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CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE  
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS  
BIOLÓGICAS (BIODIVERSIDADE NEOTROPICAL)



EWERTON FINTELMAN DE OLIVEIRA

ECOLOGIA FUNCIONAL DAS COMUNIDADES ZOOPLANCTÔNICAS DE  
RESERVATÓRIOS DO SUDESTE DO BRASIL

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SUDESTE DO BRASIL

Dissertação apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Biodiversidade Neotropical) da Universidade Federal do Estado do Rio de Janeiro como requisito parcial para obtenção do título de Mestre em Ciências Biológicas.

Orientadora: Prof<sup>ª</sup> Dr<sup>ª</sup> Christina Wyss Castelo Branco

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## **ECOLOGIA FUNCIONAL DAS COMUNIDADES ZOOPLANCTÔNICAS DE RESERVATÓRIOS DO SUDESTE DO BRASIL**

Dissertação apresentada ao curso de Mestrado em Ciências Biológicas do Programa de Pós-Graduação em Ciências Biológicas (Biodiversidade Neotropical) da Universidade Federal do Estado do Rio de Janeiro no dia 25 de janeiro de 2019, como requisito parcial para a obtenção do título de Mestre em Ciências Biológicas. A mesma foi avaliada pela banca examinadora composta pelos Professores Dr. Reinaldo Luiz Bozelli (UFRJ), Dr. Luciano Neves dos Santos (UNIRIO) e Dra. Christina Wyss Castelo Branco (UNIRIO), sendo suplentes os Professores Jayme Magalhães Santangelo (UFRRJ) e Betina Koslowski-Suzuki e \_\_\_\_\_ com o conceito \_\_\_\_\_.

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Prof. Dr. Reinaldo Luiz Bozelli

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Prof. Dr. Luciano Neves dos Santos

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Prof.<sup>a</sup> Dr.<sup>a</sup>. Christina Wyss Castelo Branco

Dedico este trabalho a todas as pessoas que, de maneira direta ou indireta, contribuíram para o meu sucesso enquanto estudante de pós-graduação.

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*“O insucesso é apenas uma oportunidade para recomeçar com mais inteligência.”*  
Henry Ford

*“Tudo é tudo e nada é nada.”*  
Tim Maia

## RESUMO

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Abordagens baseadas em atributos funcionais tem sido utilizadas extensivamente em ecossistemas límnicos para elucidar como variáveis ambientais afetam a dinâmica de comunidades. Entretanto, estudos em regiões tropicais e particularmente referentes a comunidades zooplanctônicas são pouco frequentes. Ecossistemas aquáticos tropicais podem ser amplamente influenciados por variações sazonais de precipitação junto as da temperatura do ar, e como resultado, as forças agindo sobre as comunidades aquáticas são diferentes de ecossistemas temperados. Nosso objetivo foi avaliar o efeito das variações sazonais do ambiente nas comunidades zooplanctônicas de reservatórios tropicais utilizando grupos funcionais do zooplâncton (ZFG) baseados em atributos funcionais individuais relacionados com morfologia, habitat, alimentação, escape à predação e reprodução. O zooplâncton e variáveis ambientais foram amostradas por três anos (estações seca e chuvosa). Uma combinação de cluster hierárquico e árvores de regressão e classificação (CART) foi usada para construir e testar os ZFG. Foram identificados seis ZFGs baseados em quatro dos oito atributos originais, em sua maioria relacionados com preferências de habitat e alimentação. A densidade e biomassa dos grupos funcionais foram significativamente explicadas pelas condições ambientais dos reservatórios. O estado trófico, influenciado pela chuva, influenciou as mudanças na dominância dos grupos funcionais de acordo com o habitat. Pelágicos raptoriais e sugadores (Prs) e pelágicos micrófagos com defesa passiva ou natação rápida (Pmi) foram dominantes na maioria dos reservatórios, com exceção do reservatório intensamente colonizado por macrófitas aquáticas, onde os litorâneos micrófagos (Lmi) prevaleceram. A chuva alterou a turbidez na coluna d'água pelo aumento da matéria particulada em habitats pelágicos, favorecendo os Pmi. Os resultados aprovam o uso de abordagens baseadas em atributos funcionais para entender e prever mudanças na comunidade zooplanctônica e ressaltam a relevância da chuva como importante força direcionadora em reservatórios tropicais. A aplicação dessa abordagem para monitorar o efeito da eutrofização e manejo de mudanças hidrológicas se mostra como uma ferramenta promissora.

**Palavras-chave:** tropical, zooplâncton, atributos funcionais, habitat, alimentação, eutrofização, precipitação



## ABSTRACT

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Trait-based approaches have been extensively used in freshwater ecosystems to elucidate how environmental conditions affect community dynamics. However, studies from tropical regions and particularly on zooplankton communities are less frequent. Tropical aquatic ecosystems can be largely influenced by seasonal variation of precipitation besides air temperature, and as a result, the driving forces acting on aquatic communities are different from temperate ecosystems. Our objective was to evaluate the effect of seasonal environmental changes on zooplankton communities of tropical reservoirs using zooplankton functional groups (ZFGs) based on individual traits related to morphology, habitat, feeding, predator avoidance and reproduction. Zooplankton and environmental variables were sampled for three years (dry and rainy seasons). A combination of hierarchical clusters and classification and regression trees (CART) was used to construct and test the ZFG. We identified six ZFGs based on four from the eight original traits, mainly related to habitat and feeding preferences. The density and biomass of the ZFGs were significantly explained by environmental conditions of the reservoirs. Trophic status, influenced by rain, influenced the changes in dominance of ZFGs according to habitat. ZFG Prs (pelagic raptors and suckers) and Pmi (pelagic microphages with passive defense or rapid swimming) were dominant in most reservoirs except in the reservoir intensively colonized by aquatic macrophytes where the ZFG Lmi (littoral microphages) prevailed. Rain altered light in the water column by increasing the amount of particulate matter in pelagic habitats favouring ZFG Pmi. Our results support both the use of trait-based approaches to understand and predict zooplankton communities' changes and the relevance of precipitation as an important driving force in tropical reservoirs. The application of this approach to monitor the effect of eutrophication and hydrological management changes seems to be a promising tool.

**Key words:** tropical, zooplankton, functional traits, habitat, feeding, eutrophication, precipitation

## LISTA DE ILUSTRAÇÕES

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**FIGURE 1:** MAP OF THE STUDY AREA SHOWING THE SOUTHEAST ATLANTIC BASIN, THE RESERVOIRS, ITS DAMS AND A DIAGRAM OF THEIR CONNECTIVITY ARE INCLUDED. KM: KILOMETERS, LAJ: LAJES, PCO: PONTE COBERTA, SAN: SANTANA, VIG: VIGÁRIO. .... 28

**FIGURE 2:** RAINFALL AND TROPHIC STATE INDEX (TSI). MONTHLY DATA FOR RAINFALL AND DATA FOR EACH SAMPLING FOR TROPHIC STATE INDEX. SAN: SANTANA, VIG: VIGÁRIO, PCO: PONTE COBERTA AND LAJ: LAJES. .... 36

**FIGURE 3:** LINEAR REGRESSIONS BETWEEN LENGTH AND WIDTH AMONG ZOOPLANKTON PHYLOGENETIC GROUPS. .... 37

**FIGURE 4:** LENGTH (MM) AMONG TAXONOMIC GROUPS (A) AND FUNCTIONAL TRAITS: HABITAT (B), FEEDING MODE (C) AND PREDATORY ESCAPE RESPONSE (D). LOW SW = SLOW SWIMMING, MED SW = MEDIUM SWIMMING, PAUSE/JUMP= PAUSING AND JUMPING, RAP SW = RAPID SWIMMING. .... 38

**FIGURE 5:** RESULTS OF THE CLASSIFICATION AND REGRESSION TREE (CART) REPRESENTING THE SIX ZOOPLANKTON FUNCTIONAL GROUPS (ZFG: A TO F) AND THE THREE CATEGORICAL TRAITS SELECTED BY THE CART TO CLASSIFY SPECIES. .... 42

**FIGURE 6:** HEATMAP SHOWING ZFG DOMINANCE BY RESERVOIR. TROPHIC STATE INDEX (TSI) SHOWED BY RESERVOIR, YEAR AND SEASON. .... 45

**FIGURA SUPLEMENTAR 1:** DENDROGRAMA OBTIDO A PARTIR DE MATRIZ DE DISTÂNCIAS EUCLIDIANAS COMPLETAS ABRANGENDO OS ATRIBUTOS COMPRIMENTO, LARGURA, BIOMASSA, HABITAT, TIPO DE ALIMENTAÇÃO E ESTRATÉGIA DE ESCAPE A PREDACÃO. .... 71

**FIGURA SUPLEMENTAR 2:** ÁRVORE DE CLASSIFICAÇÃO E REGRESSÃO (CART) DOS GRUPOS FUNCIONAIS OBTIDOS NA FIGURA SUPLEMENTAR 1, ONDE (LIFE; S=SHORT), (HABITAT; P=PELÁGICO), (FEEDING; F=FILTRATION, R=RAPTORIAL, S=SUCKER, SC=SCRAPER), (PER=PREDATORY ESCAPE RESPONSE; LS=SLOW SWIMMING, RS=RAPID SWIMMING). .... 72

## LISTA DE TABELAS

---

**TABLE 1:** MORPHOMETRIC AND HYDROLOGICAL FEATURES OF THE FOUR STUDIED RESERVOIRS. OPER.: START OF OPERATION (YEAR) AREA: AVERAGE AREA (KM<sup>2</sup>); LEVEL.: RANGE OF WATER LEVEL VARIATION (A.S.L.), FROM JANUARY 2011 TO APRIL 2014; TWV: TOTAL WATER VOLUME (HM<sup>2</sup>); WRT: WATER RETENTION TIME (DAYS); TOTAL P: TOTAL PHOSPHOROUS RANGE (MG/L); CHL-A: CHLOROPHYLL-A RANGE (µG/L); SECCHI D: SECCHI DISK DEPTH RANGE (M); TURB: TURBIDITY RANGE (NTU); TROPH ST. INDEX: TROPHIC STATE INDEX AVERAGE BY SEASON (DRY/RAIN), WHERE OLIGO: OLIGOTROPHIC, MESO: MESOTROPHIC AND EUTR: EUTROPHIC. .... **32**

