basis of the results of the statistical analyses, the influence of daily flow peaking on sediment composition (hypothesis two) appears to be negligible; however, there was partial influence of daily flow peaking on some water column variables (hypothesis one) and on benthic macroinvertebrate traits and metrics (hypothesis three) in the dry period. Our results confirmed hypothesis four, namely, that traits provide the best way to evaluate the impact of daily flow peaking on macroinvertebrate communities. A trait-based approach has considerable potential for assessing anthropogenic impacts on aquatic ecosystems by river regulation. However, we recommend further studies in other river basins, countries and continents during more hydrological cycles and with higher levels of taxonomic resolution to substantiate the results of this study.

Finally, it is vital that decision makers pay close attention to the influence of reservoir operations on the processes that determine substrate composition (habitat availability) downstream when determining environmental flow regimes. Substrate composition is an important factor that determines patterns in the structure and function in aquatic ecosystems. Suitable flow regimes and restoration measures promote the input of fine, medium and coarse organic particulate matter, increasing ecosystem complexity and providing habitats and services for the biota, thereby mitigating the impacts caused by dams.

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Appendix 1.

Mean and standard deviation of main benthic macroinvertebrates taxa sampled in the wet period (January of 2010), in three habitat types (BW = backwater, FB = fluvial beach and RN = running water) under fixed flow and daily flow peaking in two distinct seasonal periods (wet and dry), downstream Itutinga reservoir, Rio Grande basin, southeast of Brazil. The *taxa* are organized on the basis of their abundance.

	Wet period					
	Fixed flow			Daily fluctuation		
	BW	FB	RN	BW	FB	RN
Chironomidae	202·6 ± 152·8	314·9 ± 449·3	128·1 ± 139·2	269·8 ± 269·4	298·9 ± 580·3	133·7 ± 156·2
Oligochaeta	18·1 ± 18·1	18·8 ± 18·8	25·0 ± 25·0	43·3 ± 43·3	21·9 ± 21·9	140·6 ± 140·6
Baetidae	42·5 ± 42·5	27·1 ± 27·1	18·8 ± 18·8	55·0 ± 55·0	25·0 ± 25·0	41·1 ± 41·1
Amphipoda	—	—	—	—	—	—
Bivalvia	—	—	—	—	—	—
Ceratopogonidae	15·6 ± 15·6	12·5 ± 12·5	12·5 ± 12·5	12·5 ± 12·5	12·5 ± 12·5	—
Chaoboridae	—	—	—	12·5 ± 12·5	12·5 ± 12·5	—
Culicidae	—	—	—	—	12·5 ± 12·5	—
Elmidae	25·0 ± 25·0	12·5 ± 12·5	12·5 ± 12·5	12·5 ± 12·5	25·0 ± 25·0	15·3 ± 15·3
Empididae	—	—	20·8 ± 20·8	—	12·5 ± 12·5	—
Gerridae	—	—	—	—	—	—
Gelastocoridae	12·5 ± 12·5	—	—	—	—	—
Gomphidae	12·5 ± 12·5	12·5 ± 12·5	—	12·5 ± 12·5	12·5 ± 12·5	—
Gyrinidae	—	—	—	—	—	—
Hidracarina	—	12·5 ± 12·5	—	—	—	12·5 ± 12·5
Hirudinea	12·5 ± 12·5	—	—	12·5 ± 12·5	—	12·5 ± 12·5
Helichopsychidae	—	—	—	12·5 ± 12·5	—	12·5 ± 12·5
Hydrophilidae	—	25·0 ± 25·0	12·5 ± 12·5	—	20·8 ± 20·8	—
Hydropsychidae	218·8 ± 218·8	15·6 ± 15·6	725·0 ± 725·0	20·0 ± 20·0	65·6 ± 65·6	640·3 ± 640·3
Hydroptilidae	25·0 ± 25·0	22·5 ± 22·5	189·6 ± 189·6	30·4 ± 30·4	25·0 ± 25·0	100·0 ± 100·0
Leptoceridae	—	12·5 ± 12·5	—	—	—	12·5 ± 12·5
Leptophlebiidae	12·5 ± 12·5	12·5 ± 12·5	—	25·0 ± 25·0	12·5 ± 12·5	—
Leptoyphidae	16·1 ± 16·1	55·6 ± 55·6	55·0 ± 55·0	31·9 ± 31·9	23·8 ± 23·8	87·5 ± 87·5
Libellulidae	12·5 ± 12·5	12·5 ± 12·5	—	—	—	12·5 ± 12·5
Naocoridae	12·5 ± 12·5	—	—	—	12·5 ± 12·5	—
Nematoda	—	12·5 ± 12·5	—	20·8 ± 20·8	12·5 ± 12·5	47·5 ± 47·5
Ostracoda	—	—	—	12·5 ± 12·5	—	—
Polycentropodidae	25·0 ± 25·0	21·9 ± 21·9	12·5 ± 12·5	25·0 ± 25·0	50·0 ± 50·0	37·5 ± 37·5
Polymitarcyidae	—	12·5 ± 12·5	—	—	12·5 ± 12·5	12·5 ± 12·5
Pyralidae	—	37·5 ± 37·5	50·0 ± 50·0	25·0 ± 25·0	16·7 ± 16·7	25·0 ± 25·0
Simuliidae	12·5 ± 12·5	12·5 ± 12·5	277·5 ± 277·5	12·5 ± 12·5	12·5 ± 12·5	60·4 ± 60·4
Staphilinidae	—	—	—	12·5 ± 12·5	—	—
Tabanidae	—	—	—	—	—	—
Tipulidae	25·0 ± 25·0	12·5 ± 12·5	12·5 ± 12·5	—	12·5 ± 12·5	—
Vellidae	—	—	—	—	12·5 ± 12·5	—

