UNIVERSIDADE ESTADUAL PAULISTA “JÚLIO DE MESQUITA FILHO”
CAMPUS DE BOTUCATU
INSTITUTO DE BIOCIÊNCIAS - DEPARTAMENTO DE ZOOLOGIA

DISSERTAÇÃO

AMBIENTES DE PEDRAIS COMO ÁREAS ESTRATÉGICAS PARA A CONSERVAÇÃO DA BIODIVERSIDADE FLUVIAL – UM ESTUDO DA ICTIOFAUNA DO RIO SAPUCAÍ-MIRIM (SP) E SUAS INTERAÇÕES TRÓFICAS

Aluno: Eduardo Meneguzzi Brambilla

Orientador: Dr. Marcos Gomes Nogueira

Coorientadora: Dra. Virginia Sanches Uieda

BOTUCATU, SP

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Eduardo Meneguzzi Brambilla

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Orientador: Prof. Dr. Marcos Gomes Nogueira

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Resumo Geral

O Rio Sapucaí-Mirim se destaca como sendo um dos principais tributários do rio Grande. Apesar de possuir cinco PCHs instaladas (três no curso principal e duas de desvio de canal), ainda apresenta trechos consideravelmente extensos que ainda são livres de barramento. Este rio possui como característica marcante a presença de vários pedrais (“knickzones”), macrohabitats pouco conhecidos ecologicamente e altamente ameaçados pela construção de usinas hidrelétricas. A fim de avaliar a importância ecológica destes macrohabitats para a conservação da biodiversidade regional, o estudo caracterizou a ictiofauna de um pedral do rio Sapucaí-Mirim, sua associação com os distintos tipos de habitats (“isolated pools” and “connected pools”) e as relações tróficas. As amostragens foram realizadas no período seco (Junho/2014) e chuvoso (dezembro/2014) através de pesca elétrica, peneira e arrasto. Simultaneamente foi realizada uma caracterização física e limnológica do pedral (“pools”, “runs” e “rapids”), através de medidas e observações *in situ*, bem como coleta de amostras e análises em laboratório. A ictiofauna deste pedral foi composta por 23 espécies, sendo cinco primeiros registros para a sub-bacia. A riqueza específica representa 23% do total da ictiofauna conhecida no rio Sapucaí-Mirim, mas pode ser considerada elevada dada a pequena dimensão deste macrohabitat (0,03 km). Houve diferença sazonal significativa dos atributos ecológicos da fauna (composição, riqueza, abundância, diversidade e equitabilidade), bem como variações específicas conforme o tipo de habitat. Destaca-se ainda o fato de terem sido encontradas formas larvais e juvenis. Através de análises de conteúdo estomacal dos peixes verificou-se que a categoria de alimento mais frequente e dominante na dieta foi matéria orgânica e hexapoda aquático. Diferenças sazonais na dieta dos peixes foram determinadas por maior consumo de algas na condição seca e matéria vegetal e matéria orgânica na condição chuvosa. Maior sobreposição de nicho ocorreu nas poças isoladas. A alta variabilidade nos parâmetros limnológicos, heterogeneidade física e a influência das variações climáticas sazonais e episódicas podem ser as principais razões para explicar a diversidade de peixes no pedral. A importância deste tipo de macrohabitat para a manutenção da diversidade regional de peixes é ressaltada, enfatizando-se a importância de incluir de forma estratégica este tipo de ambiente nos planos de conservação da biodiversidade, visando a sua proteção contra interferências antrópicas, principalmente instalação de pequenas centrais hidrelétricas.

Apresentação

O sistema do alto rio Paraná pertence à região ictiofaunística da bacia do Paraná-Prata (Géry, 1969) que inclui as bacias hidrográficas dos rios da Prata, Uruguai, Paraná e Paraguai e representa a segunda maior drenagem hidrográfica na América do Sul, com 3,2 milhões de km² (Lowe-McConnell, 1987, 1999). O alto Paraná corresponde à porção da bacia do rio Paraná situada a montante de Sete Quedas (inundada pelo Reservatório de Itaipu), incluindo grandes tributários como os rios Grande, Paranaíba, Tietê e Paranapanema.

Em relação a ictiofauna, Bonetto (1986) relatou a presença de 130 espécies na bacia do alto Paraná, Agostinho & Júlio-Jr (1999) citam mais de 250 (incluindo as que ascenderam as Sete Quedas inundadas por Itaipu) e Langeani et al. (2007) ampliaram esse número para 310, adicionando que ainda existem lacunas a serem preenchidas quanto a descrição da ictiofauna regional.

O rio Grande, um dos principais formadores da bacia do alto rio Paraná, nasce na Serra da Mantiqueira, na região limítrofe entre os Estados de São Paulo e Minas Gerais, a aproximadamente 1.500 m de altitude (22º15’S 44º34’W). Apresenta extensão total de 1.050 km (Ziesler & Ardizzone, 1979) e uma área de drenagem de aproximadamente 143 mil km² (CEMIG & CETEC, 2000), desaguando no rio Paraná, na confluência com o rio Paranaíba. O rio Sapucaí-Mirim, objeto do presente estudo, é um importante tributário do rio Grande (Fig. 1).

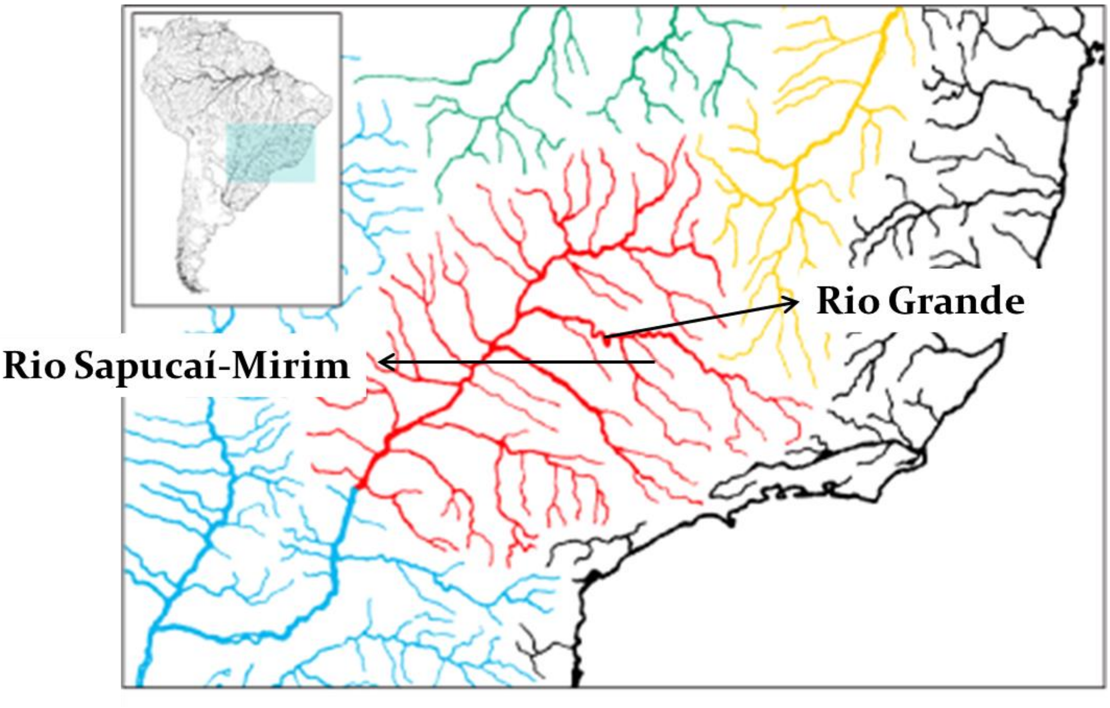

Figura 1. Sistema do Alto rio Paraná (vermelho) e bacias vizinhas do Paraguai e Baixo Paraná (azul), Araguaia/Tocantins (verde), São Francisco (amarelo) e rios costeiros (preto). Destaque para o Rio Grande e Rio Sapucaí-Mirim. Mapa modificado de Langeani et al., 2007.

De acordo com Pompeu et al. (2009) a bacia do rio Grande possui pelo menos 105 espécies de peixes. Esse número se baseia no conjunto de levantamentos existentes para o rio Grande (CEMIG & CETEC, 2000), reservatório de Itutinga (Alves et al., 1998), porção mineira da bacia (Pompeu et al., 2009) e afluentes do rio Grande que drenam o Estado de São Paulo (Castro et al., 2004).

Assim como os demais grandes rios da região sudeste, o rio Grande foi bastante impactado pela construção de um número elevado de barragens hidrelétricas (UHEs de Água Vermelha, Marimbondo, Porto Colômbia, Volta Grande, Igarapava, Jaguara, Estreito, Peixoto, Furnas, Funil, Camargos e Itutinga), com uma potência total instalada de 5.616 MW (CEMIG & CETEC, 2000).

Esses barramentos causam profundas modificações no ambiente aquático e nas comunidades presentes (Carvalho & Silva, 1999; Panarelli et al., 2003; Casanova & Henry, 2004; Nogueira et al., 2006). O novo ambiente, formado após o barramento, apresenta características muito diferentes do original e as comunidades distinguem-se significativamente daquelas que ocorriam nos trechos lóticos originais ou remanescentes. Assim, o resultado inevitável destes empreendimentos em relação à fauna aquática, é a alteração na abundância e riqueza de espécies, com proliferação de algumas e redução ou mesmo eliminação de outras (Agostinho, 1994).

Entre as comunidades aquáticas, os peixes se destacam por serem organismos facilmente visualizáveis no ambiente, por apresentarem valor econômico e por serem sensíveis a mudanças ocorridas em outros componentes do sistema aquático. Em geral, a fauna de peixes que habita reservatórios é composta primariamente por espécies sedentárias de pequeno porte, com tendência de redução das espécies migradoras de grande porte (Agostinho et al., 2007).

O grupo dos migradores inclui os maiores peixes de nossa fauna, com predadores de topo de cadeia alimentar que podem determinar padrões de transferência energética ao longo das cadeias tróficas (Carpenter & Kitchell, 1993). Por serem os mais prejudicados pelos represamentos, apresentarem um elevado interesse social, econômico e ecológico, os peixes migradores devem ser de especial interesse nas ações de manejo (Agostinho et al., 2007).

As espécies sedentárias e endêmicas que se concentram em áreas de represamento ou nos primeiros quilômetros a jusante da barragem também são importantes socialmente. Para esse grupo os impactos decorrentes do represamento podem ser compensados, visto que muitas dessas espécies podem proliferar no ambiente represado e ser mantida uma pesca sustentável, desde que adequadamente controlada (Agostinho et al., 2007).

Frente ao cenário atual observado na bacia do rio Grande, com múltiplos barramentos, amplia-se a importância de tributários para manutenção dos estoques pesqueiros e conservação da biodiversidade regional, uma vez que esses trechos podem representar rotas alternativas para migração reprodutiva das espécies de grande porte (Vazzoler et al., 1997). Esses tributários possuem, ao longo do gradiente longitudinal, uma gama de habitats funcionais que atuam como áreas de desova, crescimento e alimentação, fundamentais para o fechamento do ciclo de vida de muitas espécies de peixes (Agostinho et al., 1993; Baumgartner et al., 2004; Viana e Nogueira, 2008).

A composição da ictiofauna do rio Sapucaí-Mirim é similar àquela encontrada em outros rios da bacia do alto Paraná, contando ainda com espécies consideradas raras e/ou ameaçadas de extinção no estado de São Paulo e outras que são importantes para a pesca de subsistência e esportiva (Cesário, 2010; Souza, 2014). Este rio apresenta importantes migradores como dourados (*Salminus brasiliensis* e *Salminus hilarii*), curimbatás (*Prochilodus lineatus*), barbados (*Pinirampus pirinampu*) e diversas espécies de piaus (família Anostomidae), o que comprova sua importância como rota reprodutiva. Uma elevada riqueza e abundância expressiva de cascudos também são encontradas neste rio, com a presença de algumas espécies novas que estão sendo descritas (Zawadzki et al., *in prep.*). Segundo Souza (2014), baseado no conjunto de levantamentos existentes, a fauna do rio Sapucaí-Mirim contém 99 espécies de peixes, cerca de 32% do total de espécies da bacia do alto Paraná, mas correspondendo a apenas 1% de sua área.

Atualmente, existem cinco pequenas centrais hidrelétricas em operação na bacia do rio Sapucaí-Mirim. Apesar de diversos estudos relatarem os impactos provocados na fauna devido à construção de reservatórios de usinas hidrelétricas (UHEs), ainda são escassos os que analisam os impactos de pequenas centrais hidrelétricas (PCHs). Essas são caracterizadas pelo pequeno porte, capacidade instalada entre 1MW e 30MW de potência, e pelo tamanho do reservatório, que deve possuir uma área total igual ou inferior a três km^2 (Resolução nº 394 de 04/12/1998 - ANEEL).

Embora a Agência Nacional de Energia Elétrica – ANEEL considere como baixos os impactos ambientais advindos da construção de uma PCH, há registro de efeitos danosos e irreversíveis para os ecossistemas locais, tão prejudiciais quanto os decorrentes de grandes barramentos (Godoy, 1975).

Nos trechos do rio Sapucaí-Mirim que não sofrem influencia direta das PCHs, destaca-se um tipo particular de ambiente complexo em termos estruturais e funcionais, conhecido regionalmente como “pedrais”. Estudos demonstram que os efeitos locais de habitats aquáticos com grande heterogeneidade, resultam no aumento regional da riqueza e abundância da fauna (Crowder et al., 1998; Kelaher & Castilla, 2005; Matias et al., 2010). No entanto, os mecanismos por trás desse efeito não são totalmente claros, com explicações que consideram a possibilidade de estabelecimento de um número maior de nichos, devido à maior disponibilidade de micro habitats, bem como o aumento da produtividade e oferta de recursos.

Baseando-se nas considerações anteriores, foram estabelecidos os temas de estudo dessa dissertação. Os dados para o desenvolvimento da pesquisa foram obtidos em um pedral localizado a montante da área de influência direta da PCH Palmeiras no rio Sapucaí-Mirim (bacia do rio Grande, SP/MG).

Em termos de estrutura da dissertação, se optou pela organização na forma de capítulos, os quais foram redigidos nos padrões de um de artigo científico (segundo as normas do periódico *Hydrobiologia*).

O objetivo do primeiro capítulo foi caracterizar e conceituar o ambiente de pedral através de observações e medidas de parâmetros físicos e limnológicos. O segundo capítulo visa caracterizar a ictiofauna deste pedral, com o intuito de avaliar a importância deste ambiente para a manutenção da diversidade de peixes do rio Sapucaí-Mirim. Por fim, o terceiro capítulo refere-se a dieta dos peixes do pedral e a importância dos recursos alimentares deste ambiente para a ictiofauna.

Cabe mencionar que o presente estudo, associado a outros concluídos e em andamento[1], integra o desenvolvimento de uma proposta estratégica de monitoramento e gestão ambiental na bacia hidrográfica do Sapucaí-Mirim e também contribui para a consolidação da linha de pesquisa de avaliação de impactos ecológicos de PCHs do Laboratório de Ecologia de Águas Continentais do Departamento de Zoologia da UNESP/Campus de Botucatu.

Área de estudo

Rio Sapucaí-Mirim

O rio Sapucaí-Mirim apresenta 290 km de extensão, possuindo suas nascentes localizadas nas encostas interiores da serra da Laje (Mantiqueira), a nordeste do Estado de São Paulo, além das nascentes de dois formadores (Esmeril e Santa Bárbara) localizadas no Estado de Minas Gerais. Trata-se de um rio de planalto, com fortes corredeiras e pequenas quedas d´agua, correndo encaixado na sua porção superior, e tornando-se menos veloz e turbulento na porção mais baixa, próxima à desembocadura na margem esquerda no

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[1] Ruocco, A. M. C., 2014. Impacto da construção de Pequenas Centrais Hidrelétricas sobre a comunidade de macroinvertebrados bentônicos associados à ambientes de pedrais: um estudo de caso no rio Sapucaí-Mirim (SP). Dissertação de mestrado. PPG Zoologia. IBB UNESP Botucatu
Souza, D. F. 2014. Interferências dos fechamentos de PCHs sobre a assembleia de peixes do Rio Sapucaí-Mirim, SP. Dissertação de mestrado. PPG Zoologia. IBB UNESP Botucatu
Zago, A.C. Biodiversidade dos helmintos parasitas de peixes provenientes do Rio Sapucaí-Mirim, Estado de São Paulo, Brasil. Tese de doutorado em andamento. PPG Zoologia. IBB UNESP Botucatu
Franceschini, L. Biodiversidade de helmintos de peixes da família Loricariidae (Teleostei: Siluriformes) procedentes do Rio Sapucaí- Mirim, Brasil. Tese de doutorado em andamento. PPG Zoologia. IBB UNESP Botucatu.
Pessotto, M. A. Alterações limnológicas, com ênfase nas comunidades planctônicas, decorrentes da construção de Pequenas Centrais Hidrelétricas: um estudo de caso no rio Sapucaí-Mirim (SP). Tese de doutorado em andamento. PPG Zoologia. IBB UNESP Botucatu.
Suiberto, R. M. & Nogueira, M.G. Identificação de habitats críticos de desova e berçários naturais de peixes em rios barrados por Pequenas Centrais Hidrelétricas (PCHs): um estudo de caso no rio Sapucaí-Mirim (SP). Projeto RHAE/CNPq em andamento.

reservatório da UHE de Porto Colômbia no médio rio Grande. O Sapucaí-Mirim tem como principais afluentes os rios Santa Bárbara, dos Bagres, Salgado, Pontal e Sete Lagoas (Paiva, 1982).