**TABLE 2:** FUNCTIONAL TRAITS OF ZOOPLANKTON SPECIES INCLUDING METHODS, CATEGORIES OF TRAITS, REFERENCES, THE LINEAR REGRESSIONS AND THE LIKELIHOOD RATIO TEST. .... **34**

**TABLE 3:** SUMMARY OF THE ZFG DESCRIPTION: NAME, BODY SIZE RANGE (BS RANGE), CATEGORICAL TRAITS (HABITAT, FEEDING, PREDATORY ESCAPE RESPONSE [SLOW SW: SLOW SWIMMING, MED SW: MEDIUM SWIMMING, RAPID SW: RAPID SWIMMING, PAUSE/JUMP: PAUSING AND JUMPING]), NUMBER OF TAXA (NUM. OF TAXA) BY ZTG (ROTIFERA, CLADOCERA AND COPEPODA) AND MAIN TAXA BY EACH ZFG. .... **40**

**TABLE 4:** MULTIPLE LINEAR REGRESSIONS (MLR) COEFFICIENTS OF DENSITY AND BIOMASS OF THE FUNCTIONAL GROUPS FROM ENVIRONMENTAL VARIABLES (SHOWED ONLY COEFFICIENTS WITH P-VALUE < 0.05) AND ITS R<sup>2</sup> AND P-VALUES. .... **44**

**TABELA SUPLEMENTAR 1:** MATRIZ DE ATRIBUTOS FUNCIONAIS UTILIZADOS E CLASSIFICAÇÃO TAXONÔMICA POR ESPÉCIE. LENGHT E WIDTH (MM) E BIOMASS (MGC.M<sup>-3</sup>)..... **67**

**TABELA SUPLEMENTAR 2:** GRUPOS FUNCIONAIS OBTIDOS NA FIGURA SUPLEMENTAR 1 E OS ERROS DE CLASSIFICAÇÃO APONTADOS PELO CART (FIGURA SUPLEMENTAR 2). .... **72**

## SUMÁRIO

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<b>AGRADECIMENTOS .....</b>	<b>V</b>
<b>RESUMO.....</b>	<b>VIII</b>
<b>ABSTRACT .....</b>	<b>IX</b>
<b>LISTA DE ILUSTRAÇÕES .....</b>	<b>X</b>
<b>LISTA DE TABELAS .....</b>	<b>XI</b>
<b>SUMÁRIO .....</b>	<b>11</b>
<b>INTRODUÇÃO GERAL .....</b>	<b>12</b>
1.    ZOOPLÂNCTON EM RESERVATÓRIOS TROPICAIS: ECOLOGIA E BIODIVERSIDADE.....	12
1.1    RESERVATÓRIOS TROPICAIS.....	12
1.2    COMUNIDADES ZOOPLANCTÔNICAS .....	13
2.    ECOLOGIA FUNCIONAL .....	14
2.1    CONCEITOS .....	14
2.2    ECOLOGIA FUNCIONAL DO ZOOPLÂNCTON .....	15
<b>OBJETIVOS .....</b>	<b>18</b>
<b>REFERÊNCIAS BIBLIOGRÁFICAS DA INTRODUÇÃO GERAL.....</b>	<b>19</b>
<b>CAPÍTULO 1: ZOOPLANKTON FUNCTIONAL GROUPS IN THE TROPICS: THE EFFECT OF TROPHIC STATE AND RAINFALL .....</b>	<b>23</b>
<b>APÊNDICES DO CAPÍTULO 1 .....</b>	<b>67</b>
1.    SEÇÃO DE MATERIAL SUPLEMENTAR .....	67
<b>CONCLUSÃO GERAL .....</b>	<b>73</b>

## INTRODUÇÃO GERAL

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### 1. Zooplâncton em reservatórios tropicais: ecologia e biodiversidade

#### 1.1 Reservatórios tropicais

Reservatórios artificiais são complexos sistemas intermediários entre rios e lagos, cuja evolução depende da entrada de inúmeras informações no tempo e no espaço as quais interferem com os processos de evolução das comunidades planctônicas, bentônicas e de peixes, e com a composição química da água (Tundisi, 1999). Estes sistemas sofrem com frequentes mudanças hidrológicas, já que são corpos d'água manipuláveis operacionalmente. Somados esses fatores às variações climáticas sazonais, os reservatórios podem apresentar características heterogêneas, mesmo quando inseridos numa mesma região hidrográfica (Nilsson, 2009). Além de sua importância econômica, reservatórios são sistemas extraordinariamente ricos no tocante a biodiversidade de alguns grupos, como peixes, algas, rotíferos e cladóceros (Agostinho, Sidinei & Gomes, 2005).

Tundisi (2003) disserta sobre ameaças para a biodiversidade em águas continentais tropicais, citando o tratamento inadequado de água, a presença de grandes áreas urbanas, indústrias e agricultura, além do desmatamento. Estas ameaças, quando atuantes em reservatórios tropicais, causam o aceleração do processo de eutrofização, que é causado pelo aporte de nutrientes, em especial nitrogênio e fósforo, provenientes da agricultura, urbanização, industrialização e o intenso uso do entorno dos ambientes aquáticos, constituindo em fontes difusas. Esse fator tem comprometido a qualidade da água desses sistemas, além da diminuição da diversidade biológica (Lodi *et al.*, 2011).

As mudanças climáticas sofridas em escala global na atualidade tornam o monitoramento de reservatórios tropicais essencial. Vale ressaltar que o monitoramento constante proporciona um conhecimento ecológico mais apurado, visto que as variações do ambiente são rápidas e, em muitos casos, bem significativas. Ao comparar as mudanças de um período para outro, podemos entender a causa de modificações no ambiente a partir da análise das variáveis. O estudo sobre as variáveis físicas, químicas e biológicas avaliam os impactos da eutrofização (Soares *et al.*, 2012). Os resultados de análises de comunidades zooplantônicas auxiliam também no entendimento do processo de eutrofização nos ecossistemas aquáticos continentais (Sampaio *et al.*, 2002).

## 1.2 Comunidades zooplanctônicas

As comunidades zooplanctônicas representam um dos grupos com maior riqueza e abundância em águas continentais (Santos, Moreira & Rocha, 2013). São quatro os principais grandes grupos de invertebrados que compõem o zooplâncton límnic: protozoários, rotíferos, cladóceros e copépodes.

O entendimento da estruturação e estabelecimento das comunidades zooplanctônicas é um dos pontos-chaves para o estudo de reservatórios artificiais, pois estas constituem bioindicadores importantes de aspectos referentes à qualidade de água (Branco *et al.*, 2002; Vieira *et al.*, 2009). Falk-Petersen *et al.* (1999) apontam que o ciclo de vida do zooplâncton facilita a assimilação das variações na qualidade do ecossistema aquático estudado devido ao ciclo ser rápido e totalmente proporcional a qualidade da água do ecossistema mensurado. Algumas espécies são mais suscetíveis a alterações no ecossistema, enquanto outras apenas se desenvolvem em águas de boa qualidade.

As espécies que vivem no plâncton de águas continentais estão submetidas, simultaneamente, a competição por recursos limitados e pressão de predação que são variáveis no tempo e no espaço (Bocaniov & Smith, 2009). O sucesso de uma espécie depende da sua capacidade de usar os recursos disponíveis (alimentos que variam em tamanho, teor de nutrientes e concentração) e na sua estratégia de história de vida para atender às diferentes restrições de alocação de recursos. Considera-se, sob a ótica de dinâmica ambiental, que o plâncton é um sistema funcional integrado à coluna d'água.

Os organismos planctônicos estão no centro de microscópicas malhas de controle com regulação feita pela existência de “feedbacks” entre os organismos e seus ambientes, que inclui também outros organismos, também planctônicos ou não. A característica desta regulação se baseia no metabolismo dos organismos, que exibem diferentes estratégias de vida. A história da estratégia de vida é um produto do conflito entre as demandas metabólicas do organismo, e condições de condições bióticas e abióticas do meio ambiente. Processos evolutivos resultaram em diferentes estratégias de alocação de recursos, como um mecanismo para o sucesso na competição com outros usuários dos mesmos ou semelhantes recursos, e na reação a predadores (Walz, 1995).

Em ambientes aquáticos, o zooplâncton desempenha um papel importante na estruturação de comunidades fitoplanctônicas (McCauley & Briand, 1979; Pinto-Coelho *et al.*, 2005; Jeppesen *et al.*, 2011) e em mediar o fluxo de energia para níveis tróficos superiores em habitats pelágicos (Tundisi, Matsumura-Tundisi & Abe, 2008). Os organismos zooplanctônicos apresentam enorme diversidade de aspectos funcionais, estratégias ecológicas e, conseqüentemente, uma variedade de potenciais impactos em outros níveis tróficos, incluindo a alça microbiana (Obertegger & Manca, 2011; Litchman, Ohman & Kiørboe, 2013).

Diversos estudos no Brasil têm caracterizado as comunidades zooplanctônicas de reservatórios e evidenciado associações com variáveis ecológicas contribuindo para a caracterização dos ecossistemas (Arcifa, 1984; Sampaio *et al.*, 2002; Pinto-Coelho *et al.*, 2005; Sendacz, Caleffi & Santos-Soares, 2006; Perbiche-Neves *et al.*, 2014).

## **2. Ecologia funcional**

### **2.1 Conceitos**

Espécies respondem às condições ambientais de acordo com suas características morfofisiológicas, conferindo a capacidade de se estabelecerem, crescerem e reproduzirem naquelas condições (Keddy, 1992). Pode-se, então, apontar que essas premissas exercem um filtro de restrição à ocorrência de espécies numa comunidade, selecionando somente os indivíduos do banco regional capazes de se desenvolverem nas condições ambientais locais. Esse processo é conhecido por filtro ambiental. O filtro ambiental pode dar origem a uma assembleia com aspectos semelhantes dentro de uma comunidade (Lortie *et al.*, 2004).