Appendix 2.

Mean and standard deviation of main benthic macroinvertebrates taxa sampled in the dry period (July of 2010), in three habitat types (BW = backwater, FB = fluvial beach and RN = running water) under fixed flow and daily flow peaking in two distinct seasonal periods (wet and dry), downstream Itutinga reservoir, Rio Grande basin, southwest of Brazil. The *taxa* are organized on the basis of their abundance.

	Dry period					
	Fixed flow			Daily fluctuation		
	BW	FB	RN	BW	FB	RN
Chironomidae	918·2 ± 726·9	824·5 ± 648·7	914·1 ± 734·6	825 ± 797·6	1104 ± 835·5	646·9 ± 578·9
Oligochaeta	26·8 ± 26·8	33·3 ± 33·3	37·5 ± 37·5	69·8 ± 69·8	46·9 ± 46·9	57·7 ± 57·7
Baetidae	12·5 ± 12·5	18·8 ± 18·8	26·8 ± 26·8	12·5 ± 12·5	12·5 ± 12·5	29·2 ± 29·2
Amphipoda	—	—	—	12·5 ± 12·5	—	—
Bivalvia	—	—	—	12·5 ± 12·5	—	—
Ceratopogonidae	22·9 ± 22·9	21·9 ± 21·9	50·0 ± 50·0	18·8 ± 18·8	13·5 ± 13·5	16·7 ± 16·7
Chaoboridae	—	—	12·5 ± 12·5	—	—	—
Culicidae	50·0 ± 50·0	—	—	—	—	—
Elmidae	12·5 ± 12·5	12·5 ± 12·5	12·5 ± 12·5	18·8 ± 18·8	—	12·5 ± 12·5
Empididae	—	—	—	—	—	12·5 ± 12·5
Gerridae	—	—	—	12·5 ± 12·5	—	12·5 ± 12·5
Gomphidae	—	—	—	—	—	12·5 ± 12·5
Gyrinidae	12·5 ± 12·5	—	—	—	—	—
Hidracarina	—	—	12·5 ± 12·5	—	—	—
Hirudinea	—	—	12·5 ± 12·5	—	—	—
Hydropsychidae	12·5 ± 12·5	25·0 ± 25·0	69·3 ± 69·3	—	12·5 ± 12·5	58·3 ± 58·3
Hydroptilidae	12·5 ± 12·5	—	12·5 ± 12·5	—	—	12·5 ± 12·5
Leptoceridae	37·5 ± 37·5	12·5 ± 12·5	—	12·5 ± 12·5	—	—
Leptophlebiidae	—	—	12·5 ± 12·5	12·5 ± 12·5	—	12·5 ± 12·5
Leptoyphidae	40·6 ± 40·6	32·3 ± 32·3	66·1 ± 66·1	55·0 ± 55·0	39·8 ± 39·8	64·6 ± 64·6
Libellulidae	37·5 ± 37·5	—	31·3 ± 31·3	12·5 ± 12·5	—	12·5 ± 12·5
Naocoridae	—	—	—	—	—	—
Nematoda	12·5 ± 12·5	—	—	15·0 ± 15·0	12·5 ± 12·5	20·8 ± 20·8
Ostracoda	—	—	12·5 ± 12·5	—	—	—
Polycentropodidae	12·5 ± 12·5	—	—	12·5 ± 12·5	—	—
Polymitarcyidae	—	12·5 ± 12·5	—	12·5 ± 12·5	—	—
Pyralidae	—	—	12·5 ± 12·5	—	—	12·5 ± 12·5
Simuliidae	12·5 ± 12·5	—	22·9 ± 22·9	12·5 ± 12·5	—	87·5 ± 87·5
Tabanidae	—	—	—	12·5 ± 12·5	—	—
Tipulidae	15·0 ± 15·0	12·5 ± 12·5	12·5 ± 12·5	15·6 ± 15·6	12·5 ± 12·5	12·5 ± 12·5
Vellidae	—	—	31·3 ± 31·3	—	—	—