Este rio é parte integrante da Unidade Hidrográfica de Gerenciamento de Recursos Hídricos 08 (UHGRH) (Fig. 2), segundo a promulgação da Lei N° 9.034/94, de 27/12/1994, que dispôs sobre o Plano Estadual de Recursos Hídricos.

Entre as cinco pequenas centrais hidrelétricas em operação na bacia do rio Sapucaí-Mirim, duas, de desvio de canal, pertencem à Companhia Paulista de Força e Luz (CPFL) – Dourados e São Joaquim. As demais foram construídas no canal do rio, sendo duas da empresa Duke Energy – PCH-Palmeiras e PCH-Retiro, e uma da Central Elétrica Anhanguera S.A – PCH Anhanguera. Com intuito de conectar novas usinas ao sistema existente e melhorar os atuais níveis de suprimento energético da região, outros seis projetos no mesmo rio encontram-se em processo de licenciamento (ANEEL, 2012).

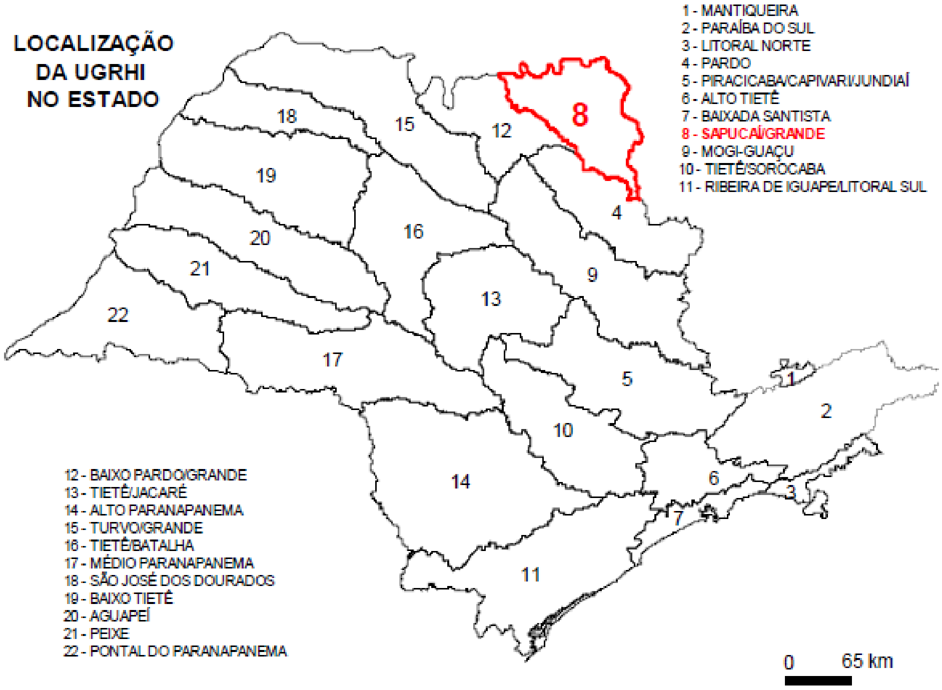


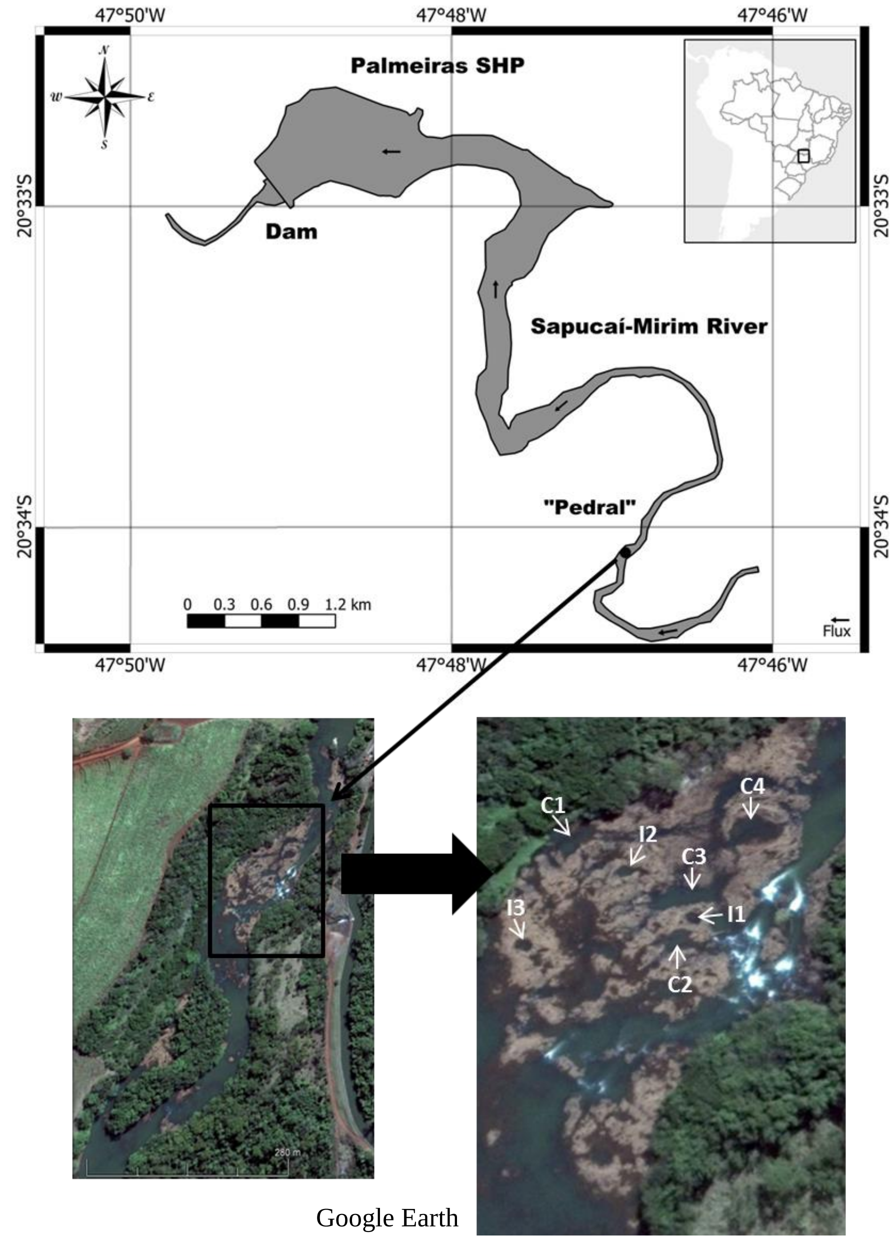
Figura 2. Unidade Hidrográfica de Gerenciamento de Recursos Hídricos (UGRHI) 08.

Pedral

O ambiente de pedral estudado localiza-se a montante da PCH Palmeiras (20°34'34,1"S 47°47'06,5"W), município de São Joaquim da Barra/SP (Fig. 3). Este pedral está fora da área de influência direta do empreendimento, apresentando assim uma dinâmica natural de flutuação no nível da água.

Poças

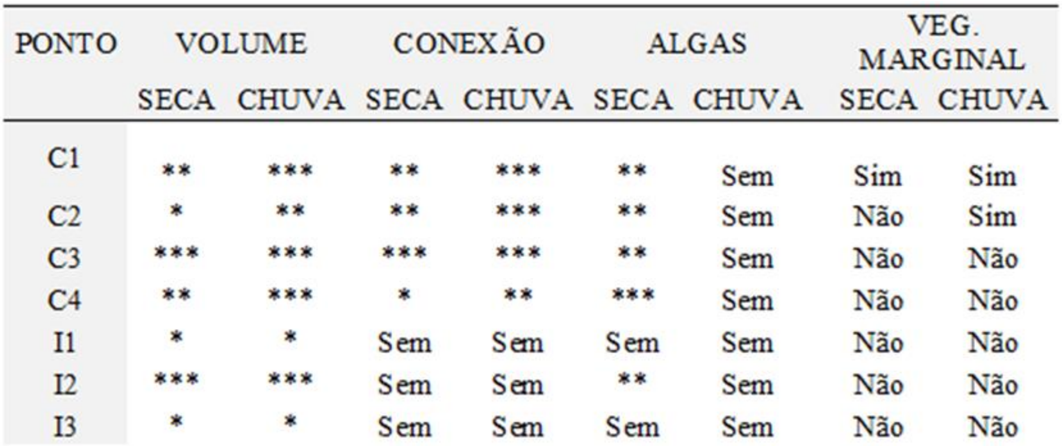
Foram selecionadas quatro poças com conexão com o fluxo do rio e três isoladas (Fig. 3), elas apresentam variações em suas características físicas: volume de água, grau de conexão com outros habitats, quantidade de algas filamentosas, entorno e presença de vegetação herbácea terrestre em contato com a água (Tab. 1 e 2).



Google Earth

Figura 3. Localização da área de estudo no rio Sapucaí-Mirim com destaque para as sete poças amostradas. C = conectadas com o fluxo do rio; I = isoladas.

Tabela 1. Características físicas das sete poças amostradas na estação seca e chuvosa em um pedral do rio Sapucaí-Mirim, Bacia do rio Grande SP/MG.



PONTO	VOLUME		CONEXÃO		ALGAS		VEG. MARGINAL	
	SECA	CHUVA	SECA	CHUVA	SECA	CHUVA	SECA	CHUVA
C1	**	***	**	***	**	Sem	Sim	Sim
C2	*	**	**	***	**	Sem	Não	Sim
C3	***	***	***	***	**	Sem	Não	Não
C4	**	***	*	**	***	Sem	Não	Não
I1	*	*	Sem	Sem	Sem	Sem	Não	Não
I2	***	***	Sem	Sem	**	Sem	Não	Não
I3	*	*	Sem	Sem	Sem	Sem	Não	Não

Volume: * = < 50 m³, **= 50 a 100 m³,***= >100m³; Conexão: * = pouca conexão, ** = média conexão, *** = alta conexão; Algas: * = quantidade baixa, ** = quantidade média, *** = quantidade alta; C = conectada e I = isolada.

Tabela 2. Imagens das sete poças amostradas na estação seca e chuvosa em um pedral do rio Sapucaí-Mirim, Bacia do rio Grande SP/MG.

POÇA	SECA	CHUVA
C1		
C2		
C3		
C4		
I1		
I2		
I3		

C = conectada e I = isolada.

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Capítulo 1

Knickzones – river bed rocky stretches: a threatened unknown environment

Eduardo Meneguzzi Brambilla, Ana Maria Cirino Ruocco, Marcos Gomes Nogueira

Universidade Estadual Paulista (UNESP) - Campus de Botucatu, Instituto de Biociências de Botucatu, Departamento de Zoologia. Distrito de Rubião Júnior, s/n – CEP: 18618-970 – Botucatu – SP. eduardo.brambilla@gmail.com, +55 14 3880 0630

Abstract

There is a gap of ecological knowledge of particular river stretches dominated by continuous rocky substrates, geologically named knickzones. These are structurally complex macrohabitats formed by dynamic interactions among pools, rapids and runs. In this study, knickzones are conceptualized and characterized based on a case study in Sapucaí-Mirim River, State of São Paulo, Brazil. Our data showed a remarkable influence of the distinct habitats and flood conditions (dry and rainy) on the limnological features. A clear discrimination in terms of habitat type and seasonality was demonstrated through the PCA analysis (69.9% explicability of data variability). Comparisons among habitats showed that pools, with distinct degrees of connectivity with the river flow, exhibited higher amplitude of variation for most limnological parameters, such as pH, dissolved oxygen, temperature, oxide reduction potential, electric conductivity, total nitrogen and organic suspended solids. Some of these variables are highly influence by internal metabolism. The variety of conditions in this restricted area supports the colonization of species with different ecological requirements, contributing for the regional biodiversity maintenance. Strategies for environmental conservation are strongly required because knickzones are in eminent threat by construction of hydropower plants.

Keywords: “pedral”, limnology, basaltic substrate, pools, runs, rapids

Introduction

The description and ordination of geographic habitats and landscapes is one of the ancient roots of the distinct areas of Ecology (Margalef, 1980). The classical typology studies decisively influenced the development and consolidation of Limnology, as a particular field of the scientific knowledge (Margalef, 1983).

Typology is conceptual, based upon *a priori* subjective judgment of class definitions and boundaries (Schmera & Baur, 2011). This approach results in an important framework for conservation planning and biodiversity management (Hawkins & Vinson, 2000; Eros, 2007) in a baseline for effective and reliable communication between distinct disciplines and non-specialists (Turak & Coop, 2008) as well as a reference for the scientific research.

Descriptive studies have been intensively used for theoretical and practical purposes, such as the classification of the Amazonian rivers (Sioli, 1950 *apud* Esteves, 2011), the typology of the southeast Brazilian reservoirs (Tundisi, 1981, 1983) and temperate streams (Allan, 1995). However, some distinctive aquatic environments have not been properly considered.

This is the case of particular river stretches dominated by continuous rocky substrates, geologically named as knickzones, widely distributed mainly in the Brazilian territory, and popularly known as “pedrais”.

This macrohabitat is formed by three types of basalt litho-structural zones: vesicular-amygdaloidal basalts, massive basalts with horizontal joints and massive basalts with a predominance of vertical joints. Some elements operate together to generate these morphologies and adjust the evolution of the profile of the river such as jointing style, tectonic fractures, faults, different erosion processes and magnitude of discharge. The combination of these elements is significantly influenced by tectonic control over the river course (Lima & Binda, 2013).

One of the reasons that motivated this study is the fact that these natural rocky platforms are propitious sites for hydroelectric dams axis positioning. Considering the ongoing energetic policy, with the perspective of construction of hundreds of new hydropower plants in the country (1871 projects in distinct stages of implementation – ANEEL, 2013), it can be assumed an eminent threat for this kind of habitat. This problem was recently evidenced during the controversial construction of the huge Belo Monte hydropower complex, with an installed capacity of 11,233 MW, which is located in the Xingu River (Amazon Basin) (Winemiller et al., 2016).

In this context, it is imperative to supply the lack of information about this kind of habitat and its role for the biodiversity maintenance. Therefore, the study aims to contribute for the physical and limnological characterization, conceptualization and diffusion of the knickzones importance as an ecological macrohabitat, based on a case study carried out in the Sapucaí-Mirim River, State of São Paulo, Brazil.

Material and Methods

Study area

The study area is located in Sapucaí-Mirim River, a tributary of Grande River basin, São Paulo/Minas Gerais States, Brazil (Fig. 1). Based on recent satellite images at least eight knickzones can be still be recognized in this river. The selected knickzone (20°34'34.1"S

47°47'06.5"W) is located in the upstream zone of Palmeiras small hydropower plant (SHP), but beyond its operational influence, thus, presenting a natural dynamic of the river flow.

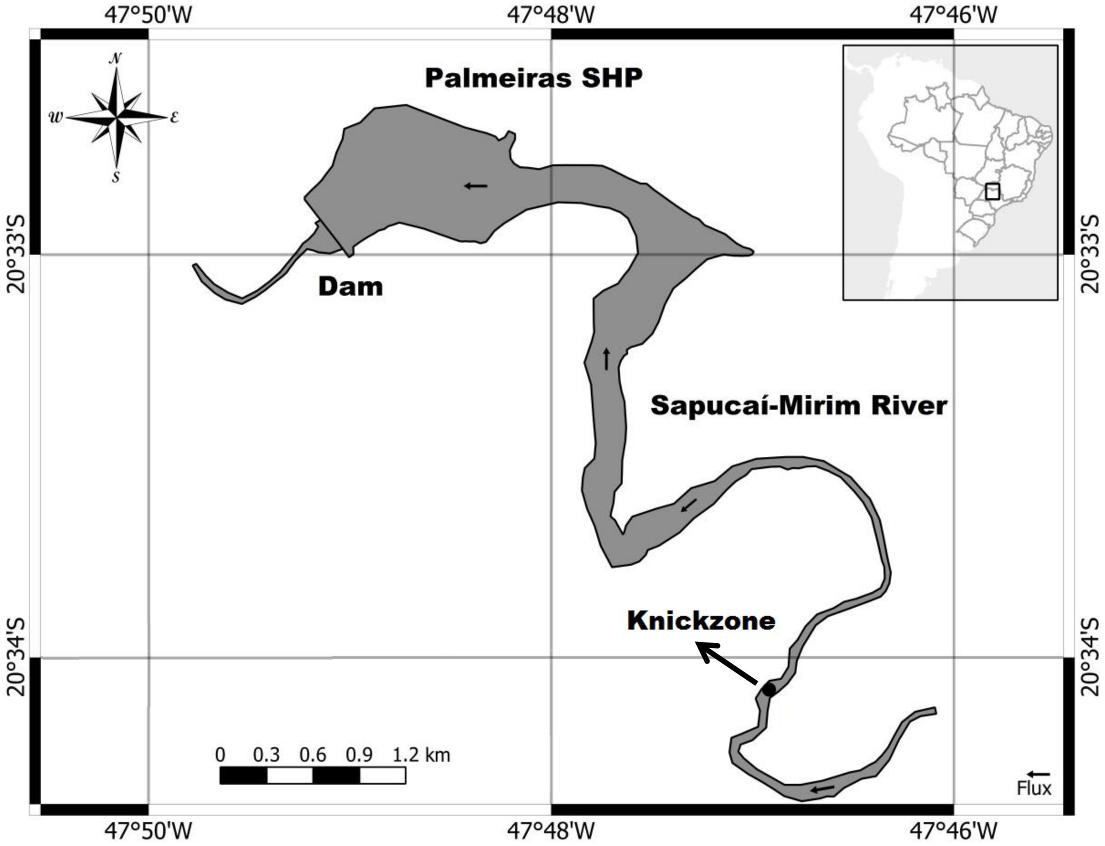


Fig. 1 Geographic positioning of the study area – a knickzone in Sapucaí-Mirim River, Southeast Brazil.