A abordagem funcional foi proposta para descortinar o papel do filtro ambiental como agente edificador dos padrões de diversidade de espécies em uma comunidade (Villéger, Mason & Mouillot, 2008). A ecologia funcional abrange o conjunto de interações tróficas e ambientais que interferem na abundância e dinâmica populacional dos organismos (Calow, 1987).

Atributos funcionais definem espécies em termos de suas funções ecológicas - como elas interagem com o ambiente e com outras espécies (Díaz & Cabido, 2001). O termo, de acordo com Geber & Griffen (2003), abrange características que influenciam a aptidão de um

organismo e podem ser selecionadas por meio de testes bioquímicos, entre características fisiológicas, morfológicas, mecanismos de desenvolvimento, ou de comportamento.

Pesquisas em comunidades de diversos ecossistemas têm mostrado que a relação entre ecologia funcional e riqueza é complexa e contexto dependente. Diferentes características funcionais podem mostrar as respostas individuais aos diferentes gradientes bióticos e abióticos, significando que importantes mudanças na diversidade funcional podem ocorrer com alteração mínima da riqueza. Além disso, considera-se que a diversidade funcional pode refletir pequenas alterações no ecossistema, mesmo quando a riqueza não (Cadotte, Carscadden & Mirotnick, 2011).

A ecologia funcional é uma subárea da ecologia com resultados bastante consolidados para alguns grupos biológicos, como o fitoplâncton e plantas terrestres (Reynolds *et al.*, 2002; Suding *et al.*, 2008; Kruk *et al.*, 2010; Beamud *et al.*, 2015; Shipley *et al.*, 2016). Na área da zoologia, destacam-se trabalhos com peixes e macroinvertebrados bentônicos (Toussaint *et al.*, 2016; Kopf, Shaw & Humphries, 2017).

Para o zooplâncton, apesar de atuais, as abordagens ainda representam um cenário em formação. O primeiro trabalho publicado de ecologia funcional do zooplâncton tem pouco mais de dez anos (Barnett, Finlay & Beisner, 2007), mas nos últimos anos foram publicados diversos artigos em revistas de alto fator de impacto discutindo abordagens funcionais (Benedetti, Gasparini & Ayata, 2015; Obertegger & Flaim, 2015; Pomerleau, Sastri & Beisner, 2015; Lokko, Virro & Kotta, 2017; Rizo *et al.*, 2017; Braghin *et al.*, 2018; Redmond, Loewen & Vinebrooke, 2018). O cenário é mais carente em regiões tropicais, onde poucos trabalhos foram publicados.

## **2.2 Ecologia funcional do zooplâncton**

Apesar da carência de bibliografia, deve ser ressaltado que os primórdios da discussão sobre ecologia funcional do zooplâncton datam antes mesmo do conceito de ecologia funcional ser amplamente difundido na academia. Dodson (1974), ao propor a “size-efficiency hypothesis”, organizou espécies zooplanctônicas em grupos levando em consideração sua alimentação e tamanho. Outros trabalhos, apesar de não direcionarem a



aspectos ecológicos, tratam as similaridades morfofisiológicas de espécies do zooplâncton (Allan, 1976; Lynch, 1980; Pejler, 1983).

O primeiro trabalho a tratar da expressão conceitual ecologia funcional do zooplâncton foi o de Barnett *et al.* (2007)<sup>1</sup>, que proporcionou uma síntese de características funcionais disponíveis para de espécies de cladóceros e copépodes com base em cerca de cinco décadas de estudos de laboratório e observações em lagos canadenses e propôs um agrupamento funcional a partir de um dendrograma.

O trabalho de Boit *et al.* (2012) seguiu na linha da ecologia funcional do zooplâncton buscando padrões na modelagem do funcionamento do Lago Constance, na Suíça, e propondo guildas zooplancônicas baseadas no tamanho de organismos. Litchman *et al.*, (2013) apresentou uma abordagem para estudos de modelagem de comunidades planctônicas pelágicas baseada em atributos funcionais do zooplâncton. Hulot, Lacroix & Loreau (2014) realizaram um estudo de meta-análise para investigar respostas de espécies pelágicas ao enriquecimento de nutrientes e propôs grupos funcionais dentro do zooplâncton constituídos por pequenos herbívoros, grandes herbívoros e onívoros. Obertegger & Flaim (2015) sintetizaram padrões de atributos funcionais em rotíferos relacionados a aquisição de alimento e defesa contra predadores em estudo em um lago na Itália.

A partir de 2017, as abordagens avançaram mais. Rizo *et al.* (2017) propuseram grupos funcionais para cladóceros em ambientes tropicais e subtropicais. Diferente de Barnett *et al.* (2007), este testou a significância dos atributos funcionais para sugerir os grupos funcionais. Em outras palavras, o autor aponta que é necessário avaliar se estes atributos possuem de fato uma correlação com o ambiente estudado e suas variáveis físicas, químicas e hidrológicas. Dentre os trabalhos de diversidade funcional de Cladocera, o de Rizo *et al.*

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1 O TRABALHO FOI CORRIGIDO E PUBLICADO CORRIGENDUM POSTERIORMENTE EM 2013.

BARNETT A.J., FINLAY K. & BEISNER B.E. (2013) FUNCTIONAL DIVERSITY OF CRUSTACEAN ZOOPLANKTON COMMUNITIES: TOWARDS A TRAIT-BASED CLASSIFICATION. *FRESHWATER BIOLOGY*, 52, 796-813. DOI: 10.1111/j.1365-2427.2007.01733.x. *FRESHWATER BIOLOGY* 58, 1755–1765.)

(2017) é o que apresenta a maior matriz de atributos funcionais. Destaca-se também o trabalho de Lokko *et al.* (2017), que sugeriu grupos funcionais para rotíferos psâmicos de três lagos na Estônia. Este último é interessante pelo fato dos três lagos formarem um gradiente de trofia, mostrando como os grupos funcionais se comportam em ambientes tróficos, mesotróficos e hipertróficos. O trabalho, além de levar em consideração atributos funcionais relacionados a trofia, faz também uma correlação dos grupos com variáveis físicas e químicas que são consideradas indicadores de trofia.

Os desafios dentro da ecologia funcional do zooplâncton se amplificam em regiões tropicais. São poucos trabalhos publicados (Rizo *et al.*, 2017; Braghin *et al.*, 2018). Para reservatórios tropicais, a abordagem é, até o momento, inédita.

## **OBJETIVOS**

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- Propor grupos funcionais para as comunidades zooplanctônicas de quatro reservatórios do sudeste do Brasil.
- Verificar a associação dos grupos funcionais das comunidades zooplanctônicas com atributos do fitoplâncton, fatores físicos, químicos e hidrológicos dos ambientes estudados.

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## **CAPÍTULO 1: Zooplankton functional groups in the tropics: the effect of trophic state and rainfall**

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Ewerton Fintelman, Carla Kruk, Gissell Lacerot, Gabriel Klippel, Christina Castelo Branco

### **Abstract**

Trait-based approaches have been extensively used in freshwater ecosystems to elucidate how environmental conditions affect community dynamics. However, studies from tropical regions and particularly on zooplankton communities are less frequent. Tropical aquatic ecosystems can be largely influenced by seasonal variation of precipitation besides air temperature, and as a result, the driving forces acting on aquatic communities are different from temperate ecosystems. Our objective was to evaluate the effect of seasonal environmental changes on zooplankton communities of tropical reservoirs using zooplankton functional groups (ZFGs) based on individual traits related to morphology, habitat, feeding, predator avoidance and reproduction. Zooplankton and environmental variables were sampled for 3 years (dry and rainy seasons). A combination of hierarchical clusters and classification and regression trees (CART) was used to construct and test the ZFG. We identified six ZFGs based on four from the eight original traits, mainly related to habitat and feeding preferences. The density and biomass of the ZFGs were significantly explained by environmental conditions of the reservoirs. Trophic status, influenced by rain, influenced the changes in dominance of ZFGs according to habitat. ZFG PR (pelagic raptors and suckers) and PM (pelagic microphages with passive defense or rapid swimming) were dominant in most reservoirs except in the reservoir intensively colonized by aquatic macrophytes where the ZFG LM (littoral microphages) prevailed. Rain altered light in the water column by increasing the amount of particulate matter in pelagic habitats favouring ZFG PM. However, in littoral sites only temperature had a significant influence on ZFG. Our results support both the use of trait-based approaches to understand and predict zooplankton communities' changes and the relevance of precipitation as a main driving force in tropical reservoirs. The application of this approach to monitor the effect of eutrophication and hydrological management changes seems to be a promising tool.

**Key words:** tropical, zooplankton, functional traits, habitat, feeding, eutrophication, precipitation



## Introduction

Zooplankton plays an important role in structuring phytoplankton communities (Pinto-Coelho *et al.*, 2005; Jeppesen *et al.*, 2011), mediating the bioavailability of nutrients and flow of energy to upper trophic levels (Hébert, Beisner & Maranger, 2017). Zooplanktonic organisms exhibit enormous diversity of physiological attributes, ecological strategies and, consequently, a variety of potential impacts on other trophic levels including the microbial loop (Obertegger & Manca, 2011; Litchman, Ohman & Kiørboe, 2013; Obertegger & Flaim, 2015). The complexity of the myriad plankton species interrelations, their relationships with other links of the aquatic trophic web and the influence of physical and chemical aspects of the water column turn the delineation of planktonic dynamics a challenge.

Trait-based approaches have been extensively used in freshwater ecosystems to elucidate how environmental conditions affect community dynamics. Functional traits are those that define species in terms of their ecological functions - how they interact with the environment and with other species (Díaz & Cabido, 2001). According to Geber & Griffen (2003), functional traits are individual features that influence fitness and include physiological, morphological, developmental, or behavioural organisms traits (Violle *et al.*, 2007; Kruk *et al.*, 2010). In phytoplankton, for instance, functional traits generally include body size, tolerance/sensitivity to environmental conditions, motility, shape, N-fixing capacity, content of silica and nitrogen compounds, growth and sinking rate, and population size and biomass attained in the field (Reynolds *et al.*, 2002; Kruk *et al.*, 2010). While phytoplankton studies have increasingly emphasized the use of functional traits in ecological research, this approach is still incipient for zooplankton. Zooplankton functional traits should also reflect the main relevant functions, including secondary production, resources acquisition (food preferences, feeding strategies), growth and reproduction, and mortality avoidance (hydrological and from predators) (Gillooly & Dodson, 2000; Le Quere *et al.*, 2005; Barnett, Finlay & Beisner, 2013). These complex features describe the ecological role of species based on how they interact with each other and with their environment (Hébert *et al.*, 2017). In a broad perspective, the challenge in the study of functional traits has been to delineate mechanisms of functional community responses to changes in trophic and environmental features (Litchman *et al.*, 2013).

Early freshwater zooplankton functional groups date back to the propose of Romanovsky (1984) for cladoceran species. Based species on their body weight at maturity, maximum birth rate, and resistance of juveniles to food deficiency and size the author classified cladocerans into: “competitors or violents (C)”, “stress tolerators or patients (S)”, and “ruderal or explerents (R)”, (Romanovsky, 1984, 1985). Since then, the application of trait-based approaches has increased both in marine and freshwater ecosystems, for the whole zooplankton community or taxonomic groups, and with traits related to size, feeding mode/selectivity, habitat and role as prey as the most commonly used. For instance, Barnett, Finlay & Beisner (2007) provided a synthesis of functional characteristics for cladoceran species based on about five decades of laboratory and observational studies in Canadian lakes, Boit *et al.* (2012) sought patterns in modelling the functioning of a widely studied lake (Lake Constance, Switzerland), suggesting possible zooplanktonic guilds based on the size of organisms, and Litchman *et al.* (2013) performed modelling studies of pelagic plankton communities including possible functional traits of zooplankton. Hulot, Lacroix & Loreau (2014), working on a meta-analysis to investigate responses of pelagic species to nutrient enrichment, proposed functional groups within the zooplankton constituted by small herbivores, large herbivores and omnivores. More detailed studies on functional diversity within the zooplankton community have been done with rotifers. Obertegger & Flaim (2015, 2018) synthesized functional trait patterns in this group related to food acquisition, defence against study predators on a lake in Italy. These authors found that different aspects of rotifer life outlined important drivers that would have been neglected by focusing only on species abundance. Lokko, Virro & Kotta (2017) characterized psammic rotifer communities in terms of taxonomic and trophic traits indicating that rotifers have different functional roles in food webs in fresh and brackish water environments. Few studies, however, analysed traits or functional groups in terms of their response to environmental changes.

All research reported above was conducted in temperate region and therefore the few studies from tropical region must be emphasised. Rizo *et al.* (2017) grouped tropical and subtropical cladocerans from Asia into eight major functional groups, each with their own ecological function and highlighted the minimal information available zooplankton functional traits in the tropics. These authors also pointed out that functional trait affect the coexistence of cladocerans. More recently, Braghin *et al.* (2018) evaluating taxonomic and functional  $\beta$ -diversity of zooplankton in lakes in a Neotropical floodplain influenced or not

by damming, used six functional traits for the categorisation of zooplankton species. This last study included continuous (mean body length), categorical (habitat, feeding type, reproduction), and ordinal (life span, predatory scape response) trait classes.

These few studies on the functional diversity of tropical zooplankton contrast with the high species richness of these systems, which may present species with several different life-history characteristics (Sarma, Nandini & Gulati, 2005; Missias *et al.*, 2017), grazing effect on phytoplankton (Pagano, 2008), and different functional grouping associations comparing with temperate counterparts (Rizo *et al.*, 2017). Besides different composition of zooplankton community and variability in trophic interactions, tropical aquatic ecosystems have been differentiated environmentally from those in temperate regions mainly by the temperature. However, despite the contrasts in temperature variation, the most pronounced difference between temperate and tropical aquatic systems can be related to the larger influence of rainfall over the last (Talling, Talling & Lemoalle, 1998). Unlike temperate regions, rainfall governs the plankton dynamics in most tropical inland waters (De Senerpont Domis *et al.*, 2013), where peculiar dynamics influencing zooplankton such as fast changes due to heavy rains bringing a greater amount of sediments, turbidity and nutrients to the aquatic ecosystems can be found (Fantin-Cruz *et al.*, 2010; Branco, Silveira & Marinho, 2018).

Artificial reservoirs constructed for hydropower generation are increasingly common throughout the world, especially in the tropical and subtropical areas where demands for energy are growing (Anderson *et al.*, 2018; Couto & Olden, 2018). These aquatic ecosystems are complex intermediate systems between rivers and lakes since they meet heterogeneous hydrological patterns. Their dynamic depends on the entrance of innumerable information in time and space which interfere with the evolutionary processes of the planktonic, benthic and fish communities and with the chemical composition of water. As a result, zooplankton communities main driving environmental factors are affected by reservoirs hydrological features (Almeida *et al.*, 2009; Guevara *et al.*, 2009) and nutrients input. Several studies have characterized the zooplankton communities of reservoirs in Brazil and evidenced that different assemblages indicate distinct environment conditions including trophic state (Sampaio *et al.*, 2002; Pinto-Coelho *et al.*, 2005; Sendacz, Caleffi & Santos-Soares, 2006).

As in other aquatic ecosystems subjected to anthropic impacts, environmental monitoring tools have been developed for reservoirs to gather information on the ecological status and/or trophic conditions. Ecological status here is defined as an expression of the quality of the structure and functioning of aquatic ecosystems based on the assessment of a series of biological quality elements and supported by a set of chemical and hydromorphological quality data (Jeppesen *et al.*, 2011). Zooplankton functional groups may be usable as a monitoring tool in tropical reservoirs as they are affected by the ecosystem processes. Although the taxonomic resolution of zooplankton has been considered important for the quality of the environmental monitoring in hydroelectric reservoirs (Missias *et al.*, 2017), the information contained in groups of species with different functionalities can bring a greater understanding of the dynamics occurring in the water column. However, to date, there is no record in the literature of the functional group approach in zooplankton studies of these systems.

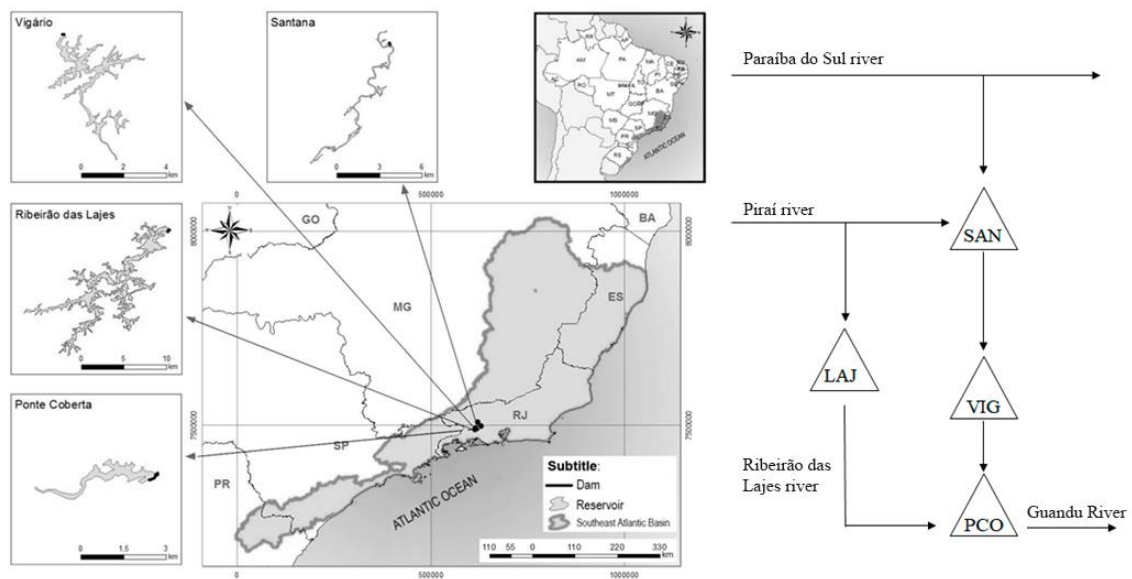
In the present study, we aimed to propose zooplankton functional groups (ZFG) for tropical reservoirs using individual functional traits. Functional traits were chosen to represent main zooplankton ecological functions related to fitness in the reservoirs, and included body size, life span, reproduction and survival related traits, as well as habitat preferences. We sampled during three years four reservoirs in southeastern Brazil. We considered zooplankton communities (copepods, cladocerans and rotifers) and environmental variables (e.g. Secchi disk depth, chlorophyll-*a*, total phosphorous). Cluster and classification trees (CART) were used to select and construct ZFG. Their relation with environmental gradients was evaluated and main drivers of zooplankton communities' assembly in reservoirs were identified.

## **Methods**

### **Study area**

We sampled five reservoirs twice a year during three years. The reservoirs are primarily used for hydropower generation, and secondarily for domestic and industrial water supply, irrigation, and artisanal fishing. Santana (SAN), Vigário (VIG) and Ponte Coberta (PCO) reservoirs are located in the Guandu River Basin (Figure 1). However, SAN also receives water transposed from the Paraíba do Sul River, which then cascades down to VIG

and PCO. Lajes reservoir (LAJ) receives water from the Pirai River, as well as contributions from small tributaries of Rio Claro Municipality (e.g. Prata and Bálamo rivers). Downstream VIG and LAJ, is the reservoir of PCO embedded in the Ribeirão das Lajes River, which forms the Rio Guandu. This last river supplies the second largest metropolitan region in Brazil, providing domestic supply for nine million people through the Water Treatment Plant of Guandu (Kelman, 2015). Because of this plant and according to demands for hydroelectric power generation the water levels of the reservoirs are artificially controlled. SAN, VIG and PCO have lower seasonal variation (2 to 3 meters), and LAJ higher (6 to 7 meters) (Guarino *et al.*, 2005; Lopes *et al.*, 2017). Water level is lower by the end of the dry season (October and November) and higher at the end of the rainy season (March and April). Morphometric and hydrological features of the reservoirs are summarized in Table 1.