Data on precipitation for the period 2012, 2013, 2014 and 2015 were provided by the INMET (National Institute of Meteorology) nearest station (Franca municipality about 47 km) and by the sugar cane processing plant named Alta Mogiana (station about 14 km). Palmeiras dam outflow was obtained from the energy company (Duke Energy Brasil) for the same period.

Sampling and analyses

Samplings were performed in three different habitats – pools, runs and rapids, under dry and rainy conditions during three consecutive years (September/2012 – dry condition; May/2013 – rainy condition; June/2014 - dry condition and December/2014 - rainy condition). Three different runs and seven different pools were selected for the study. In case of pools, four were connected with the river flow, and three were isolated. Six different rapids were sampled only in the dry condition, due to the access impossibility during high flow periods.

The maximum length, maximum width and maximum depth dimensions were measured with graduated tape and ruler, for pools volumes calculation. For rapids and runs, the water velocity was measured with a Flowatch current meter or through the time displacement of a floating object.

Surface measurements of temperature, dissolved oxygen (DO), conductivity, oxide reduction potential (ORP), total dissolved solids (TDS) and pH were obtained using a daily calibrated Horiba probe (U-52). Simultaneously, water samples were collected for determination of total nitrogen and total phosphorus (Strickland & Parsons, 1960; Mackreth et al., 1989; Valderama, 1981), total solids (TS) (APHA, 2005), organic suspended solids (OSS), inorganic suspended solids (ISS), total suspended solids (TSS) (*sensu* Cole, 1979), and chlorophyll-*a* (Golterman et al., 1978).

After checking the non-normality of data, a Spearman correlation analysis was performed between monthly accumulated rain precipitation and daily mean outflow per month for the definition of dry and rainy seasons. Another Spearman correlation analysis was performed between daily values of rain precipitation and outflow in the same day, one day, two days and three days after precipitation for the evaluation of variation in outflow by rainy precipitation.

The sampling sites were arranged in seven groups: isolated pools in dry condition (PDI), connected pools in dry condition (PDC), isolated pools in rainy condition (PRI), connected pools in rainy condition (PRC), runs in dry condition (RuD), runs in rainy condition (RuR) and rapids in dry condition (RaD). The mean values differences were tested by a one way ANOVA. When differences were detected, the Tukey test was used for significance analyses ($p < 0.05$). Previously, Kolmogorov Smirnov test was used to check the data normality.

For data ordination and identification of temporal and spatial tendencies, a principal components analysis (PCA) was performed after data transformation using log x + 1 (except pH).

Results

Knickzone ecological concept

Knickzone is a geologic name used for denomination of shallow stretches located in upstream and middle river basins, which are characterized by large rock outcrops forming a complex of habitats composed by rapids, runs and pools with distinct magnitudes (Fig. 2a). The substrate immersion or exposition condition is highly variable in terms of volume and level, even seasonally (dry and rainy seasons) or short term variation (occasional storm events and dry spells) (Fig. 3).

Rapids are distributed discontinuously along the knickzone macrohabitat and are characterized by relatively narrow channels, with steep slopes and high turbulence, velocity, and water flow (Fig. 2b). Runs are continuous habitats, deeper than rapids, with lower turbulence and velocity (Fig. 2c). Finally, the pools, such as the rapids, are heterogeneously distributed, with distinct degrees of connectivity with the running waters (runs and rapids). The pools exhibit low or no turbulence, the water flow tends to zero and deepness is highly variable, as well as the limnological characteristics which can be strongly influenced by the internal metabolism due to intensive colonization of periphyton (filamentous algae), macro invertebrates and fish (Fig. 2d).

Fig. 2 General view of a knickzone (a) formed by rapid (b), run (c) and pool (d) habitats in Sapucaí-Mirim River, Brazil.

Fig. 3 Study area – knickzone of the Sapucaí-Mirim River, Brazil, during dry (a) (July/2010) and flood condition (b) (May/2013).

Fig. 4 shows the fluctuation of rain precipitation and river flow during the studied period. Both variables were positively correlated (r = 0.618; $p < 0.05$). The precipitation exhibits a well-marked seasonal pattern, with high volumes in summer and maximum peaks in December and January. Annual mean precipitation for the three year period was 1.454 mm.

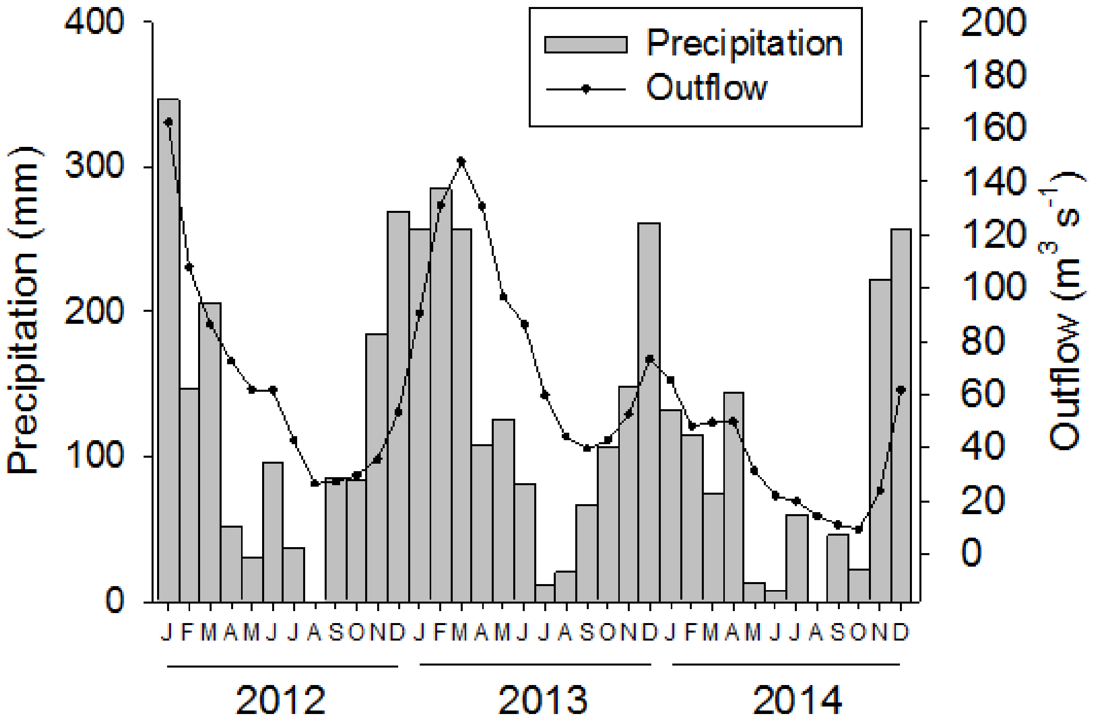


Fig. 4 Monthly accumulated rain precipitation in Franca meteorological station and daily mean outflow per month downstream Palmeiras dam in Sapucaí-Mirim River, Brazil.

Simultaneous daily values of river flow and rain precipitation along the rainy season - October 2014 to March 2015, are shown in Fig. 5. Higher correlation occurs two days after a precipitation event ($r = 0.422$; $p < 0.05$). A comparison between visits, satellite images and river flow suggest that this particular knickzone is totally under water when river flow values reach 90 $m^3 s^{-1}$. Between October 2014 and March 2015 the knickzone exhibited this condition during 15 days.

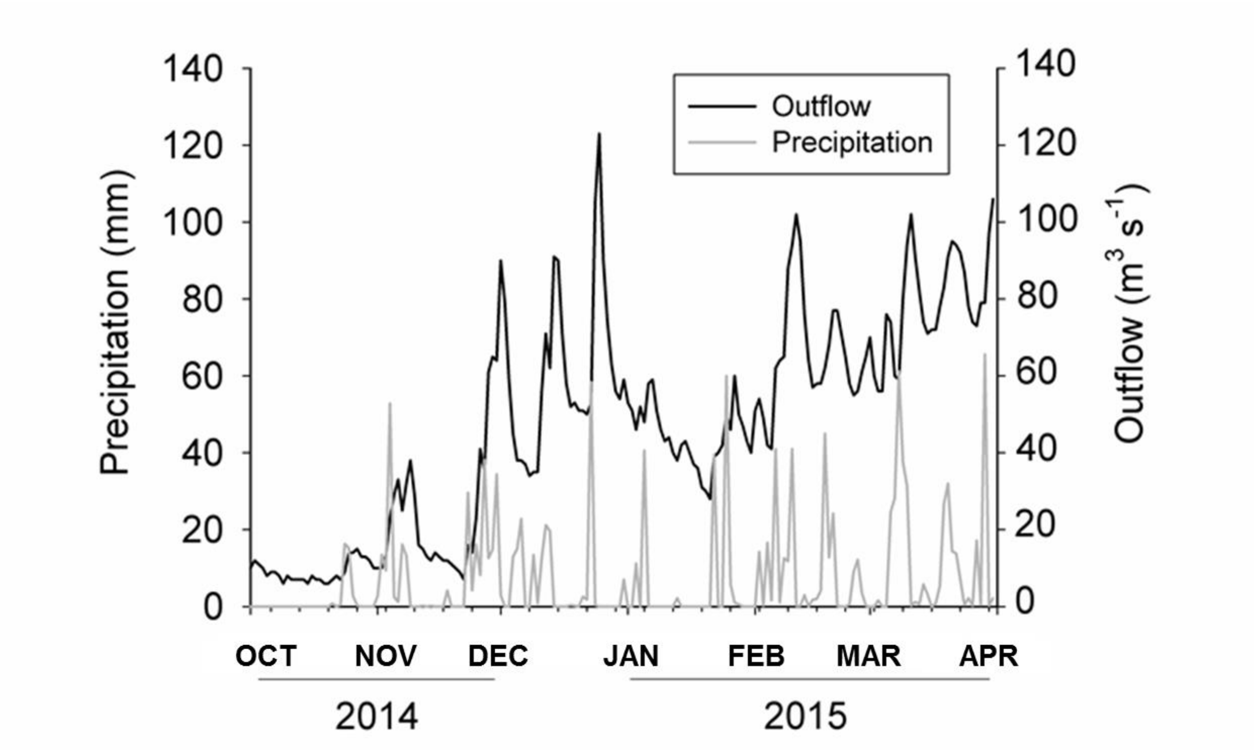


Fig. 5 Daily values of rain precipitation (Alta Mogiana sugar cane plant station) and outflow (downstream Palmeiras dam) in Sapucaí-Mirim River, Brazil, along the rainy season (October 2014 to April 2015).

Limnological analyses

The amplitude of variation for all limnological measurements was higher in pools compared to rapids and runs, except for total phosphorus. Conversely, the runs were more conservative habitats, with lower variability. For comparison among habitats data obtained in dry conditions (rapids were not accessed in rain conditions) are presented in Table 1.

Table 1 Environmental variables (maximum and minimum values) for each type of habitat in the dry condition.

VARIABLES	RAPIDS (n=6)	RUNS (n=3)	POOLS (n=7)
Length (m)	3.0 – 10.5	-	3.2 – 31.7
Width (m)	1.8 – 3.5	-	4.6 – 10.5
Depth (m)	0.1 – 0.55	-	0.3 – 1.5
Volume (m^3)	-	-	5.9 - 200.3
Water velocity (m s^{-1})	0.4 - 2	0.7 - 0.8	-
Water temperature (ºC)	17.9 - 19.3	22.4 - 22.8	19.4 - 24.2
pH	7.1 - 7.8	7.1 - 7.2	7.0 - 9.1
ORP (mV)	181.0 - 222.0	264.0 - 272.0	68.0 - 202.0
Conductivity (µS cm^{-1})	68.0 - 70.0	94.0 - 94.0	65.0 - 96.0
Turbidity (NTU)	8.6 - 269.0	11.3 - 17.5	1.9 - 37.5
DO (mg L^{-1})	8.8 - 12.8	8.8 - 10.0	5.7 - 14.7
DO (%)	97.5 - 140.9	104.3 - 117.8	67.8 - 164.3
TDS (mg L^{-1})	44.0 - 46.0	61.0 - 61.0	42.0 - 63.0
TSS (mg L^{-1})	2.9 - 7.2	5.0 - 5.7	1.2 - 8.1
ISS (mg L^{-1})	2.0 - 5.2	3.4 - 4.1	0.2 - 8.1
OSS (mg L^{-1})	1.0 - 2.0	1.5 - 1.6	1.0 - 6.0
TS (mg L^{-1})	54.0 - 66.0	64.0 - 70.0	44.6 - 67.0
Total phosphorous (µg L^{-1})	13.2 - 74.1	19.7 - 20.4	14.1 - 59.2
Total nitrogen (µg L^{-1})	1649.0 - 2235.5	1797.0 - 2176.0	846.0 - 2055.0
Chlorophyll-*a* (µg L^{-1})	1.0 - 8.0	0.5 - 0.5	0.7 - 9.9

n = number of sampling habitats; “-“ = It does not apply.

Most limnological measurements were statistically different among habitats ($p < 0.05$), except for total solids and total phosphorus (Table 2). Higher water temperature occurred in the pools during the rainy condition and lower values were observed in the rapids (Fig. 6a). Connected pools during dry condition exhibited higher pH values opposite to runs in the rainy condition (Fig. 6b). Lower ORP values occurred in the connected pools during dry condition and higher in pools (connected and isolated) and runs during the rainy condition (Fig. 6c). Lower values of total dissolved solids occurred in pools and runs during the rainy condition (Fig. 6d). For total nitrogen higher values were observed in the dry condition for connected pools, rapids and runs (Fig. 6e).

In terms of electric conductivity higher values were measured in runs and isolated pools in dry condition contrasting to pools (isolated and connected) and runs in rainy condition (Fig. 6f). Isolated pools in dry condition were the least turbid habitat different from connected pools and runs in the rainy condition (Fig. 6g). Runs and connected pools in dry condition, as well as rapids (only sampled in dry condition), were the most oxygenated habitats (Fig. 6h). Higher concentrations of total suspended solids in the runs during rainy condition contrasted with low values in isolated pools, rapids and runs during dry period (Fig. 6i). Remarkable higher values of inorganic suspended solids were observed for pools and runs in the rainy condition (Table 2). For organic suspended solids lower mean values occurred in rapids and runs and higher in connected pools, both during dry conditions (Table 2). Chlorophyll-*a* higher concentration was measured in isolated pools during dry condition and the lowest value in runs during the same period (Table 2).

Table 2 Mean, standard deviation and statistical similarity (same letter) for environmental variables measured in distinct habitats of a knickzone in Sapucaí-Mirim River, Brazil.

VARIABLES	POOL				RAPID	RUN	
	PDI	PDC	PRI	PRC	RaD	RuD	RuR
Water temperature (°C)	21.9^{a}	20.9^{a}	28.5^{b}	27.2^{b}	18.7^{c}	22.5^{a}	20.1^{ac}
	(1.5)	(1.7)	(2.2)	(0.6)	(0.5)	(0.2)	(0.0)
pH	7.3^{a}	8.5^{b}	7.4^{a}	7.2^{a}	7.4^{a}	7.2^{a}	6.0^{c}
	(0.3)	(0.3)	(0.1)	(0.4)	(0.3)	(0.1)	(0.1)
ORP (mV)	188.0^{c}	94.5^{d}	319.7^{a}	322.8^{a}	206.8^{bc}	266.7^{ab}	325.7^{a}
	(12.2)	(23.6)	(6.5)	(14.4)	(15.6)	(4.6)	(3.5)
Conductivity (µS cm^{-1})	82.7^{ab}	74.0^{a}	56.3^{c}	57.8^{c}	69.2^{a}	94.0^{b}	57.3^{c}
	(15.9)	(2.6)	(1.5)	(0.5)	(0.8)	(0.0)	(0.6)
Turbidity (NTU)	6.8^{a}	18.4^{ab}	36.8^{ab}	52.6^{a}	55.5^{ab}	13.4^{ab}	48.8^{a}
	(4.2)	(16.6)	(14.5)	(17.3)	(104.6)	(3.6)	(1.3)
DO (mg L^{-1})	6.6^{ab}	11.9^{c}	6.5^{a}	7.0^{ab}	10.8^{c}	9.3^{bc}	9.1^{abc}
	(0.8)	(2.7)	(0.7)	(0.3)	(1.9)	(0.6)	(0.3)
TDS (mg L^{-1})	53.7^{ab}	48.0^{a}	36.7^{c}	37.8^{c}	45.0^{a}	61.0^{b}	37.3^{c}
	(10.7)	(1.7)	(0.6)	(0.5)	(0.6)	(0.0)	(0.6)
TSS (mg L^{-1})	4.1^{a}	11.8^{a}	18.6^{bc}	18.8^{c}	4.5^{a}	5.3^{ab}	25.1^{c}
	(3.6)	(18.0)	(10.8)	(3.3)	(1.6)	(0.4)	(3.6)
ISS (mg L^{-1})	1.0^{b}	1.5^{ab}	14.6^{cd}	15.2^{c}	3.1^{a}	3.7^{ad}	19.5^{c}
	(1.0)	(0.4)	(8.8)	(2.5)	(1.3)	(0.4)	(3.1)
OSS (mg L^{-1})	3.1^{abcde}	10.2^{ace}	3.9^{bce}	3.7^{bd}	1.4^{a}	1.6^{acde}	5.6^{b}
	(2.6)	(17.8)	(2.0)	(0.8)	(0.4)	(0.1)	(0.6)
TS (mg L^{-1})	57.3^{a}	58.1^{a}	70.0^{a}	69.5^{a}	60.3^{a}	67.0^{a}	66.0^{a}
	(8.4)	(9.3)	(3.6)	(4.2)	(4.5)	(3.0)	(10.4)
Total phosphorous (µg L^{-1})	31.3^{a}	18.8^{a}	26.7^{a}	23.2^{a}	27.2^{a}	20.0^{a}	17.0^{a}
	(24.4)	(2.8)	(3.8)	(8.0)	(23.3)	(0.4)	(0.4)
Total nitrogen (µg L^{-1})	1045.4^{a}	1803.4^{b}	1102.0^{a}	1170.6^{a}	1883.6^{b}	1950.0^{b}	588.6^{c}
	(216.7)	(236.3)	(199.2)	(67.2)	(234.5)	(199.8)	(24.7)
Chlorophyll-*a* (µg L^{-1})	6.2^{a}	2.1^{ab}	2.1^{ab}	2.4^{ab}	3.1^{ab}	0.5^{b}	2.4^{ab}
	(4.7)	(2.1)	(0.0)	(1.2)	(2.8)	(0.0)	(0.4)

PDI = isolated pools in dry condition; PDC = connected pools in dry condition; PRI = isolated pools in rainy condition; PRC = connected pools in rainy condition; RuD = runs in dry condition; RuR = runs in rainy condition and RaD = rapids in dry condition.