**Figure 1:** Map of the study area showing the southeast Atlantic Basin, the reservoirs, its dams and a diagram of their connectivity are included. Km: kilometers, LAJ: Lajes, PCO: Ponte Coberta, SAN: Santana, VIG: Vigário.

### Sampling strategy and analysis

Samplings covered three dry seasons and three rainy seasons, between July 2011 and January 2014. The number of sampling sites in the limnetic zone of each reservoir was selected in accordance with its size. SAN and VIG reservoirs included three sampling sites, at the upper part (head) of the reservoir, in the middle, and near the dam. In PCO one

sampling point was located at the head and near the dam. In LAJ, four points were included following the same gradient from the head of the reservoir to the dam.

### Sample analyses

Total phosphorus was analysed by persulfate digestion according to APHA (2005). Chlorophyll-*a* was determined by extraction with ethanol 90% according to Lush & Palmer (1975). For zooplankton quantitative analysis, five subsamples were analysed in the laboratory in a 1-mL Sedgewick-Rafter chamber, under an Olympus BX51 optical microscope. If the counting of five subsamples did not reach 200 organisms, the entire sample was counted. The entire sample was inspected for rare species. Nauplii, copepodites and adults of Calanoida and Cyclopoida copepod species were counted separately. Adults were identified at species level, when possible. Taxonomical identifications followed (Koste, 1978; Streble & Krauter, 1987; Dussart & Defaye, 1995; Segers, 1995; Elmoor-Loureiro, 1997). Results were expressed in ind.m<sup>-3</sup>. Taxa obtained were separated in three zooplankton phylogenetic groups Cladocera, Copepoda and Rotifera.

Biomass of rotifers was estimated by volume according to Ruttner-Kolisko (1977). Individual dry weight was calculated as the percentage of fresh weight according to (Pauli, 1989), being specific for each taxon. At least 20 individuals of each taxon of rotifers were measured. The dry weight of the microcrustaceans (cladocerans and copepods) was obtained with a microbalance (Mettler UMT-5), after being dried at 60°C for 24 hours. At least 30 individuals of each taxon of cladocerans or copepods were weighted. Due to the low abundance of Harpacticoid copepods, calculation of their dry weight was estimated by a regression equation according to Dumont, Velde & Dumont (2012). The method of Manca & Comoli (1999) was used to calculate the dry weight of copepods nauplii (dry weight=10% volume). The carbon content of the biomass was expressed in micrograms of carbon per liter (µgC.L<sup>-1</sup>), assuming that the organic carbon content for all zooplankton species is 50% of their dry weight (Latja & Salonen, 1978).

### **Estimation of the reservoirs trophic state**

We adopted the modified Carlson Trophic State Index (TSI) by Toledo Jr. *et al.* (1983) for tropical systems, to estimate the trophic conditions of the reservoirs in each sampling. The equations for the trophic state index (TSI) include water transparency (Secchi Disk), chlorophyll-*a*, total phosphorus and soluble reactive phosphate. The proposed limits for the trophic categories were oligotrophic:  $TSI \leq 44$ ; mesotrophic:  $44 \leq TSI \leq 54$ ; eutrophic:  $TSI \leq 54$ .

### **Identifying functional traits**

Functional traits were chosen to represent main zooplankton ecological functions in the reservoirs related to fitness and included growth, reproduction and survival related traits, as well as habitat (Litchman *et al.*, 2013). Three continuous traits (length, width and biomass) and five categorical traits (habitat preferences, feeding mode and preferences, predatory escape response, life span and reproduction) were estimated for each specie (Table 2). Length ( $\mu\text{m}$ ), width ( $\mu\text{m}$ ) and biomass ( $\mu\text{gC}$ ) were estimated as explained above for each species and considering information from all studied period. Categorical traits were determined for each species from literature information (Allan, 1976; Koste, 1978; Lynch, 1980; Fryer, 1996; Barnett, Finlay & Beisner, 2013; Bradley *et al.*, 2013; Obertegger & Flaim, 2015; Perbiche-Neves *et al.*, 2015; Rizo *et al.*, 2017). For habitat preferences, we used a combination of literature and information of occurrence in the studied reservoirs and other tropical systems.

### **Data analysis**

The relations among traits were analysed using linear regressions. The change in average and variance values of continuous traits among different values of categorical traits (habit, feeding, predatory scape response) and groping species into rotifers, cladocerans and copepods was analysed through the likelihood ratio test (LRT) and the R-package 'nlme' (Pinheiro *et al.*, 2018).

To construct zooplankton functional groups (ZFGs) a combination of techniques was applied including hierarchical cluster and classification and regression trees (CART). Traits with non-normal distribution were standardized by the 0-1 range method, proposed by

Hedrick (2005). The information of average traits ( $n=8$ ) for each species ( $n=121$ ) was transformed into a distance matrix. A hierarchical clustering was done using Gower (1971) distances to combine categorical and continuous traits (Legendre & Gallagher, 2001).



**Table 1:** Morphometric and hydrological features of the four studied reservoirs. OPER.: Start of operation (year) AREA: Average Area (km<sup>2</sup>); LEVEL.: Range of water level variation (a.s.l.), from January 2011 to April 2014; TWV: Total Water Volume (hm<sup>3</sup>); WRT: Water Retention Time (days); TOTAL P: Total Phosphorous range (mg/L); CHL-A: Chlorophyll-*a* range (µg/L); SECCHI D: Secchi Disk depth range (m); TURB: Turbidity range (NTU); TROPH ST. INDEX: Trophic State Index average by season (Dry/Rain), where OLIGO: oligotrophic, MESO: mesotrophic and EUTR: eutrophic.

RESERVOIR	OPER. year	AREA km <sup>2</sup>	LEVEL VAR. (a.s.l.)	TWV hm <sup>3</sup>	FLOW m <sup>3</sup> /s	WRT days	TOTAL P mg/L	CHL-A µg/L	SECCHI D m	TURB NTU	TROPH. ST. INDEX	
											Dry	Rain
<b>Santana</b>	1954	5.23	361.6 - 363.5	15.2	174.8	1.0	0.04 - 0.16	0.1-3.4	0.1 - 1.8	7.3 - 491	51.3	57.9
											MESO	EUTR
<b>Vigário</b>	1954	3.33	396.9 - 398.9	27.6	158.0	2.0	0.06 - 0.14	0.1-5.9	0.2-1.3	6 - 126	50.3	54.2
											MESO	EUTR
<b>Ponte Coberta</b>	1962	1.09	83.2 - 86.5	16.9	170.0	1.1	0.05 - 0.14	0.1 - 3.1	0.3 - 1.6	5.4 - 45	45.24	54.2
											MESO	EUTR
<b>Lajes</b>	1908	30.7	409.4 - 415.4	467.3	17.99	300.6	0.01 - 0.05	0.1 - 5.9	0.2 - 7.0	0 - 38	38.1	38.3
											OLIGO	OLIGO

To select the best number of groups, k-means partitions were generated and partitions with at least 75% of total variance were selected (Legendre & Legendre, 1998).

To identify which traits best influence groups differences and to evaluate the accuracy of the ZFG established by hierarchical clustering, CART analyses were done (Kruk & Segura, 2012) using the R “rpart” package (Warnes *et al.*, 2018). In a first CART analysis the classification errors (E) were estimated for each ZFG ( $E = [\text{misclassified cases} / \text{total number of cases}] \times 100$ ). ZFGs with E larger than 5% were revised and the misclassified species reclassified with the tree into ZFG with higher similarity. Then, a second CART analysis with the improved classification was performed to construct a classification key to classify new entries.

The values of density ( $\text{ind.m}^{-3}$ ) and biomass ( $\mu\text{gC.L}^{-1}$ ) of the ZFG were obtained by adding the respective values of each taxon classified into the group in each reservoir.

The dominance of each ZFG ( $\text{Dom}_{\text{ZFG X}}$ ) was estimated as  $\text{Dom}_{\text{ZFG X}} (\%) = D_{\text{ZFG X}} / (\sum D_{\text{ZFG X}} 100)$ , where  $D_{\text{ZFG X}}$  represents the density of ZFG and  $\sum D_{\text{ZFG}}$  represents the sum of densities of all ZFGs. To evaluate the degree of similarity and distribution of the ZFG dominance in the reservoirs, we constructed a heatmap using the "gplots" R package (Warnes *et al.*, 2018).

All data was tested for normality if applicable (Shapiro-Wilk tests) and transformed if necessary. All analysis were performed in R (R Core Team, 2017).

**Table 2:** Functional traits of zooplankton species including methods, categories of traits, references, the linear regressions and the likelihood ratio test.

	<b>CATEGORIES</b>	<b>REFERENCES (range)</b>	<b>Linear Regression / Likelihood Ratio Test</b>	
<b>LENGTH</b>	Continuous variable ( $\mu\text{m}$ )	This study – (70 $\mu\text{m}$ – 1340 $\mu\text{m}$ )	<b>Width</b>	$R^2=0.51$ ; $Y = 116.63 + 1.48x$ ; $p < 0.0001$
			<b>Biomass</b>	$R^2=0.50$ ; $Y = 2.73 + 0.26x$ ; $p < 0.0001$
<b>WIDTH</b>	Continuous variable ( $\mu\text{m}$ )	This study – (32 $\mu\text{m}$ – 810 $\mu\text{m}$ )	<b>Length</b>	$R^2=0.51$ ; $Y = 116.63 + 1.48x$ ; $p < 0.0001$
			<b>Biomass</b>	$R^2=0.61$ ; $Y = -5.26 + 1.98x$ ; $p < 0.0001$
<b>BIOMASS</b>	Continuous variable ( $\mu\text{gC.m}^{-3}$ )	This study – (0,002 $\mu\text{gC.m}^{-3}$ – 4,5 $\mu\text{gC.m}^{-3}$ )	<b>Length</b>	$R^2=0.52$ ; $Y = 2.73 + 0.26x$ ; $p < 0.0001$
			<b>Width</b>	$R^2=0.61$ ; $Y = -5.26 + 1.98x$ ; $p < 0.0001$
<b>HABITAT</b>	Pelagic and Littoral	Koste, 1978; Barnett <i>et al.</i> , 2007; Perbiche-Neves <i>et al.</i> , 2015	<b>Length</b>	LR=7.64; $p < 0.005$
			<b>Width</b>	LR=5.33; $p = 0.02$
			<b>Biomass</b>	LR=8.59; $p < 0.005$
<b>FEEDING TYPE</b>	Filtration, Microphagous, Raptorial, Scraper, and Sucker	Brooks & Dodson, 1965; Koste, 1978; Elmoor-Loureiro, 1997	<b>Length</b>	LR=60.80; $p < 0.0001$
			<b>Width</b>	LR=55.39; $p < 0.0001$
			<b>Biomass</b>	LR=94.87; $p < 0.0001$
<b>LIFE SPAN</b>	Short and Long	Allan, 1976	<b>Length</b>	LR=30.58; $p < 0.0001$
			<b>Width</b>	LR=38.92; $p < 0.0001$
			<b>Biomass</b>	LR=17.57; $p < 0.0001$
<b>PREDATORY ESCAPE RESPONSE</b>	Slow Swimmersing, Medium Swimmersing, Rapid Swimmersing, Pause/Jump, and Passive	Bradley <i>et al.</i> , 2013; Obertegger & Flaim, 2015; Rizo <i>et al.</i> , 2017	<b>Length</b>	LR=59.92; $p < 0.0001$
			<b>Width</b>	LR=46.89; $p < 0.0001$
			<b>Biomass</b>	LR=43.98; $p < 0.0001$
<b>REPRODUCTION</b>	Asexual and Sexual	Allan, 1976; Lynch, 1980; Fryer, 1996	<b>Length</b>	LR=9.63; $p < 0.005$
			<b>Width</b>	LR=2.65; $p = 0.10$
			<b>Biomass</b>	LR=4.70; $p = 0.03$

## Multiple linear regressions (MLR)

Multiple linear regression (MLR) models were used to evaluate the relationship between ZFGs density and biomass and explanatory environmental variables. Variables were standardized with the same methodology proposed for the traits (0-1 range). To avoid multicollinearity, variables with a Variance Inflation Factor  $> 20$  were removed from the following MLR models (ter Braak, 1986), using the R package 'HH' (Heiberger, 2018). To select the most appropriate models we applied Akaike Information Criteria (AIC) using the R package 'MASS' (Ripley *et al.*, 2011). The finally selected models were those with the lowest AIC with at least one significant coefficient ( $p < 0.05$ ) (Kruk *et al.*, 2017).

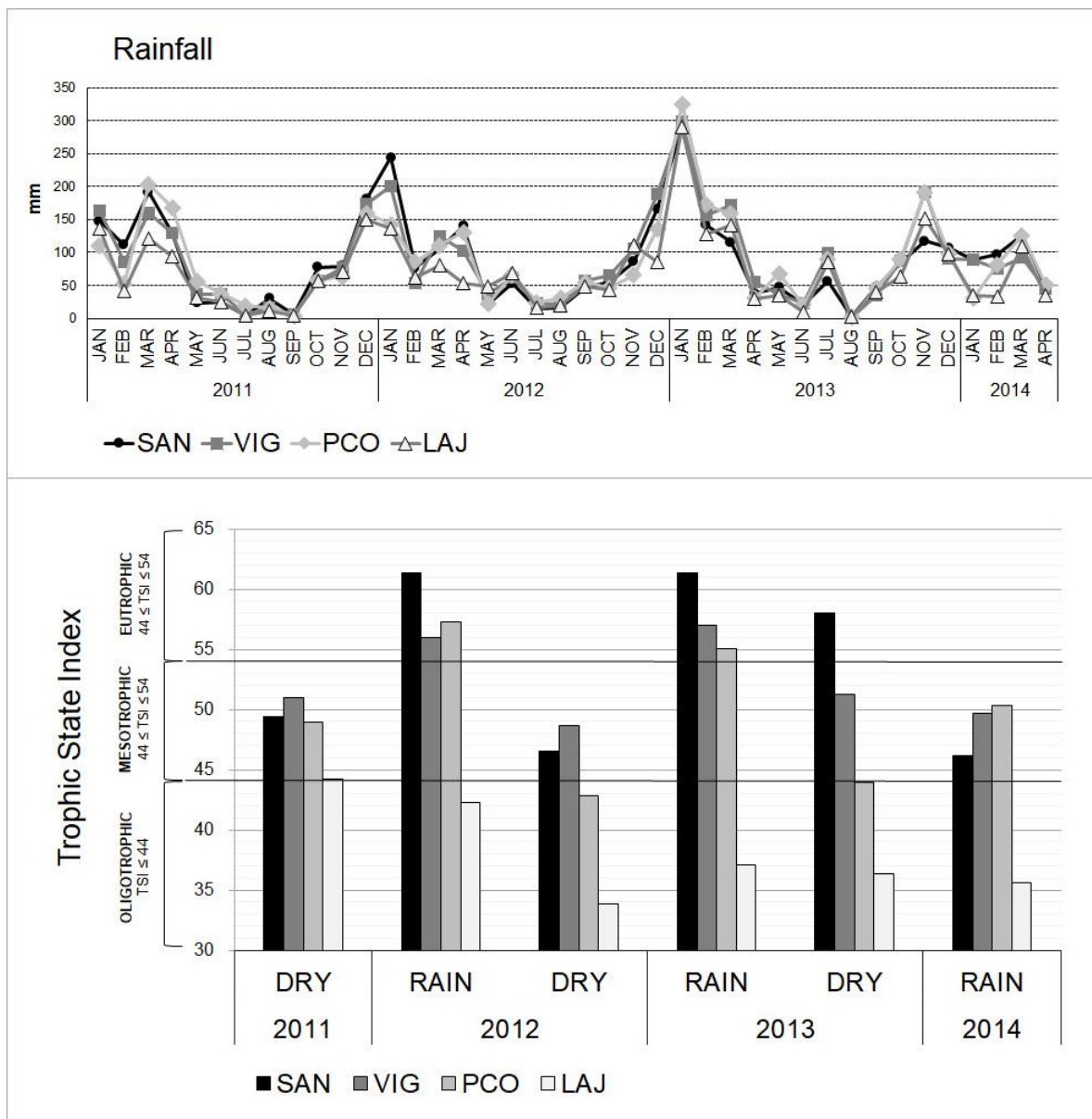
## Results

### Environmental variables and trophic conditions

SAN, VIG and PCO reservoirs presented the highest values of total phosphorus, chlorophyll-*a* and lower Secchi disk depth (Table 1). LAJ presented lower values for these variables, and higher Secchi disk depth representative of oligotrophic conditions during dry and rainy seasons. All reservoirs but LAJ had different trophic states during dry (mesotrophic) and rainy (eutrophic) seasons (Table 1, Figure 2). Precipitations values during dry seasons (June/July) were often  $< 100$  mm, while during rainy seasons (December/January)  $> 150$  mm (Fig. 2). However, there were some exceptions to this pattern. During rainy season 2013, rainfall values approached 250 mm in SAN, and in the same season of 2013, it rained approximately 300 mm in all the reservoirs. The latter was the highest amount of rain recorded for the entire study. The opposite occurred in 2014, as rainfall values during rainy season did not increase in relation to the dry season, with values close to 100 mm.

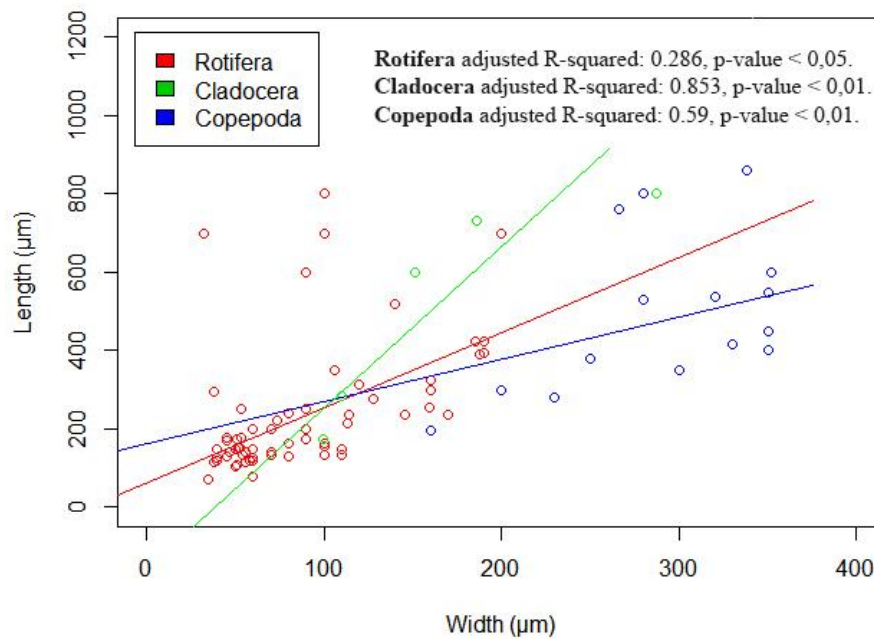
### Zooplankton body size and functional traits

We identified 121 zooplankton taxa during the 3 sampling years, including Rotifera (86 taxa), Cladocera (23 taxa) and Copepoda (12 taxa). Length and width were significantly related in each zooplankton main taxonomic group, resulting also in significantly different adjusted models (Figure 3). Linear regressions showed that rotifers, cladocerans and copepods have similar size variations.