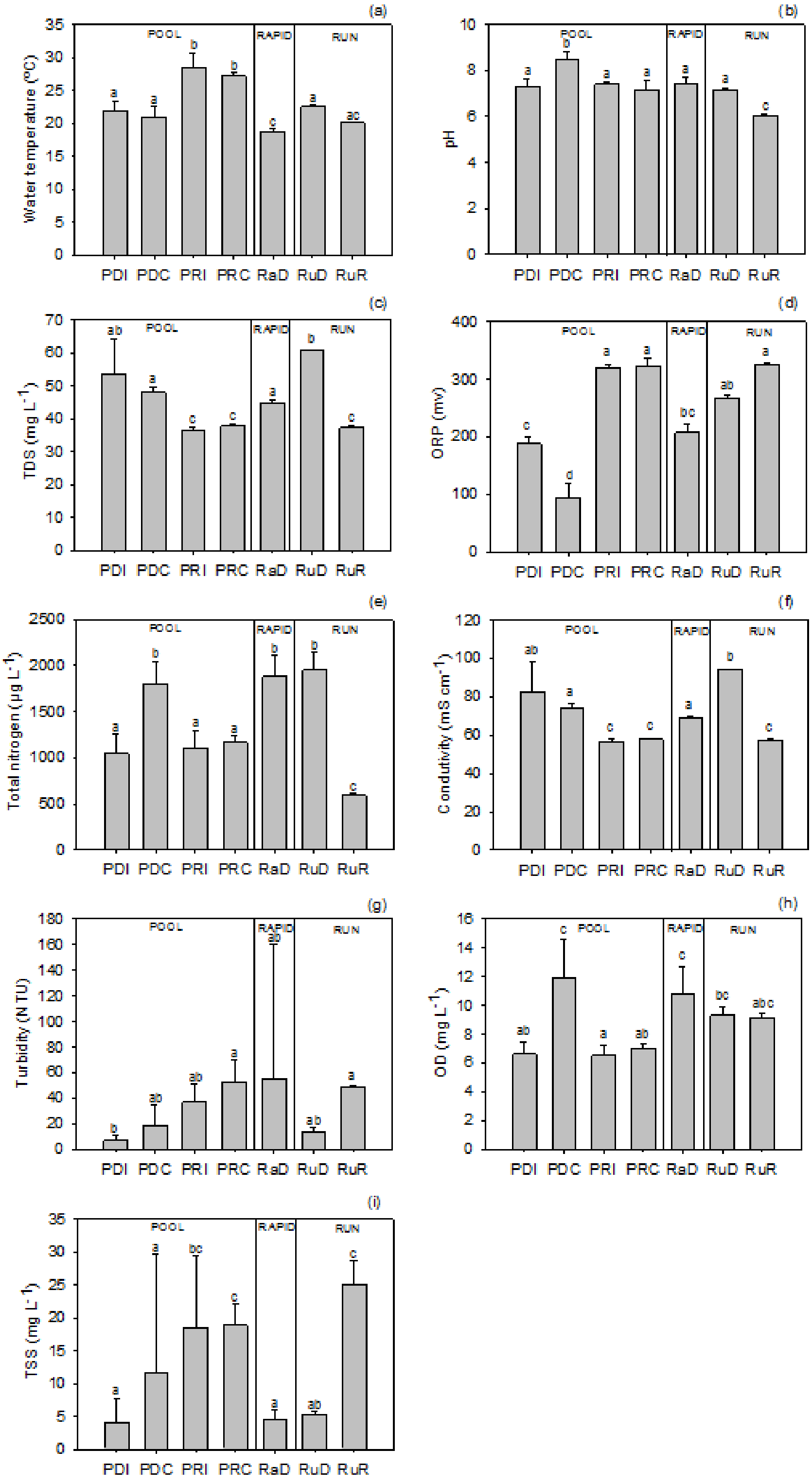
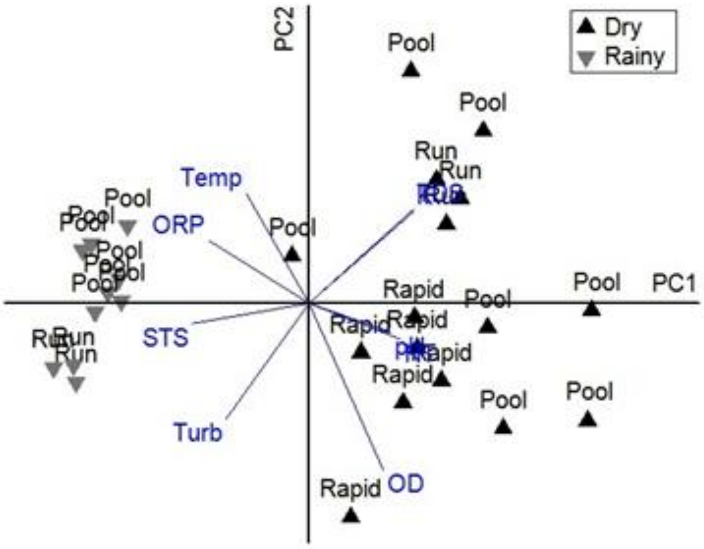


Fig. 6 Mean, standard deviation and statistical similarity (same letter) for (a) water temperature, (b) pH, (c) ORP, (d) TDS, (e) total nitrogen, (f) electrical conductivity, (g) turbidity, (h) dissolved oxygen, (i) total suspend solids among the sampling sites of a knickzone in Sapucaí-Mirim River, Brazil. PDI = isolated pools in dry condition; PDC = connected pools in dry condition; PRI = isolated pools in rainy condition; PRC = connected pools in rainy condition; RuD = runs in dry condition; RuR = runs in rainy condition and RaD = rapids in dry condition.

The PCA (Fig. 7) explained 69.9% of data variability, considering the PC1 (54.4%) and PC2 axis (15.5%). The seasonal influence was clearly evidenced by the PC1 axis. Rainy condition was plotted on the negative side associated with high values of turbidity, total suspend solids, oxide reduction potential and temperature. The dry condition, on the positive side, was positively associated with dissolved oxygen, pH, conductivity, total dissolved solids and total nitrogen.

In the rainy condition the habitats distribution is more aggregated than in the dry period. Pools were grouped on the positive side of PC2 axis associated with high values of temperature and oxide reduction potential and runs were grouped on the negative side associated with high values of turbidity and total suspend solids. During the dry condition habitats did not exhibit a well-defined distribution related to this axis.



Variable	PCA 1	PCA 2
Watertemperature	-0,227	0,397
pH	0,296	-0,104
ORP	-0,36	0,225
Conductivity	0,377	0,331
Turbidity	-0,299	-0,415
DO	0,269	-0,602
TDS	0,375	0,338
TSS	-0,421	-0,073
Total nitrogen	0,332	-0,13
Eigenvalues	4,9	1,4

Fig. 7 Principal components analysis showing the distribution of the sampling sites in the rainy and dry condition, according to the limnological variables.

Discussion

Despite the fact that the knickzones are widely distributed in upper and middle river stretches in the neotropics, especially in plateau conditions, there is a surprisingly lack of ecological information on this kind of macrohabitat. This fact could be partially explained by the inherent difficulties to access this environment, including total impossibility of safe navigation, and by the fact that it is a mosaic of distinct habitats. Knickzones are also different when compared with certain habitats such as streams and temporary pools. Riffles, runs and pools in streams ecosystems have a sequential distribution, in a continuous longitudinal organization (Allan, 1995). In case of inland temporary pools the location is generally apart from main water bodies, like river channels. Therefore, the possibilities for comparisons of our results are limited, basically restricted to the literature on lateral river habitats and their interactions with the central channel.

The knickzones exhibit a unique complex structure due to the occurrence of distinctive kind of habitats: pools, rapids and runs of different magnitudes and degree of connectivity, distributed in relatively short river stretches. The limnological characteristics in knickzones are highly influenced by the seasonality – especially the alternation between dry and rainy periods. The river flow is promptly influenced by the rain precipitation.

In the rainy period the similarity between habitats is expected to be higher because of considerable exchanges of water, sediment, nutrients, and organisms. The opposite occurs in the dry period when the homogenization process is less effective with a higher differentiation among habitats. This dynamics is evidenced when compared river channels and lateral ecosystems such as floodplains and lagoons (Neiff, 2001;

Carvalho et al., 2001; Rodrigues et al., 2002; Domitrovic, 2003; Britto, 2006; Thomaz et al., 2007; Granado & Henry, 2012; Ferrareze et al., 2014).

The knickzone macrohabitat exhibited a high limnological variability. From 17 analyzed variables only the total solids and total phosphorus did not varied significantly among the distinct habitats.

The pools exhibit higher amplitude of variation in terms of limnological characteristics when compared to runs and rapids. This is explained by their particularities, such as small volume and low water renovation, but also by the considerable physical and biotic variability features (e.g. surface area; volume; degree of connection with adjacent running channels; presence of marginal vegetation; quantity of periphyton and fish biomass).

In addition to the predictable seasonal changes the knickzone habitats are exposed to erratic weather variation – sporadic short term events of significant precipitation and dry spell. Therefore, this environment has a high disturb frequency. For more confined habitats (pools), certainly the hourly variation (nictemeral), especially in warmer periods plenty of sunshine, is also significant and would justify an additional investigation.

Particularly in case of freshwater rock pools the highly variable environmental conditions in such small restricted water volumes, in addition to exposition of seasonal an erratic weather, require high stress tolerance of the biota, with adaptations for surviving the dry phase such as the production of resistant stages and active emigration followed by quick re-colonization (Jocque et al., 2010).

For characterization purposes, it is important to note that each limnological factor can vary in different ways for each particular habitat and time period.

Among habitats the higher temperatures were attained in pools during the rainy condition, which is coincident with the warmer period (late spring and summer), due to the smaller volume and low exchange rate with running waters and atmosphere. The lowest temperature occurred in rapids, habitat with the highest water flow/velocity, in the dry condition (autumn and late winter).

Pools, under dry condition, exhibited higher values of pH, organic suspended solids and oxygen values. This is probably associated to the intense periphyton colonization, resulting in high photosynthesis rate and organic detritus accumulation. In some lateral river ecosystem and lagoons, the oxygen reduction in the rainy condition is associated due to the decomposition process of organic matter coming from the adjacent plain (Granado & Henry, 2012). This process may also occur in knickzone pools.

In general ORP is higher in the rainy season (pools and runs), probably due to the entrance of allochthonous material (high turbidity) from catchment, as already mentioned. An opposite tendency was observed for oxygen, which reached higher values during the dry condition in connected pools and rapids.

The lowest electrical conductivity of water (pools and runs), TDS (pools and runs) and total nitrogen (runs) in the rainy condition can be explained by the dilution effect. This pattern also occurs regionally in river lateral lagoons (Martins & Henry, 2004; Granado & Henry, 2012; Ferrareze et al., 2014).

Regarding turbidity, total and inorganic suspend solids, higher values occurred in rainy condition (mainly in connected pools and runs), while lower values (except for rapids due excessive turbulence) were seen in dry period (isolated pools). High loads of external material from the drainage basin are introduced into the river system during rains, especially in habitats with more intensive water exchange. Similar findings are reported for floodplains (Oliveira & Calheiros, 2000; Rodrigues et al., 2002; Taniguchi et al., 2004, 2005; Alho, 2008).

The chlorophyll-*a* distribution was contrasting between pools and runs. Higher values occurred in isolated pools (phytoplankton colonization) and lower in runs (washout effect), both during the dry condition. The increase of chlorophyll-*a* during the dry period is a common pattern for large rivers and lakes of tropical/subtropical floodplains (Bonetto, 1986; Welcome, 1986; Garcia de Emiliani, 1990; Neiff, 1990; Carvalho et al., 2001), but this seems not to be applied for all knickzone habitats.

The wide limnological variability observed in the knickzone macrohabitat results from the inherent high complex structure with distinct interacting habitats: pools, runs and rapids, and an intense functional dynamics at distinct temporal scales – seasonal and short term fluctuations in flood/exposition conditions. Comparisons with limnology of non knickzone stretches, which predominates in the river, could also be a strategy to highlight the particularities of this kind of macrohabitat.

The remarkable knickzone heterogeneity certainly promotes conditions for the colonization of species with different ecological requirements, contributing for a great biodiversity in a proportional small area of a river. As a consequence of this hypothesis this environment should be considered as potentially important for regional biodiversity conservation.

Efforts must be undertake in order to provide the scientific ecological knowledge of this kind of macrohabitat – structure and functioning, especially due to the fact that knickzones are in eminent threat by construction of hundreds of hydropower plants all over the country.

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Capítulo 2

Importance of knickzones - river bed rocky stretches - for ichthyofauna conservation

Eduardo Meneguzzi Brambilla, Virginia Sanches Uieda, Marcos Gomes Nogueira

Universidade Estadual Paulista (UNESP) - Campus de Botucatu, Instituto de Biociências de Botucatu, Departamento de Zoologia. Distrito de Rubião Júnior, s/n – CEP: 18618-970 – Botucatu – SP.

eduardo.brambilla@gmail.com, +55 14 3880 0630

Abstract

In this study we characterized the ichthyofauna of a knickzone macrohabitat in Sapucaí-Mirim River (Southeast Brazil) and discussed about their importance for the maintenance of regional diversity of fishes. Samplings were performed in seven pools during rainy and dry conditions. The ichthyofauna of this knickzone was composed by 23 species, 82% are of small size and five of them represent the first report in this sub-basin. Due to its small area (0.03 km²) it can be assumed that the knickzone sustain a great specific richness, with 23% of Sapucaí-Mirim River total ichthyofauna. The high physical heterogeneity and the strong influence of seasonality and episodic climatic events may be the main reasons for the great fish diversity maintenance. The presence of larvae and juveniles of several fish species also indicates the potential importance of this environment as a nursery area. The importance of knickzones for the regional diversity of fish fauna was demonstrated. The inclusion of knickzones in strategic plans for regional biodiversity conservation it is an immediate need because they are in eminent threat by construction of hydropower plants.

Keywords: “pedral”, fish, basaltic substrate, pools

Introduction

Composition and diversity of fish species is highly influenced by habitat heterogeneity (Winemiller et al., 2008). Local variation in habitat structure, such as water velocity, substrate characteristics, bathymetry, shelter, marginal vegetation, declivity (Gorman & Karr, 1978; Angermeier & Karr, 1983; Winemiller et al., 2008) and physical and chemical variables of water (Araújo et al., 2009), are factors that contribute to the habitat heterogeneity. This heterogeneity has been associated with spatial segregation among species, which is further influenced by selection of morphological specializations (Winemiller et al., 2008) that allow species coexistence and diversity maintenance.

Other attribute that influence on the composition and diversity of fish species is the seasonal hydrologic pulse, which is the main natural seasonal factor driving the dynamics of neotropical aquatic communities (Junk et al., 1989). The flood pulse increases the lateral connectivity among habitats (opportunity for dispersion), the physical space for colonizers and the availability of shelter and resources (Thomaz et al., 2007). As water level decreases, some habitats become isolated and the effect of biological interactions on fish communities become more intensive, resulting in fine segregation patterns (co-existence) or exclusion of some species (Fernandes et al., 2009; Ferrareze & Nogueira, 2011).

Aquatic environments that combine high habitat heterogeneity and intensive temporal dynamics are potentially important for biodiversity maintenance. The investigation and conservation of such areas should be considered as a priority (Sendacz & Monteiro Júnior, 2003).