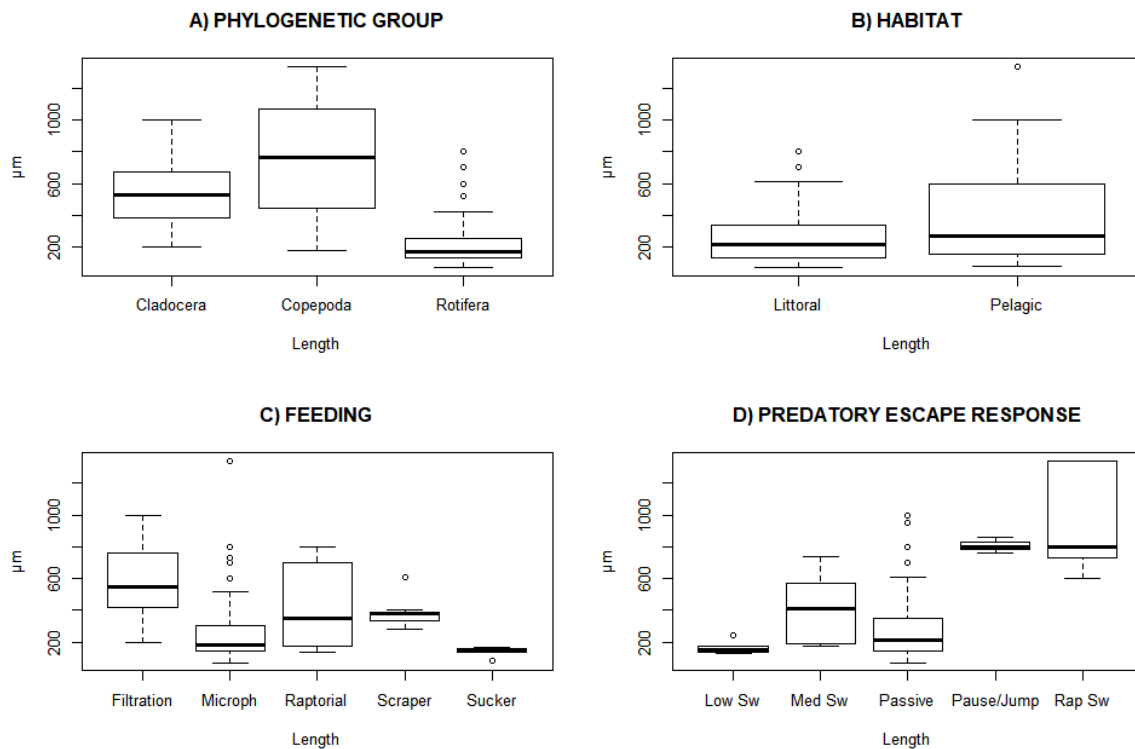
**Figure 2:** Rainfall and Trophic State Index (TSI). Monthly data for rainfall and data for each sampling for Trophic State Index. SAN: Santana, VIG: Vigário, PCO: Ponte Coberta and LAJ: Lajes.

Among zooplankton taxonomic groups (Figure 4a), copepods had the largest size range (175-1340  $\mu\text{m}$ ) and rotifers the smaller size range (70-800  $\mu\text{m}$ ), although most values were between 70 and 520 $\mu\text{m}$ . Cladocerans showed a length range of between 197 and 1000 $\mu\text{m}$ . By habitat, pelagic had larger size range than littoral (Figure 4b). In feeding (Figure 4c), filter feeders (70-610 $\mu\text{m}$ ) and raptorial (140-800 $\mu\text{m}$ ) had larger size range than microphages, suckers and scrapers. Predatory escape responses (Figure 4d) showed rapid swimmers as the larger size range (520-1340 $\mu\text{m}$ ) and the slow swimmer as the smaller (170-175 $\mu\text{m}$ ).



**Figure 3:** Linear regressions between length and width among zooplankton phylogenetic groups.

Eight zooplankton functional traits were evaluated including three continuous (length, width, biomass) and five categorical variables (habitat, feeding type, life span, predatory scape response and reproduction) (Table 3). Two-habitat type, littoral and pelagic, occurred in the three main taxonomic groups. Five feeding types were identified. Rotifers were mostly microphages, some raptors and suckers taxa species were also recorded. Cladocerans were represented mainly by filter-feeders (Bosminidae, Daphnidae and Sididae families) and scrapers species (Chydoridae family). Among copepods, microphages and raptorials species were observed. Span of life was classified in two: short and long. Short encompassing rotifers and cladocerans and long the copepods. For reproduction, rotifers and cladocerans were defined as asexual and sexual and copepods only sexual.



**Figure 4:** Length (µm) among taxonomic groups (A) and functional traits: habitat (B), feeding mode (C) and predatory escape response (D). Low Sw = Slow swimming, Med Sw = medium swimming, Pause/Jump= Pausing and jumping, Rap Sw = rapid swimming.

We recorded six predatory escape responses including three classes of swimming capacity, according to literature (Allan, 1976; Obertegger & Flaim, 2015; Rizo *et al.*, 2017). Most rotifers are considered passive but some species including in the genera *Hexarthra*, *Filinia* and *Polyarthra* have slow swimming with the ability to escape from predation through jumps. They were defined as slow swimmers because this capacity is significantly less developed than that of cladocerans and copepods. In cladocerans, we found swimming capacities stronger than rotifers, but smaller than copepods (rapid swimmers).

As for rotifers, we found non-swimmer cladocerans defined also as passive (eg. *Coronatella* and *Simocephalus* genera). For the genus *Diaphanosoma*, we attributed a strategy described by Rizo *et al.* (2017) as "pausing and jumping". Among copepods, copepodites and adults were defined as rapid swimmers. Medium swimming was attributed to the nauplii, since in the literature they were found for these average values of swimming speed were similar ( $3.0\text{mm}\cdot\text{s}^{-1}$ ) to like that of cladocerans (Bradley *et al.*, 2013).

For reproduction, rotifers and cladocerans were defined as asexual and sexual and copepods only sexual. Regarding life span, rotifers and cladocerans were catalogued as short life and copepods as long life (Allan, 1976). It was also found relationships of body size with life span. The pattern was not fully observable in our study, as we found a high size range between the two types of life span.

Length, width and biomass were significantly related in a positive manner, for example length increased with width and with biomass. Linear models constructed combining them showed high redundancy and in all cases explained variance was higher than 50%.

Average and variance values of length, width and biomass were significantly different among different attributes of most categorical traits except width for reproduction ( $p$ -value = 0.11). Continuous traits also showed significant differences among categorical traits (Table 3). For example, pelagic, raptorial and filtration feeders, as well as rapid swimmers were larger. Differently, littoral, microphagous and sucker feeders, and low swimming species were smaller (Figure 4).

### **Zooplankton functional groups (ZFG)**

A first preliminary hierarchical cluster analysis using all eight traits (3 continuous and 5 categorical, Table 2) classified species into 8 groups with a 76.7% of k-means significance. Reproduction and life span traits did not vary among the zooplankton taxonomic groups and were removed from the trait list. A new cluster excluding these traits had a k-means significance of 83.4% and produced ten ZFG.

These ten ZFG (from A to J) and the selected six traits were analysed with a CART. This CART had a global error (E) of 17.8% and classified very well six groups. Three out of the six traits were finally selected by the CART. Habitat was the first variable influencing groups' separation. Then feeding type and after predatory escape response. Length, width and biomass traits were not selected by the CART analyses to organize the species into the groups. From the original 10 groups, four were well classified (E = 0%) and four were misclassified (E = 100%). Group A showed E = 44.8% with three poorly classified species and Group G had an E= 6.6% with one misclassified species. Despite the errors, these groups were kept in well classified and species responsible for the errors were redistributed in other



**Table 3:** Summary of the ZFG description: name, body size range (BS range), categorical traits (habitat, feeding, predatory escape response [Slow Sw: Slow swimming, Med Sw: Medium swimming, Rapid Sw: Rapid swimming, Pause/Jump: Pausing and Jumping]), number of taxa (NUM. OF TAXA) by ZTG (Rotifera, Cladocera and Copepoda) and main taxa by each ZFG.

ZFG	Name	BS range ( $\mu\text{m}$ )	CATEGORICAL TRAITS			NUM. OF TAXA			MAIN TAXA
			HABITAT	FEEDING	PRED. ESC. RESP.	ROT	CLA	COP	
<b>Pms</b>	Pelagics microphages with slow swimming	150- 240	Pelagic	Microphagous	Slow sw	7	0	0	<i>Filinia longiseta</i> and <i>Hexarthra mira</i>
<b>Prs</b>	Pelagics raptors and suckers	80-800	Pelagic	Raptorial and Sucker	Passive, Slow sw, Med Sw and Rapid Sw	15	0	4	<i>Ascomorpha ecaudis</i> , Cyclopoida nauplii, Cyclopoida Copepodit and <i>Thermocyclops</i> sp.
<b>Pfi</b>	Pelagics filter-feeders	197-1000	Pelagic	Filtration	Passive, Med Sw and Pause/Jump	0	15	0	<i>Ceriodaphnia silvestrii</i> , <i>Daphnia gessneri</i> and <i>Moina minuta</i>
<b>Pmi</b>	Pelagics microphages with passive defense or rapid swimming	110-1340	Pelagic	Microphagous	Passive, Med Sw and Rapid Sw	24	0	5	<i>Brachionus falcatus</i> , Calanoida nauplii, <i>Kellicottia bostoniensis</i> , <i>Keratella americana</i> and <i>Notodiaptomus cearensis</i>
<b>Lrs</b>	Littoral raptors, scrapers and filters	135-800	Littoral	Filtration, Raptorial and Scraper	Passive, Med Sw and Rapid Sw	7	8	3	<i>Alona</i> sp., <i>Macrothrix</i> sp., Harpacticoida nauplii and <i>Trichocerca cylindrica</i>
<b>Lmi</b>	Littoral microphages	70-800	Littoral	Microphages	Passive	33	0	0	Bdelloidea, <i>Brachionus dolabratus</i> , <i>Euchlanis dilatata</i> , <i>Lecane bulla</i> , <i>Lepadella</i> sp., <i>Ptygura libera</i> and <i>Sinantherina ariprepes</i>

groups. Based on traits similarity, the 18 misclassified species were located in the well reproduced groups from, and a final CART was done (Figure 5). In this CART, the first trait evaluated is the habitat. If habitat is littoral, feeding is considered to determine the species classification to E or F. If habitat is pelagic, feeding is a same way evaluated. However, in this case, if feeding is microphagous, it is also necessary to observe the predatory escape response.