In this context, it is important to distinguish the knickzones macrohabitats. These are shallow stretches of upland and mid-section rivers dominated by the presence of large rock outcrops creating a complex of habitats mainly composed by rapids, runs and pools of distinct magnitudes. The immersion condition of the substrate is highly variable in terms of volume and level, seasonally (drought and rain periods) and episodically (storm events and dry spells) (Chapter 1).

The threat of knickzones in Brazil, regionally named as “pedrais”, was recently evidenced by the controversial construction of the huge hydroelectric plant of Belo Monte, in Xingu River (Amazon Basin) (Winemiller et al., 2016). The geological substrate associated to the knickzones is technically appropriated for the location of river dams. Considering the presently large amount (hundreds) of hydropower plant projects in the country (http://www.aneel.gov.br/) and the lack of ecological information about this kind of macrohabitat, the aim of this work is to characterize the ichthyofauna of knickzones and discuss their importance for the regional diversity maintenance. For this purpose a knickzone macrohabitat in Sapucaí-Mirim River, SP, Brazil, was selected as a case study.

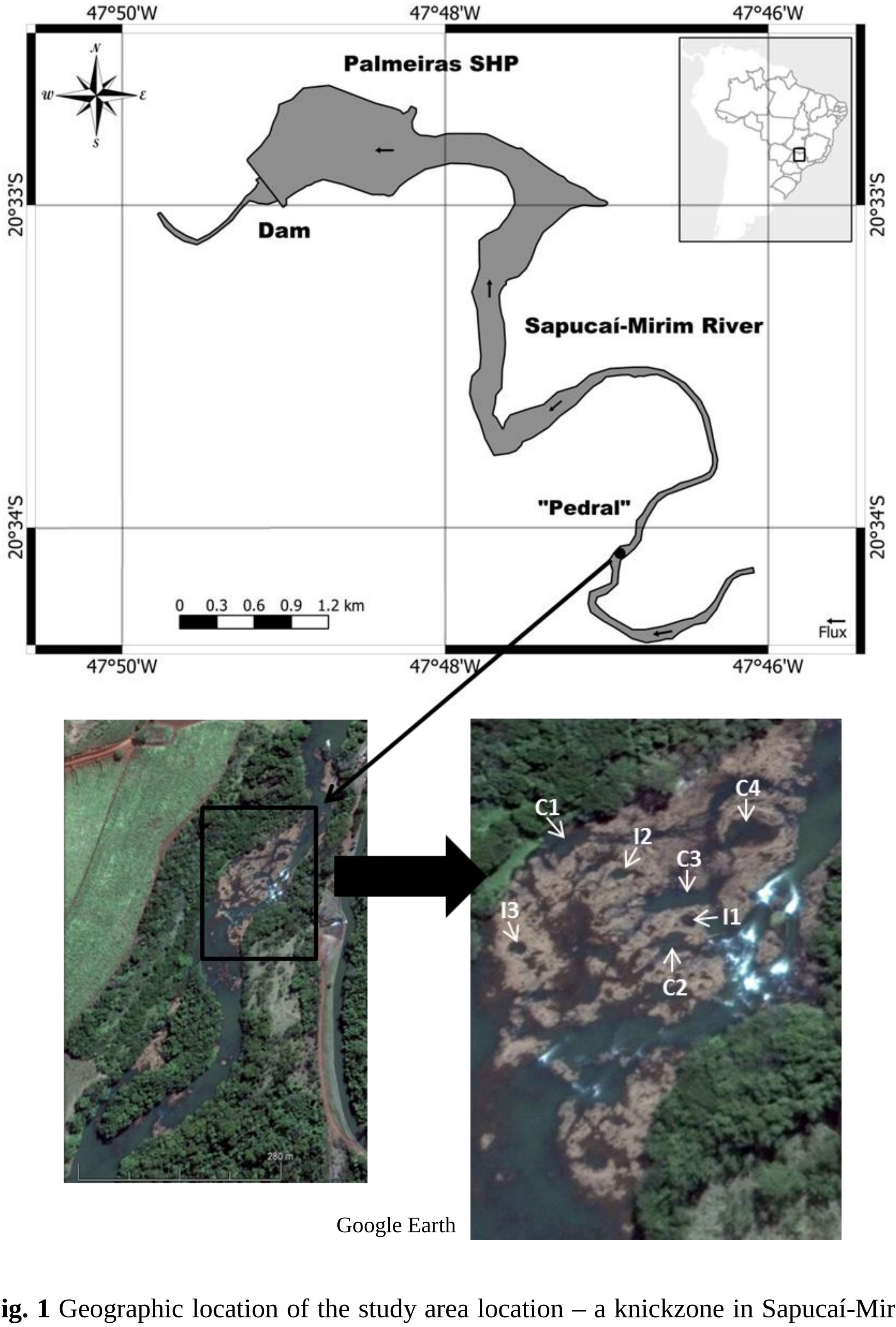
Material and Methods

Study area

The study area is located in Sapucaí-Mirim River, a tributary of River Grande basin, São Paulo/Minas Gerais States, Brazil (Fig. 1). Presently five small hydropower plant (SHP) are operating in this river, generating 70 MW, and another six potential sites are inventoried for future construction. Based on recent satellite images, at least eight knickzones can be recognized in this river. The selected knickzone (20°34'34.1"S 47°47'06.5"W) is in the upstream zone of Palmeiras SHP, but beyond its operational influence, thus, presenting a natural dynamic of the river flow (Fig. 1).

Sampling

Samplings were performed in seven different pools (Fig. 1) during the dry (June/2014) and rainy (December/2014) seasons (Fig. 2). Four selected pools were connected with the river flow and three were isolated.



Google Earth

Fig. 1 Geographic location of the study area location – a knickzone in Sapucaí-Mirim River, Southeast Brazil, with the positioning of the sampling habitats (pools). C = connected with river flow; I = isolated.

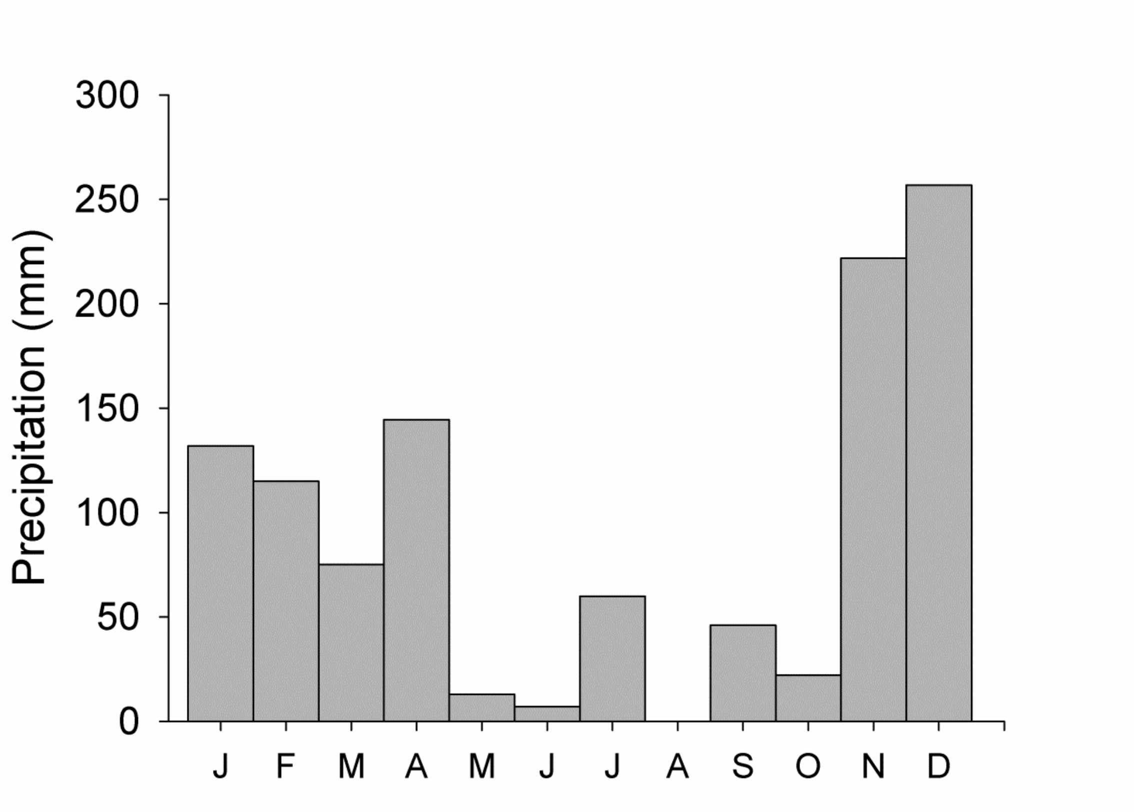


Fig. 2 Monthly rain precipitation in Sapucaí-Mirim basin, Brazil, during 2014.

In each pool it was applied a combination of several sampling methods in order to obtain an integrated and representative sample of the whole ichthyofauna community. It was used seine, sieve (mesh size 0.5 cm) and electrofishing. The sampling effort applied for each method was standardized for the distinct pools and both seasons. Sampled fish were immediately sacrificed in a hiperconcentrated solution of eugenol, fixed in formaline 10%, and subsequently transferred to alcohol 70^{o} GL.

In laboratory fish were discriminated according to morphological and meristic features and identified was based on specific keys (Britto, 2003; Castro et al., 2004; Britski et al., 2007; Graça & Pavanelli, 2007). The identifications were checked through scientific collections and confirmed by specialists (State University of São Paulo – Campus Rio Preto and State University of Maringá).

Analyses

For statistic comparisons the pools were firstly arranged in four groups, according to season and connection condition with the river flow: isolate pools in dry condition (DI), connect pools in dry condition (DC), isolate pools in rainy condition (RI) and connect pools in rainy condition (RC). A second arrangement was performed only considering dry and rainy conditions.

The differences among mean values of ecological attributes (richness, abundance, Shannon-Wiener diversity index and Pielou Evenness) were tested by a one-way ANOVA and T-STUDENT test, respectively, for connection condition in each season and for the dry and rainy data independent of connectivity. When differences were detected, the Tukey test was used for significance analyses ($p < 0.05$). Previously, Kolmogorov-Smirnov test was used to check the data normality.

In order to discriminate the fish assemblage structure in terms of the considered metrics we used Non-Metric Multidimensional Scaling (NMDS) derived from Bray-Curtis similarity matrices. One-way analysis of similarity (ANOSIM) (Clarke & Warwick, 2001), a permutation test, was used a posteriori to test the null hypothesis of no difference in fish assemblage among DI, DC, RI and RC and between dry and rainy condition. Similarity Percentages (SIMPER) was used to determine the contribution of individual taxa to the average similarity (typifying species) among DI, DC, RI and RC and also between dry and rainy condition (Clarke & Warwick, 2001).

Results

The ichthyofauna of the studied knickzone of Sapucaí-Mirim River was composed by 23 species from 11 families and five orders (Table 1), 82% are small size and the others medium size, according to Britto, 2003 and Vazzoler, 1996. The most abundant species were *Knodus moenkhausii* and *Astyanax bockmanni*, comprising, 43.09% and 30.10%, respectively, in a total of 608 specimens captured. The other specimens represented 26.81% (Table 2).

The presence of larvae and juveniles of several fish species, mainly during the rainy season, was observed.

Table 1 Taxonomic list of the fish species sampled in the Sapucaí-Mirim River knickzone.

ORDER CHARACIFORMES

Family Anostomidae

Schizodon nasutus Kner, 1858

Family Characidae

Astyanax bockmanni Vari & Castro, 2007

Astyanax altiparanae Garutti & Britski, 2000

Bryconamericus stramineus Eigenmann, 1908

Bryconamericus turiuba Langeani, Lucena, Pedrini & Tarelho-Pereira, 2005

Knodus moenkhausii (Eigenmann & Kennedy, 1903)

Piabina argentea Reinhardt, 1867

Planaltina britskii Menezes, Weitzman & Burns, 2003

Family Curimatidae

Steindachnerina insculpta (Fernández-Yépez, 1948)

Family Erythrinidae

Hoplias malabaricus (Bloch, 1794)

FamilyParadontidae

Apareiodon cf. *piracicabae* (Eigenmann, 1907)

ORDER CYPRINODONTIFORMES

FamilyPoeciliidae

Poecilia reticulata Peters, 1859*

ORDER GYMNOTIFORMES

FamilyGymnotidae

Gymnotus sylvius Albert & Fernandes-Matioli, 1999

ORDER PERCIFORMES

Family Cichlidae

Geophagus brasiliensis (Quoy & Gaimard, 1824)

Laetacara araguaiae Ottoni & Costa, 2009

Oreochromis niloticus (Linnaeus, 1758)*

Tilapia rendalli (Boulenger, 1897)*

ORDER SILURIFORMES

Family Heptapteridae

Imparfinis schubarti (Gomes*, 1956)*

Rhamdia quelen (Quoy & Gaimard, 1824)

Family Loricariidae

Hypostomus ancistroides (Ihering, 1911)

Hypostomus cf. *fluviatilis* (Schubart, 1964)

Hypostomus nigromaculatus (Schubart, 1964)

Family Trichomycteridae

Parastegophilus paulensis (Miranda Ribeiro, 1918)

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*Indicates non-native fish species.

Table 2 Total and relative abundance of the fish species sampled in the Sapucaí-Mirim River knickzone.

Species	N	N%
Knodus moenkhausii	262	43,09
Astyanax bockmanni	183	30,10
Apareiodon cf. *piracicabae*	38	6,25
Piabina argentea	23	3,78
Geophagus brasiliensis	19	3,13
Hypostomus nigromaculatus	19	3,13
Bryconamericus turiuba	8	1,32
Hypostomus ancistroides	8	1,32
Astyanax altiparanae	7	1,15
Hypostomus cf. *fluviatilis*	7	1,15
Hoplias malabaricus	6	0,99
Poecilia reticulata	6	0,99
Schizodon nasutus	5	0,82
Steindacnerina insculpta	5	0,82
Gymnotus silvius	2	0,33
Laetacara cf. *araguaie*	2	0,33
Planaltina britskii	2	0,33
Bryconamericus stramineus	1	0,16
Imparfinis schubarti	1	0,16
Oreochromis niloticus	1	0,16
Parastegophilus paulensis	1	0,16
Rhandia quelen	1	0,16
Tilapia rendalli	1	0,16

The most specious order was Characiformes comprising 11 species, followed by Siluriformes (6), Perciformes (4), Gymnotiformes (1) and Cyprinodontiformes (1). The most specious family was Characidae (7), followed by Cichlidae (4) and Loricariidae (3).

The habitat with higher percentage of Characiformes was RI (71.4%), Siluriformes in DC (55.6%) and Perciformes in RC (21.0%) (Fig. 3). Four orders were found in the samplings performed during the dry condition, and the most specious were Siluriformes (41.7%) and Characiformes (41.7%). Fiver orders occurred in the rainy condition and Characiformes were the most specious order (50%) followed by Perciformes (20%) and Siluriformes (20%) (Fig. 3).

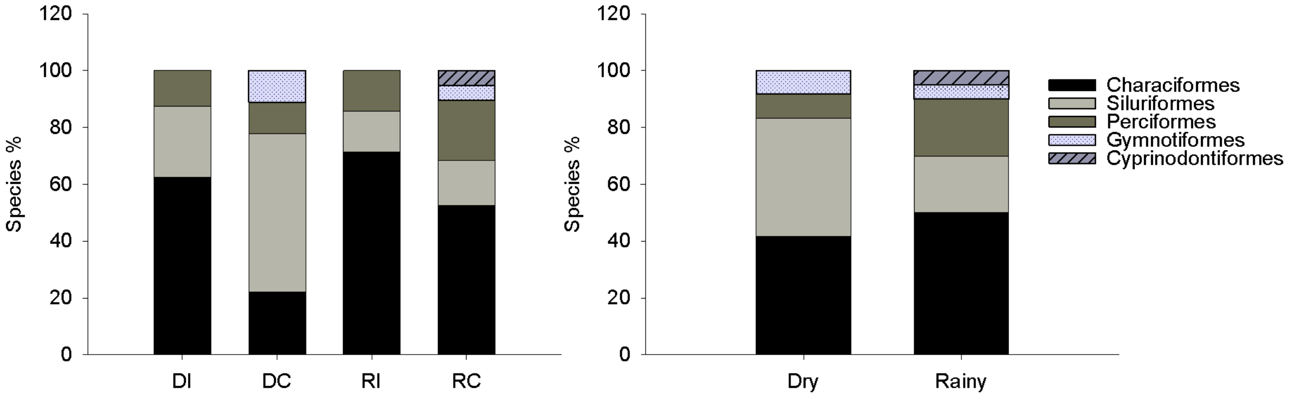

Fig. 3 Percentage of fish species richness per order sampled in distinct habitats (left) and seasonal conditions (right) in the Sapucaí-Mirim River knickzone. DI = isolated pools in dry condition; DC = connected pools in dry condition; RI = isolated pools in rainy condition and RC = connected pools in rainy condition.

Significant difference ($p<0.05$) was detected only for abundance, with higher values in the rainy condition compared to the dry condition. In terms of richness and diversity, higher values were associated to connection condition in both seasons of the year, but the differences were not significant. The evenness did not follow the same pattern, as the abundance was concentrated in a few species (Table 3).

Table 3 Means and standard deviations for abundance, richness, Shannon-Wiener diversity index (H') and Pielou Evenness index (J') of fish assemblage in the Sapucaí-Mirim River knickzone.

		Abundance	Richness	H'	J'
Habitats	DI	25.67 ± 41.86	2.67 ± 2.08	0.89 ± 0.83	0.51 ± 0.50
	DC	21.00 ± 11.92	4.50 ± 1.73	1.69 ± 0.90	0.75 ± 0.26
	RI	44.00 ± 36.01	4.00 ± 2.00	1.50 ± 0.71	0.58 ± 0.16
	RC	78.75 ± 52.28	7.25 ± 4.57	1.70 ± 0.79	0.50 ± 0.17
Season	Dry	23.00 ± 25.72*	3.71 ± 1,98	1.34 ± 0.91	0.65 ± 0.37
	Rainy	63.86 ± 46.30*	5.86 ± 3.85	1.62 ± 0.70	0.54 ± 0.16

* indicates $p<0.05$ according to T STUDENT test. DI = isolated pools in dry condition; DC = connected pools in dry condition; RI = isolated pools in rainy condition; RC = connected pools in rainy condition.

A non-metric multidimensional scaling analysis applied to abundance data indicated a clear separation of the ichthyofauna assemblage in terms of seasonality, with rainy samples more aggregate than dry ones (Fig. 4).

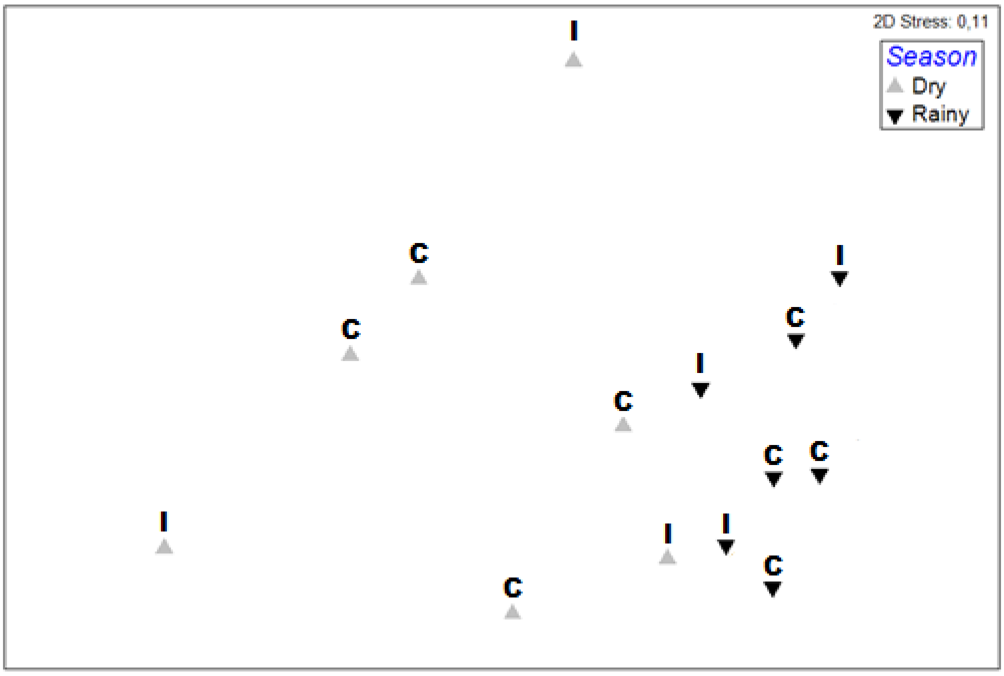

Fig. 4 Non-metric multidimensional plots of the abundance of fish assemblage in isolated (I) and connected (C) pools during the rainy and dry condition in the Sapucaí-Mirim River knickzone.

ANOSIM analyses showed significant differences only between the comparisons of DC - RI and DC - RC ($p<0.05$). According to SIMPER, the taxon that most contribute to similarity in DC were *Astyanax bockmanni*, *Hypostomus nigromaculatus* and *Hypostomus* cf. *fluviatilis*; for RI were *Knodus moenkhausii*, *A. bockmanni* and *Piabina argentea*, and for RC were *K. moenkhausii*, *A. bockmanni* and *Apareiodon* cf. *piracicabae* (Table 4).

Dry and rainy conditions also presented significant composition differences ($p<0.05$). The species that contribute to similarity in dry condition were *A. bockmanni*, *K. moenkhausii* and H. *nigromaculatus*, and in the rainy condition were *A. bockmanni*, *K. moenkhausii* and *P. argentea* (Table 4).

Table 4 Fish species that contribute to average similarity for each habitat and season in the Sapucaí River Knickzone, according to Simper analysis.

Groups	DI		DC		RI		RC		Dry		Rainy	
	Av. Sim. 1.8		Av. Sim. 27.3		Av. Sim. 40.9		Av. Sim. 46.7		Av. Sim. 17.6		Av. Sim. 44.5	
Species	Av.Ab.	Cont.%	Av.Ab.	Cont.%	Av.Ab.	Cont.%	Av.Ab.	Cont.%	Av.Ab.	Cont.%	Av.Ab.	Cont.%
A. bockmanni	16.3	50.0	10.0	49.2	18.0	72.2	10.0	7.28	12.7	55.6	13.4	10.9
K.moenkhausii					18.0	9.5	46.3	82.0	3.3	7.3	34.1	74.7
A. cf. *piracicabae*	1.0	50.0					6.3	3.9				
P. argentea					3.0	9.1					2.9	6.3
H. nigromaculatus			3.8	34.5					2.3	28.0		
H. cf. *fluviatilis*			1.0	11.1								

DI = isolated pools in dry condition; DC = connected pools in dry condition; RI = isolated pools in rainy condition; RC = connected pools in rainy condition; Av. Sim. = Average Similarity; Av. Ab. = Average Abundance; Cont. = Contribution.

Discussion

Previous studies on the ichthyofauna of Sapucaí-Mirim River sub-basin have reported distinct values for richness. Castro et al. (2004) found 41 fish species sampling six low order streams. Cesário (2010) observed 76 species and Souza (2014) 66 species, both studies in the Sapucaí-Mirim.

From the 23 species observed in this study, 13 are common to the ones found by Castro et al. (2004), 14 to Cesário (2010) and 14 to Souza (2014). It is important to notice that five species are the first record for Sapucaí-Mirim sub-basin (Table 5). Probably the new fish records are related to the knickzones structural and functional particularities which may attend specific ecological requirements.

Table 5 Common fish species among different studies carried out in the Sapucaí-Mirim River.

Species	Present study	Souza (2014)	Cesário (2010)	Castro et al. (2004)
Apareiodon cf. *piracicabae*	X	-	X	-
Astyanax altiparanae	X	X	X	X
Astyanax bockmanni	X	X	X	X
Bryconamericus stramineus	X	X	X	X
Bryconamericus turiuba	X	-	-	-
Geophagus brasiliensis	X	X	X	X
Gymnotus sylvius	X	X	-	X
Hoplias malabaricus	X	X	-	X
Hypostomus ancistroides	X	X	X	X
Hypostomus nigromaculatus	X	X	X	X
Hypostomus cf. *fluviatilis*	X	-	X	-
Imparfinis schubarti	X	-	X	X
Knodus moenkhausii	X	-	-	-
Laetacara araguaie	X	-	-	-
Oreochromis niloticus	X	X	-	-
Parastegophilus paulensis	X	-	-	-
Piabina argentea	X	X	X	X
Planaltina britskii	X	-	-	-
Poecilia reticulata	X	-	X	X
Rhamdia quelen	X	X	X	X
Schizodon nasutus	X	X	X	
Steindachnerina insculpita	X	X	X	X
Tilapia rendalli	X	X	-	-

The orders Characiformes and Siluriformes were the most representative in studied knickzone. This is the common pattern for the upper Paraná basin (Lowe-McConnell, 1975; Agostinho & Júlio Jr., 1999; Langeani et al., 2007), which is also recurrent in the Sapucai-Grande basin (Castro et al., 2004; Cesário, 2010; Souza, 2014).

The presently known fish richness of Sapucai-Grande basin comprises 99 species and represents 32% of the richness registered in the upper Paraná basin, although corresponding to only 1% of this basin area (9,175,42 km² of 891,309 km²) (Souza, 2014). This relation is even more prominent if we considered that in the studied knickzone [(0.00032% (0.03 km²) of the Sapucaí-Mirim area)] we found 23% of the river fish richness.

Great specific richness in such small area could be explained by the high limnological variability, complex interactions of physically different habitats (pools, runs and rapids) in terms of depth, area, volume and connectivity with the river flow, as well as the presence of a variety of structures such as rocks and marginal vegetation (Chapter 1). A great abundance of small size species and larval and juveniles of some species was also found, showing to be an important macrohabitat for the life cycle of this species. The knickzone is plentiful of shelters, reducing pressure from predators (Schlosser, 1987) and providing suitable conditions for rearing grounds (Bain et al., 1989; Gore et al., 1989; Flebbe & Dolloff, 1995). Another important factor is the availability of a wide spectrum of food resources (Chapter 3).

The most evident impacts in ichthyofauna by damming of rivers are related to medium and large size migratory species, comprising the interruption of migratory routes and the lost and degradation of spawning and nursery habitats (Agostinho et al., 2007).

The flood of knickzones by damming of rivers also affects small size species, which are very important in energetic transfer in food chain.

The presence of three non-native species in a natural environment like knickzone is rare. A preserved environment with natural condition has a well-established native biota, making difficult the presence of non-native species (Keller et al., 2011). Probably *Tilapia rendali* and *Oreochromis niloticus* were introduced in Sapucaí-Mirim River by fish farm escapes and *Poecilia reticulata* by aquarists. It is something worrying because the dispersion potential of non-native species apparently is under estimated.

Simultaneous analyzes of the limnological parameters demonstrated a remarkable variation among pools considering the distinct degrees of connectivity (Chapter 1). Nevertheless, the ichthyofauna of knickzone was moderately influenced by this condition. Despite higher values of abundance, richness and diversity in connected habitats, differences (ANOVA test) were not significant. But temporally, there was significant differences in abundance were, with higher values in rainy condition.

When analyzed in detail the composition of assemblages (ANOSIM), significant differences were observed for DC - RI and DC - RC and also between dry and rainy conditions. Species contributed for these differences in different proportions, according to SIMPER analyses.

During the phase of water retraction (low hydrometric level), higher elevation or more distant areas from the river channel, become disconnected, and aquatic organisms remain confined within these habitats for different time periods (Lake 2003; Humphries and Baldwin 2003). During this period of isolation, stressful abiotic conditions intensify progressively until the following flood (Tockner et al., 2000). At the same time, biotic interactions, such as competition and predation, are expected to become more intense, mainly among individuals restricted to habitats of restricted proportions (small lagoons and pools). Therefore, non-random patterns of species co-occurrence (aggregation/segregation) are expected between natural disturbance events, basically due to harsh abiotic/biotic conditions that lead some species to local extinctions (Arrington et al., 2005).

As the river level rises, aquatic environments are expanded reestablishing connection between isolated sites and the main channels of rivers. Fish may thereby disperse to different floodplain environments for a variety of reasons, such as reproductive migration or searching for food, because flood increases accessible to different habitats (Fernandes et al., 2009). In a gradient of hydrological connections, it is expected that communities shift from structured patterns in low-water periods to random patterns in high-water periods (Arrington et al., 2005; Fernandes et al., 2009).

The species *K. moenkhausii* and *A. bockmanni* were the most abundant species in the Sapucaí-Mirim River knickzone. The first one had higher contribution to the similarity in terms of composition in the rainy condition (74.7%) and the second during the dry condition (55.6%).

In relation to feeding habits these species are omnivorous or generalists, with a greater trophic plasticity (Bennemann et al., 2005; Ceneviva-Bastos and Casatti, 2007). They remain positioned in the water column for food consumption of items transported by the water current or even floating on the water surface, such as terrestrial insects and plants. The foraging strategy, especially for small characids in streams, has been reported previously, since these species are usually trophic opportunists and may change their diet according to spatial variations and interactions with other species (Silva et al., 2012).

Other aspect that justifies the success of colonization of this two species is their reproduction. They have premature maturation and continuous reproduction (Winemiller & Rose, 1992), with split spawning along the whole year in small water bodies and with total spawning in large water bodies (Garutti, 1989).

The knickzone macrohabitat is also very important for species of genus *Hypostomus,* due to the rocky substrate and the availability of food resources. The species *H. nigromaculatus,* particularly, contributed with 28% of the similarity among habitats during the dry condition according to SIMPER analyses. In Sapucaí-Mirim River it was reported 12 species of this genus, occurring in high abundance (Souza., 2014).

Species of genus *Hypostomus* are iliophagous and are favored by the presence of higher plants, phytoplankton and periphyton (Bennemann et al., 2005). The knickzone rocky substrate and the high transparence in dry season promote ideal conditions for an abundant growth of filamentous algae. The lower transparence in the rainy season, and consequently less algae grow, should have influence on a lower abundance of *Hypostomus*.

This study shows the importance of knickzone as a differentiated environment for the river ichthyofauna. It was observed a high fish richness and abundance, when considered such proportionally small area, and even the presence of species exclusive to this macrohabitat in Sapucaí-Mirin River sub-basin. There were also evidences that this is a nursery and growth area for some species. These characteristics are supported by the intrinsic structural heterogeneity of habitats and intensive functional dynamics - seasonal and random.

Further studies on knickzones are required for the better ecological understanding of this particular kind of macrohabitat. They should also be considered as strategic environments in the regional planning for biodiversity conservation, especially due to the eminent threat by intensive hydropower reservoir construction.

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Capítulo 3

Use of food resources by ichthyofauna in a knickzone macrohabitat

Eduardo Meneguzzi Brambilla, Virginia Sanches Uieda, Marcos Gomes Nogueira

Universidade Estadual Paulista (UNESP) - Campus de Botucatu, Instituto de Biociências de Botucatu, Departamento de Zoologia. Distrito de Rubião Júnior, s/n – CEP: 18618-970 – Botucatu – SP.

eduardo.brambilla@gmail.com, +55 14 3880 0630

Abstract

Ichthyofauna trophic ecology studies of knickzones can generates fruitful insights to supply the lack of ecological knowledge in this kind of macrohabitat. The aim of this study was to analyze the trophic structure of a selected knickzone ichthyofauna in the Sapucaí-Mirim River (Southeast Brazil). Fish were sampled in four pools connected to the river flow and three isolated, during rainy and dry conditions. The stomach contents of 20 species were analyzed. The most frequent and dominant food category in the fish diet were organic matter and aquatic hexapod. Seasonal differences in the fish diet composition were determined, with higher contribution of algae in dry condition and vegetal matter and organic matter in rainy condition. The isolated pools exhibited higher proportion of high niche overlap, related to more intensive biotic interactions among individuals confined in physically restricted habitats. Seasonal conditions in combination with the connectivity degree of pools with river flow influenced the trophic structure of fish assemblage in the knickzones.

Keywords: “pedral”, fish, basaltic substrate, pools, diet

Introduction

Knickzone is a geologic name used for denomination of shallow stretches, in upstream and middle river basins, characterized by large rock outcrops creating a complex of habitats mainly composed by rapids, runs and pools with distinct magnitudes. The substrate immersion or exposition condition is highly variable in terms of volume and level, even seasonally (dry and rainy seasons) or short term (episodically storm events and dry spells) variation. This macrohabitat also exhibits a high limnological and physical heterogeneity (Chapter 1).

Despite the wide distribution, there is a lack of knowledge about the structure and ecological functioning of this particular river macrohabitat. Nevertheless, such kind of information is essential for the developing of management strategies focusing on environmental conservation and sustainable use of the biological resources (Guedes et al., 2015). Presently, hundreds of Brazilian knickzones are threatened by the intensive construction of small hydropower plants (ANEEL, 2013).

Investigations on ichthyofauna trophic dynamics generates fruitful information on community structure and functioning, including interactions among different species and their habitat (Stephens et al., 2007; Ferrareze et al., 2015), environment integrity, food availability, behavioral features and the ecological role of individual species (Hahn et al., 1997).

Spatial factors greatly affect the trophic organization of the fish community in a particular area (Elliott et al., 2002). As feeding resources are distributed in patches along the spatial dimensions (MacArthur & Pianka, 1966; Schoener, 1971; Meyer & Posey, 2009), it is reasonable to suppose that the distribution of the fish community follows resource availability and that the niche dimension is a major determinant of community organization (Guedes et al., 2015).

Seasonality can also promote shifts in diets of several species. The increase of feeding activity can be related with the rainy period, when prey availability is generally higher (Abilhoa et al., 2010). Higher temperatures also take to an increase in energy requirements for metabolism maintenance, reproduction and growth (Frenkel & Goren, 1997, 2000; Esmaeili & Shiva, 2006).

The aim of this study is to analyze the trophic structure of the ichthyofauna in a knickzone macrohabitat, based on a case study in Sapucaí-Mirim River, SP, Brazil.

Material and Methods

Study area

The study area is located in Sapucaí-Mirim River, a tributary of River Grande basin, São Paulo/Minas Gerais States, Brazil (Fig. 1). Presently, five small hydropower plant (SHP) are operating in this river, generating 70 MW, and another six potential sites are already inventoried for future constructions. Based on recent satellite images, at least eight knickzones can be recognized in this river. The selected knickzone (20°34'34.1"S and 47°47'06.5"W) is in the upstream zone of Palmeiras SHP, but beyond its operational influence, thus, presenting a natural dynamic of water flow (Fig. 1).

Sampling and analysis

Samplings were performed in seven different pools of the selected knickzone (Fig. 1) during the dry (June 2014) and rainy season (December 2014) (Fig. 2). Four were connected with river flow and three were isolated.

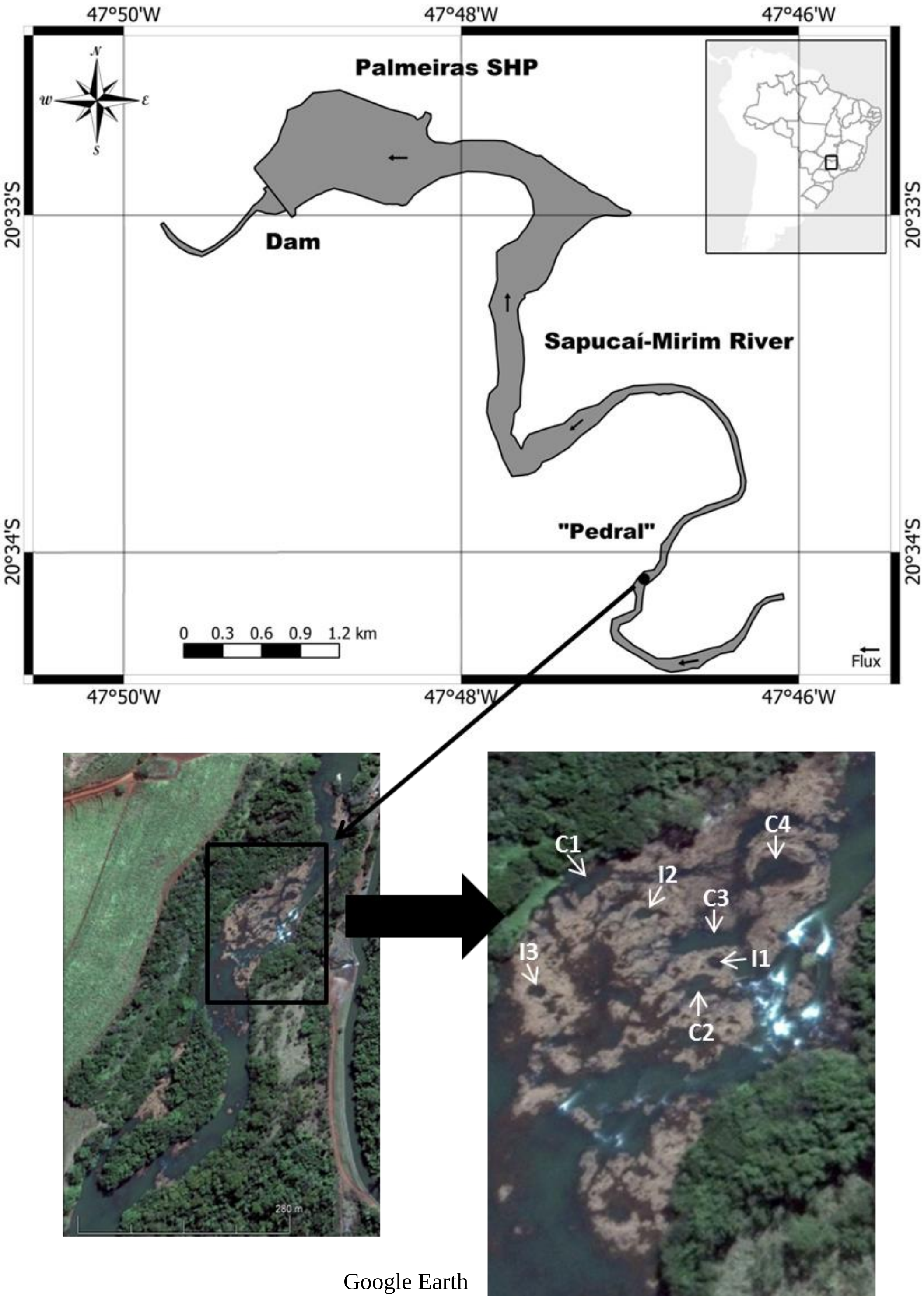

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Fig. 1 Geographic location of the study area location – a knickzone in Sapucaí-Mirim River, Southeast Brazil, with the positioning of the sampling habitats (pools). C = connected with river flow; I = isolated.

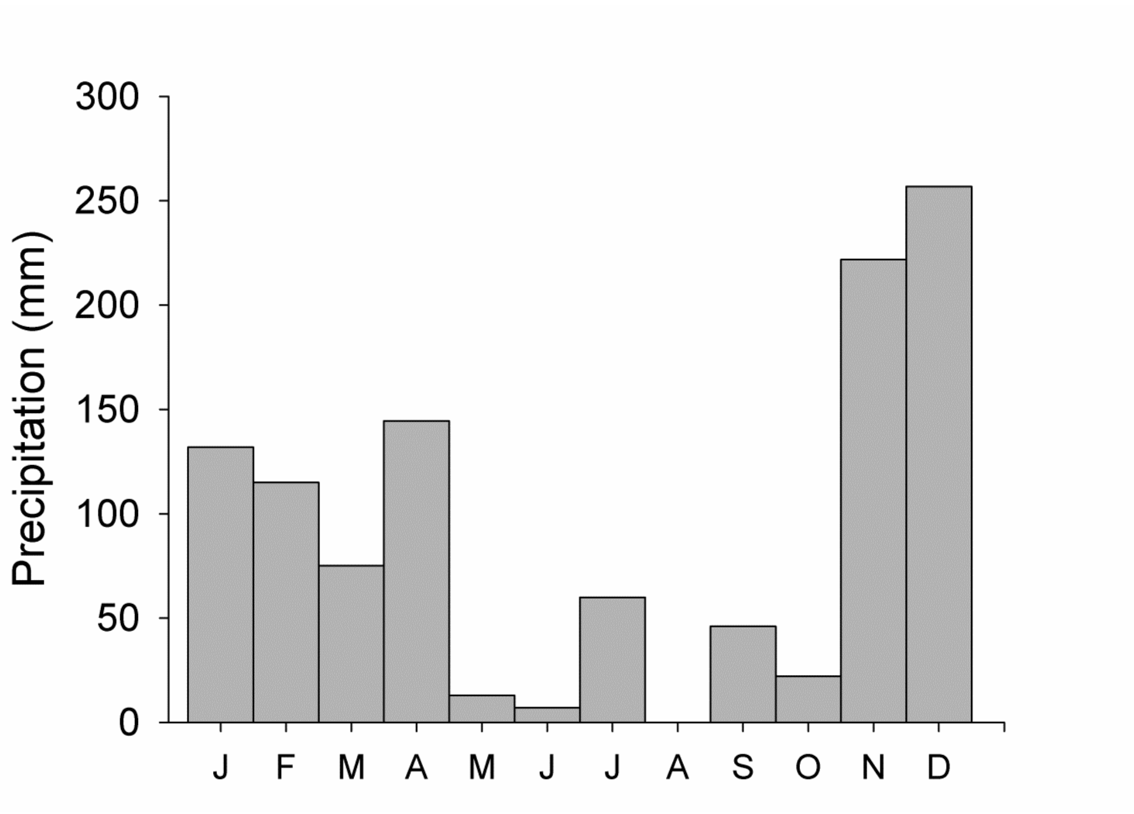

Fig 2. Monthly rain precipitation in the in the Sapucaí-Mirim basin, Brazil, during 2014.

In each pool it was applied a combination of several methods in order to obtain an integrated representative sample of the whole ichthyofauna community. It was used seine, sieve (mesh size 0.5 cm) and electrofishing. The sampling effort applied for each method was standardized for each distinct pool. Sampled fish were immediately sacrificed in a hiperconcentrated solution of eugenol, then fixed in formaline 10% and subsequently transferred to alcohol 70^{o} GL.

In laboratory fish were discriminated according to morphological and meristic features and identified was based on specific keys (Britto, 2003; Castro et al., 2004; Britski et al., 2007; Graça & Pavanelli, 2007). The identifications were checked through scientific collections and confirmed by specialists (State University of São Paulo – Campus Rio Preto and State University of Maringá).

For statistic comparisons, the pools were firstly arranged in four groups, according to season and connection condition with the river flow: isolate pools in dry condition (DI), connect pools in dry condition (DC), isolate pools in rainy condition (RI) and connect pools in rainy condition (RC). A second arrangement was performed only considering dry and rainy periods.

Food items of stomach contents were identified until the most detailed taxonomic level which was possible, counted and measured in terms of area (mm^2) using a graded dish.

The diet composition was evaluated by frequency of occurrence (Hyslop, 1980) and biovolume (adapted from Esteves & Galetti Junior, 1995) combined in an alimentary index (IAi) (Kawakami & Vazzoler, 1980) for each species and for species grouped in DI, DC, RI and RC.

The food items were grouped into 12 categories: Crustaceans - Ostracoda, Cladocera and Copepoda; Aquatic hexapod - aquatic stages of Diptera, Ephemeroptera, Trichoptera, Hemiptera, Lepidoptera, Odonata, Coleoptera, Collembola; Terrestrial Insects; Terrestrial Arachnid - Aranae and Acarina; Aquatic Acarina; Fragment of exoskeleton - debris of aquatic hexapods; Vegetal matter - stalks, leaves, roots, and seeds; Algae - filamentous and unicellular algae; Mollusca - Bivalvia, Gastropoda; Protozoa - tecameba; Fish - entire fish and debris (scales, muscles, and bones) and Organic matter - organic material so digested making impossible to define its origin.

Fish species were classified into four trophic guilds according to preferential consumed food category (IAi> 15%): omnivores, detritivores, insectivores and herbivores (Uieda, personal communication).

A Bray-Curtis matrix was performed to evaluate the similarity among the diet composition of species grouped by pool connection-season condition (DI, DC, RI and RC). A

Non-Metric Multidimensional Scaling (NMDS) derived from this matrix was performed in order to visualize the arrangement of groups. One-way analysis of similarity (ANOSIM) (Clarke & Warwick, 2001), a permutation test, was used a posteriori to test the null hypothesis of no difference in fish diet composition among DI, DC, RI and RC; between dry and rainy condition and between isolated and connected pools. Similarity Percentages (SIMPER) was used to determine the contribution of individual taxa to the average similarity (typifying food categories) among DI, DC, RI and RC and between dry and rainy condition (Clarke & Warwick, 2001).

The niche breadth (Bi) was calculated by the Levin's index (Hurlbert, 1978). This index varies from 0 (species consumed mainly one food resource) to 1 (species consumed all food resources in similar proportions). The species was considered specialist feeder when $Bi < 0.5$ and generalist feeder when $Bi > 0.5$.

The niche overlap (Pianka, 1973) was calculated among species in each group (DI, DC, RI and RC). The niche overlap value ranges from 0 (no overlap) to 1 (total overlap). Niche overlap was considered high if higher than 0.6, intermediate if 0.4-0.6, or low if lower than 0.4 (Novakowski et al., 2008).

Results

We analyzed the stomach contents of 359 individuals, comprising 20 fish species (Table 1). Vegetal matter was the food category consumed by most species (85%), followed by aquatic hexapods (75%) and crustaceans (65%).

The diet composition for all species grouped together indicated that the most frequent and dominant food category consumed was organic matter (IAi = 31.7%), followed by aquatic hexapod (IAi = 27.2%), exoskeleton fragment (IAi = 19.1%) and vegetal matter (IAi = 12.2%). The other food resources represented 9.8%.

A Bray-Curtis similarity analyses showed a high degree of similarity in IAi values among RC, RI and DC, especially between RI and RC (79.4%) (Fig. 3).

ANOSIM analyses was performed to compare IAi values of diet composition among DI, DC, RI and RC, exhibiting significant differences between DI and RC ($p<0.05$). According to SIMPER the food categories that most contribute to similarity in DI were algae, organic matter and vegetal matter and in RC were organic matter, vegetal matter, aquatic hexapod and exoskeleton fragment (Table 2).

When performed a comparison of IAi values of diet composition between dry and rainy conditions a significant difference was found too ($p<0.05$). The food categories that contribute to similarity in dry condition were organic matter, algae, aquatic hexapods and exoskeleton fragment and in rainy condition were organic matter, aquatic hexapod, vegetal matter and exoskeleton fragment (Table 2). There was no significant differences ($p<0.05$) in the comparison between isolate and connect pools.

Table 1 Results of the diet analysis of fish sampled in four knickzone pools located in Sapucaí-Mirim River, Southeast Brazil, showing the trophic guild, niche breadth and the values of Alimentar index (%) for each food category identified per species.

Species	Pool group	Trophic guild	N	B	Food Categories											
					Crus	AqHe	TeIn	TeAr	AqAr	FrEx	VeMa	Alga	Moll	Prot	Fish	OrMa
Apareiodon cf.*piracicabae*	DI	Det	3	0.097	0.19	1.88	-	-	-	1.51	5.65	9.42	-	-	-	81.36
Apareiodon cf.*piracicabae*	DC	Omn	3	0.333	2.88	31.40	-	-	-	5.19	-	3.46	-	-	-	57.07
Apareiodon cf. *piracicabae*	RI	Det	10	0.011	-	1.08	-	-	-	0.10	0.37	-	-	-	-	98.45
Apareiodon cf.*piracicabae*	RC	Det	24	0.071	-	3.14	-	-	-	-	6.30	0.01	-	-	-	90.56
Astyanax altiparanae	RC	Omn	8	0.223	0.18	12.45	4.99	0.53	*	24.69	52.70	-	-	*	4.45	-
Astyanax bockmanni	DI	Ins	49	0.158	5.30	14.54	2.68	0.83	*	66.35	0.30	10.00	-	-	-	-
Astyanax bockmanni	DC	Omn	38	0.166	0.10	25.11	0.29	0.09	*	18.56	3.15	52.68	0.01	*	0.00	-
Astyanax bockmanni	RI	Omn	23	0.17	-	7.17	0.13	-	*	13.06	15.45	0.01	-	-	0.16	64.02
Astyanax bockmanni	RC	Omn	26	0.185	0.03	1.76	0.68	-	-	4.00	59.99	0.01	-	-	-	33.52
Bryconamericus turiuba	DI	Omn	8	0.383	0.17	42.07	0.11	0.07	-	25.76	9.17	22.65	-	-	-	-
Geophagus brasiliensis	DI	Omn	1	0.454	22.18	9.56	-	-	-	-	-	-	-	-	-	68.26
Geophagus brasiliensis	RI	Omn	1	0.244	0.09	0.55	-	-	-	-	2.19	-	35.58	-	-	61.59
Geophagus brasiliensis	RC	Omn	14	0.121	0.29	32.18	-	-	0.41	0.65	0.17	-	-	0.08	0.01	66.22
Gymnotus silvius	RC	Omn	1	0.522	1.34	21.48	-	-	-	53.69	23.49	-	-	-	-	-
Gymnotus silvius	DC	Ins	1	0.219	0.13	16.03	-	-	-	70.40	3.20	10.24	-	-	-	-
Hoplias malabaricus	RC	Omn	4	0.839	*	31.62	-	-	-	-	20.11	-	-	-	48.27	-
Hypostomus ancistroides	DC	Det	7	0.06	0.01	-	-	-	-	-	0.17	8.18	-	-	-	91.64
Hypostomus ancistroides	RC	Det	1	0.003	-	-	-	-	-	-	0.20	0.10	-	-	-	99.70
Hypostomus nigromaculatus	DC	Det	14	0.101	-	-	-	-	-	-	0.56	8.62	-	-	-	90.82
Hypostomus nigromaculatus	RC	Det	2	0.046	-	-	-	-	-	-	1.65	2.75	-	-	-	95.60
Hypostomus cf. *fluviatilis*	DI	Det	1	0.365	-	-	-	-	-	-	0.10	30.04	-	-	-	69.86
Hypostomus cf. *fluviatilis*	DC	Det	4	0.02	0.01	-	-	-	-	-	0.23	2.69	-	-	-	97.07
Hypostomus cf. *fluviatilis*	RI	Det	2	0.055	-	-	-	-	-	-	0.10	5.15	-	-	-	94.75

Imparfinis schubarti	DC	Ins	1	-	-	100.00	-	-	-	-	-	-	-	-	-	-
Knodus moenkhausii	DI	Ins	9	0.24	0.44	29.12	0.01	-	-	56.21	6.61	6.72	-	-	-	0.88
Knodus moenkhausii	DC	Ins	11	0.13	0.79	70.84	0.06	0.04	*	24.25	1.48	2.53	-	-	-	-
Knodus moenkhausii	RI	Omn	25	0.084	0.00	75.10	0.33	0.02	*	6.23	0.60	-	-	-	*	17.70
Knodus moenkhausii	RC	Omn	38	0.245	0.05	34.27	0.35	0,03	*	27.81	2.13	1.16	-	*	-	34.20
Laetacara cf *araguaie*	RC	Omn	2	0.606	-	32.40	-	-	-	-	22.35	-	-	0.56	-	44.69
Oreochromis niloticus	RC	Det	1	0.042	-	0.21	-	-	-	-	3.84	-	-	-	-	95.95
Piabina argentea	DI	Omn	3	0.323	0.25	28.16	-	-	0.01	43.04	1.00	27.47	0.06	-	-	-
Piabina argentea	RI	Omn	2	0.633	-	9.56	-	-	-	34.45	*	-	-	-	-	55.99
Piabina argentea	RC	Omn	4	0.281	0.05	3.49	-	-	-	1.24	56.64	-	-	-	-	38.58
Poecilia reticulata	RC	Ins	6	0.006	0.11	99.15	-	-	0.03	0.72	-	-	-	-	-	-
Rhandia quelen	DC	Omn	1	0.443	-	18.92	-	-	-	-	81.08	-	-	-	-	-
Schizodon nasutus	RC	Omn	5	0.21	0.02	7.01	-	-	-	-	76.23	-	-	-	-	16.74
Steindacnerina insculpta	RC	Det	3	0.004	0.22	-	-	-	-	-	-	-	-	-	-	99.78
Steindacnerina insculpta	RI	Det	2	-	-	-	-	-	-	-	-	-	-	-	-	100.00
Tilapia rendali	RC	Herb	1	-	-	-	-	-	-	-	100.00	-	-	-	-	-

Food Categories: Crus: Crustacean, AqHe: Aquatic Hexapod, TeIn: Terrestrial Insect, TeAr: TerrestrianAracnid, FrEx: Fragment of exoskeleton, VeMa: Vegetal Matter, Alga: Algae, Moll: Mollusca, Prot: Protozoa, Fish: Fish, OrMa: Organic Matter; Trophic guilds: Omn: omnivores, Det: detritivores, Ins: insectivores and Herb: herbivores; N: number of analysed stomachs; B: niche overlap; Sampling habitat: DI: dry isolate, DC: dry connect, RI: rainy isolate, RC: rainy connect; * : values < 0,01.

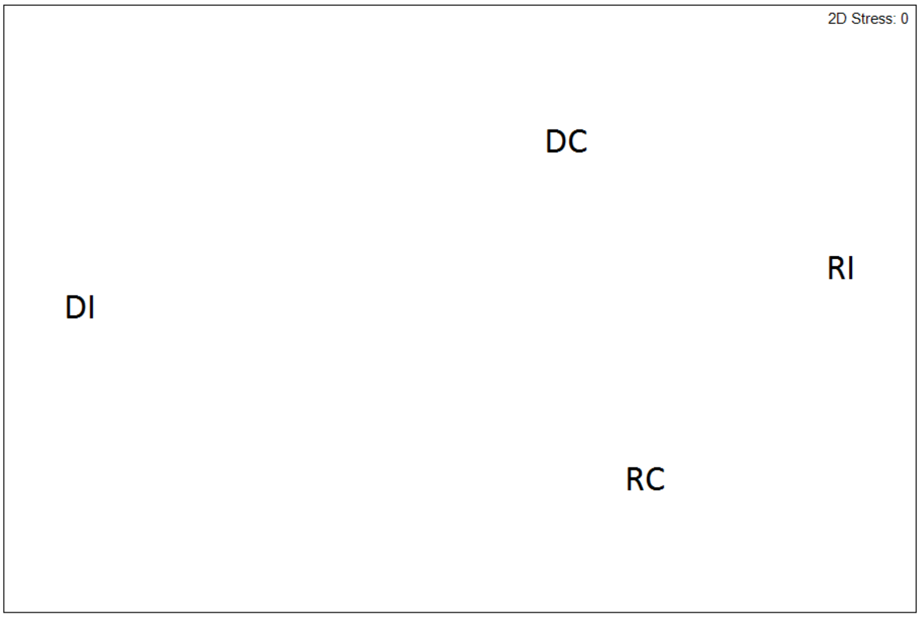

Fig. 3 Non-metric multidimensional plots of the bray-curtis similarity of alimentary index (IAi) in DI, DC, RI and RC. See text for abbreviations.

According to preferential food category (IAi> 15%), fish species were classified into four trophic guilds: omnivores, detritivores, insectivores and herbivores. Omnivorous was the trophic guild represented by most species (9), feeding on different food categories, generally a combination of animal and vegetal or animal and organic matter. Pools during the rainy condition exhibited higher proportion of species in this guild, RI (57.1%) and RC (56.3%) (Fig. 4).

Detritivores was the second most important guild in terms of number of species (6). The species in this group fed on a high quantity of organic matter, complemented by algae or vegetal matter. Also RI was the habitat with higher proportion of this group (42.8%).

Table 2 Average similarity of food categories, according to Simper analysis, for each season and knickzone habitat in Sapuací-Mirim River, Southeast Brazil.

	DI		DC		RI		RC		Dry		Rainy	
Food	Av. Sim. 1.8		Av. Sim. 27.3		Av. Sim. 40.9		Av. Sim. 46.7		Av. Sim. 17.6		Av. Sim. 44.5	
Categories	Av.Ab.	Cont.%	Av.Ab.	Cont.%	Av.Ab.	Cont.%	Av.Ab.	Cont.%	Av.Ab.	Cont.%	Av.Ab.	Cont.%
Organic Matter	13.0	22.1	21.4	39.5	40.8	55.3	44.3	51.6	27.6	35.1	42.8	52.2
Aquatic Hexapod			20.4	23.8	36.4	30.1	17.6	14.2	14.6	19.4	25.7	19.5
Algae	21.7	62.5	23.7	21.5					22.9	28.7		
Fragment of exoskeleton			11.5	10.8	8.7	12.8	13.0	13.1	14.9	11.1	11.2	12.7
Vegetal Matter	3.4	13.3					23.1	20.5			18.7	15.0

DI = isolated pools in dry condition; DC = connected pools in dry condition; RI = isolated pools in rainy condition; RC = connected pools in rainy condition; Av. Sim. = Average Similarity; Av. Ab. = Average Abundance; Cont. = Contribution.

Insectivorous were represented by four species, which fed on aquatic hexapods and exoskeleton fragments. The habitat with higher proportion of this group was DC (33.33%). Herbivorous was represented only by *Tilapia rendalli* in RC, which fed only on vegetal matter.

Considering fish species in DI, DC, RI and RC, only *Piabina argentea* in RI and *Hoplias malabaricus* and *Laetacara araguaie* in RC presented high values of niche breadth (>0.5), indicating a generalist diet. The others species in all sampling habitats presented low values of niche breadth (<0.05), indicating a specialist diet.

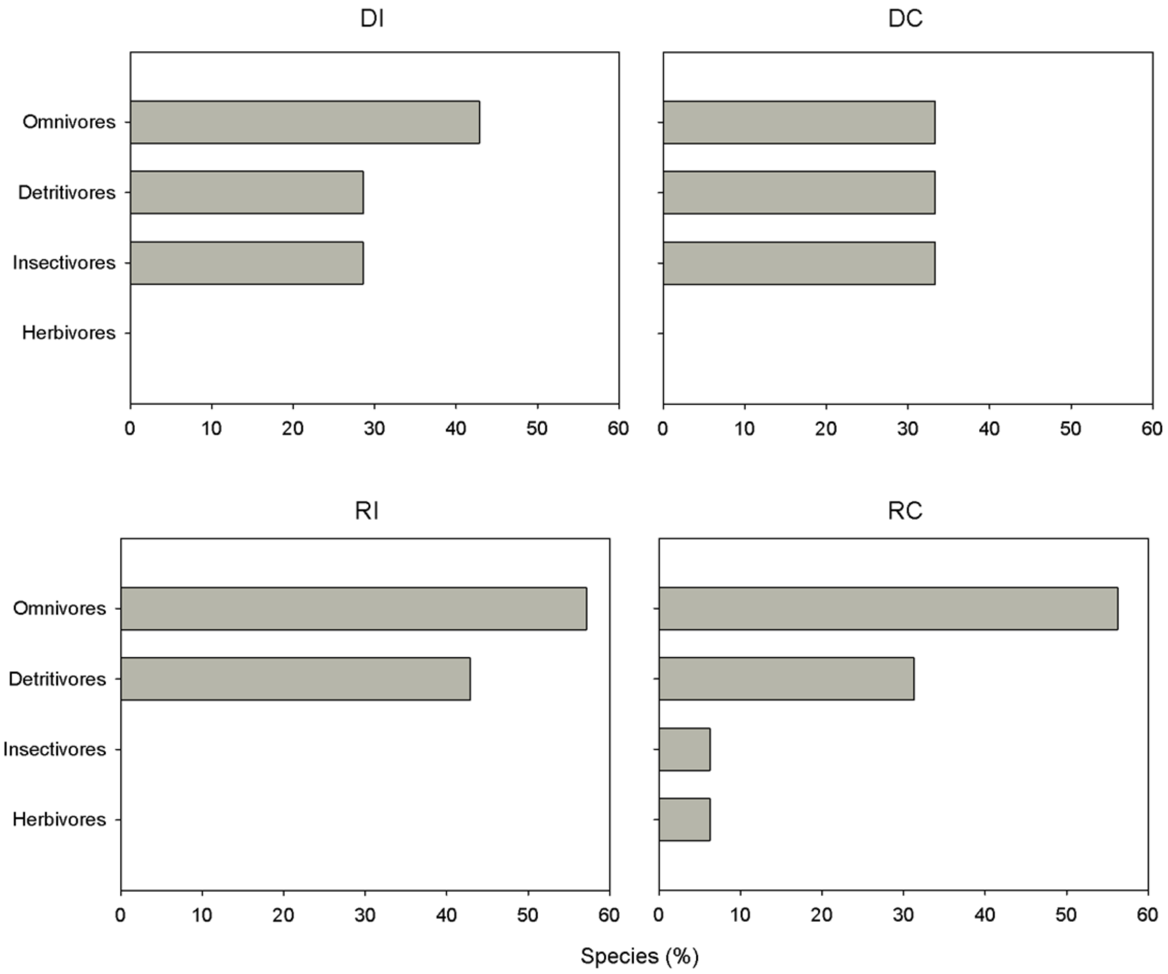

Fig. 4 Percentage of fish species in each trophic guild for all knickzone habitats sampled in Sapucaí-Mirim River, Southeast Brazil. DI = isolated pools in dry condition; DC = connected pools in dry condition; RI = isolated pools in rainy condition; RC = connected pools in rainy condition.

Most sampling habitats exhibited higher frequency of low niche overlap values between species pairs (<0.4). RI was the only habitat which presented high niche overlap values (>0.6) in a higher frequency (55%). The isolate pools presented a higher frequency of high niche overlap values (>0.6) than connect pools in the same seasonal condition (Fig. 5).

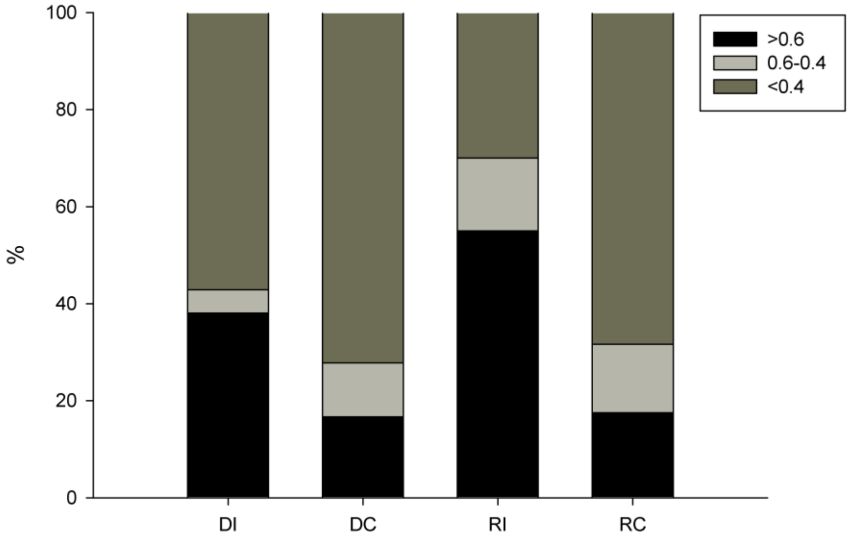

Fig. 5 Relative frequency (%) of niche overlap for all species pairs for each knickzone habitat sampled in Sapucaí-Mirim River, Southeast Brazil. DI = isolated pools in dry condition; DC = connected pools in dry condition; RI = isolated pools in rainy condition; RC = connected pools in rainy condition.

Discussion

The fish species of knickzones fed on a great variety of food items, which were grouped in 12 food categories. The availability of these trophic resources is supported by the intrinsic macrohabitat structural complexity (distinct kinds of pools, runs and rapids) and high limnological spatial and temporal variability (Chapter 1). Three food categories, organic matter, aquatic hexapod and exoskeleton fragment, comprised almost 80% of all consumed food.

When compared the diet composition similarity among habitats with distinct degrees of hydrological connectivity for both seasonal periods, the group DI showed low similarity with the others and significant differences with RC. This kind of pools keep isolated from the river flow during relatively long periods without water renovation, resulting in abiotic stressful conditions (Tockner et al., 2000) which limit the availability of several food resources. The SIMPER analyses showed that the food category whit higher contribution in terms of diet similarity for this kind of habitat (DI) is algae, followed by organic matter and vegetal matter. These could be considered resources of low energetic value, but abundant in stress abiotic conditions.

Comparisons between dry and rainy conditions showed the occurrence of remarkable difference in the fish diet composition. During the dry condition the water transparency is higher, favoring the presence of unicellular and filamentous algae, which are consumed in great quantities by fish. In rainy condition considerable loads of external material from the drainage basin is introduced into the fluvial systems (Granado & Henry, 2012; Ferrareze et al., 2014), including vegetal matter and organic matter that are incorporated in the fish diet in much higher proportion compared to the dry condition.

Despite the variety of food items, a relatively low trophic diversity was found in the fish assemblage of the Sapucaí-Mirim River knickzone. Fish were distributed only in four trophic guilds. This number is lower than the observed in streams (Zeni & Casatti, 2014), lateral lagoons (Ferrareze et al., 2015) and reservoirs (Vidotto-Magnoni, 2009). Trophic diversity is positively influenced by the stability of available food resources, mainly in environments with higher and more diverse supplies of food resources and higher quantities of opportunistic and generalist species (Angermeier & Karr, 1984).

In the rainy condition a higher proportion of omnivores and during the dry condition a higher proportion of insectivores occurred. This is because some species like *Knodus moenkhausi*, *Astyanax bockmanni* and *Gymnotus silvius* changed their insectivore food habit to omnivore habit in rainy season. During the rainy condition the availability of food resources is higher than in the dry condition (Deus & Petrere Jr., 2003), directly influencing on the fish diet.

Most species in all sampled habitats had low niche breadth values, indicating a specialized diet, with preference on a restricted number of food items. In the neotropical region, generally higher values of niche breadth are observed in the rainy condition compared to the dry season (Deus & Petrere Jr., 2003), but this pattern was not observed in knickzones.

Higher proportions of high values of niche overlap occurred in the isolate pools compared to connected pools in the same seasonal period. In isolate pools, biotic interactions are expected to become prominent, as individuals are confined in habitats of restricted physical dimensions. When the food resource is scarce, the species need to converge toward a nearly identical use of them; consequently, a high degree of niche overlap is observed (Lawlor, 1980; Matthews, 1998). In contrast, when a resource is abundant several species may use it opportunistically, generating lower niche overlap values (Mathews, 1998).

Even when species have high niche overlap, other factors may promote their coexistence such as spatial heterogeneity and habitat complexity; then species can be spatially segregated during activity for food capture (May, 1986; Schoener, 1974).

Connected pools have a continuous water renovation, reducing abiotic stressors and increasing the entrance of food resources through the river flow. The high proportion of low values of niche overlap presented in these pools in combination with low niche breadth suggest a high degree of food partitioning (Ferrareze et al., 2015), in agreement with other studies on neotropical fish communities (Uieda et al., 1997; Esteves et al., 2008; Novakowski et al., 2008).

Species segregation into different microhabitats, differences in the feeding period and the selection of particular feeding tactics contribute to minimize the overlap among species with similar diet (Casatti & Castro, 1998; Sabino & Zuanon, 1998). Segregation into different microhabitats may be determined by preferences in relation to substrate, water velocity and depth, among other variables (Herder & Freyhof, 2006); or even by the presence of competitors or predators. A high degree of variation in foraging strategies may differentiate feeding patterns (Barili et al., 2011).

In conclusion, seasonal conditions in combination with the differential degree of connectivity of pools with the river flow influenced the trophic structure of the fish assemblage in the knickzones. The seasonality influenced mainly the diet composition and the feed habits of species. Connectivity modulates the trophic relation among the species affecting the niche overlap values.

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Considerações finais

Os pedrais são macrohabitats formados por um complexo de habitats de diferentes magnitudes, desta forma apresentando uma grande heterogeneidade física e limnológica em um trecho limitado dentro do rio. Cada fator limnológico varia de forma diferente de acordo com o tipo de habitat e a condição sazonal.

Nesse macrohabitat, os peixes se alimentam de diversos tipos de itens alimentares, indicando uma grande disponibilidade e variedade de recursos alimentares. Os diferentes tipos de habitat e a condição sazonal influenciam no uso dos recursos, explorados pelos peixes e também na estrutura da comunidade.

A heterogeneidade física e limnológica somada a grande disponibilidade e variedade de recursos alimentares propicia condições que permitem o estabelecimento de espécies de peixes com diferentes requisitos ecológicos, resultando em uma elevada riqueza especifica de peixes em uma pequena área.

A importância dos pedrais para a manutenção da diversidade regional de peixes foi comprovada neste estudo e estes ambientes devem ser considerados como áreas estratégicas para programas locais/regionais de conservação e preservação ambiental, principalmente em um contexto onde são altamente ameaçadas pela instalação de PCHs.

Levando em consideração que a conservação dos tributários de grandes rios impactados por barramentos é uma das melhores alternativas para a conservação da ictiofauna da bacia hidrográfica, o rio Sapucaí-Mirim, incluindo seus pedrais, se torna uma importante área de preservação da diversidade de peixes da Bacia do rio Grande.