The main features of the six finally constructed ZFG are shown in Table 4. Groups Pms, Prs, Pfi and Pmi represent groups of pelagic taxa and groups Lrs and Lmi represent littoral taxa, and differentiation within each group is related to feeding type and predatory escape response. Although size related traits were not necessary to classify the species into ZFG, significant differences were observed among groups (Table 4; LR=44.75, p-value<0.0001). Group Pms was composed by pelagic microphages with slow swimming and consisted of six species of rotifers belonging to the genera *Filinia* and *Hexarthra*. Although group Pmi also encompasses pelagic microphages, group Pms differs in that these rotifers have appendages that allow them to swim more actively. Group Prs included pelagic raptors and sucking feeders, and included different genera of rotifers, and copepods of the order Cyclopoida. Group Pfi was composed of pelagic filtering cladocerans (Daphnidae and Bosminidae). Group Pmi corresponded to pelagic microphages, including Brachionidae rotifers and copepods of the order Calanoida. The ZFG Lrs comprised littoral raptors, scrapers and filterers and the Lmi littoral microphages. Group Lrs was the only that had representatives from all zooplankton taxonomic groups, Chydoridae family species (Cladocera), the genus *Trichocerca* (Rotifera) and Harpacticoid copepods. Group F was mainly composed by species from the rotifer genus Lecanidae.

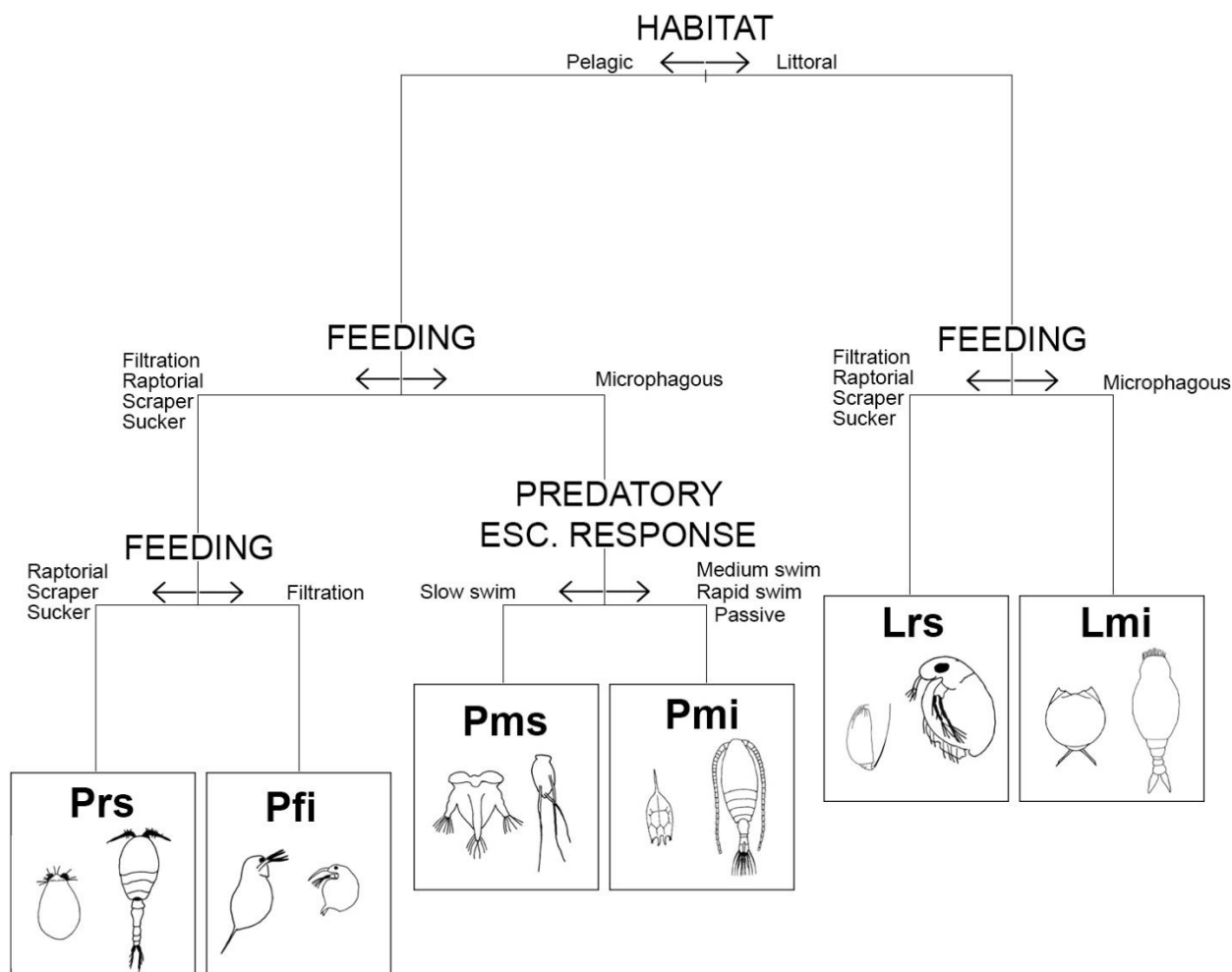
For hierarchical cluster analysis, preliminary CART and error adjustments, see supporting information.

### **Relation between constructed ZFG and environmental variables**

Variance inflation factor (VIF) test detected multicollinearity for several variables among the original 24 considered in the models. Only total phosphorous, chlorophyll-*a*, temperature, Secchi disk depth and rainfall had VIF< 20 and were retained for further modelling

density and biomass of the six ZFG also including the reservoir as a categorical explaining variable.

Multiple linear regression (MLR) coefficients are expressed on a case-by-case basis in table 5. MLR models for all ZFG density and biomass were significant and had  $R^2 > 0.5$ , except for Lrs density ( $R^2 = 0.38$ ). The changes in all ZFG biomass and density, and their responses to environmental variables varied according to the reservoir considered.



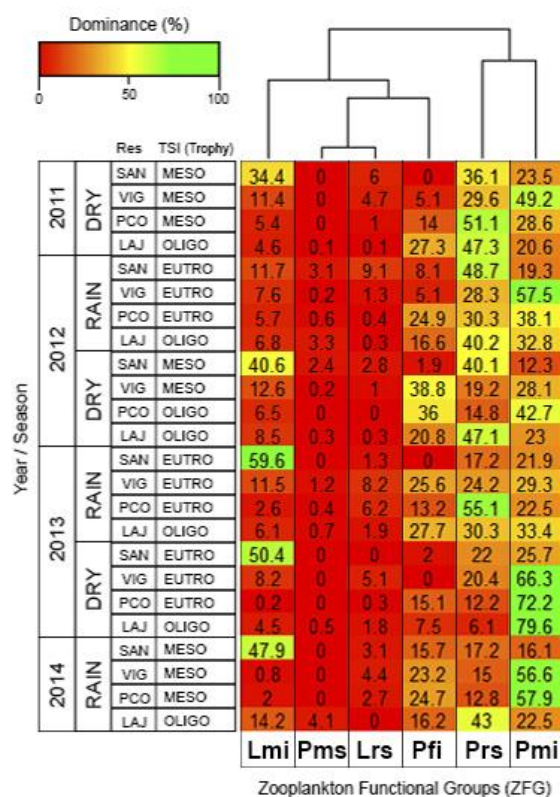
**Figure 5:** Results of the classification and regression tree (CART) representing the six zooplankton functional groups (ZFG: A to F) and the three categorical traits selected by the CART to classify species.

ZFG Prs (density and biomass) had a negative effect of rain in LAJ reservoir. Pfi density and biomass had a negative relation with chlorophyll-*a* in VIG. ZFGs Pmi and Lrs density and biomass were mainly affected by rainfall. Biomass and density of this group had positive association with rains in LAJ and negative in SAN. In VIG density was associated positively and biomass negatively with rains. Pmi density had a negative relation with chlorophyll-*a* in Santana. Finally, Lrs models included the effect of all variables in a negative shape, including rainfall (VIG, PCO) and chlorophyll-*a* (SAN).

Heatmap of dominance (Figure 6) showed ZFG Prs and Pmi as dominants for all reservoirs, except for SAN, where ZFG Lrs dominated. ZFG Pms, Lrs and Pfi had similar dominance in space and time, while Lmi, Prs and Pmi showed less similarity in this sense. In the first year of study, Prs or Pmi were dominant in most reservoirs. From the dry season of 2013, the ZFG Pmi was mostly dominant. This pattern can be observed explicitly in the reservoirs PCO and LAJ. In SAN, during most of the study, ZFG Lmi was the dominant. As showed in Table 5, this pattern is related to rainfall. Favored by high rainfall in the rainy season of 2013, Pmi increased their abundance in detriment of Prs. This pattern was maintained until the end of the study.

Variable (unit)	Reservoir	ZFG Pms		ZFG Prs		ZFG Pfi		ZFG Pmi		ZFG Lrs		ZFG Lmi	
		Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
		$R^2=0.563$ p-value < 0,001	$R^2=0.346$ p-value = 0,02	$R^2=0.535$ p-value < 0,001	$R^2=0.294$ p-value < 0,001	$R^2=0.515$ p-value < 0,001	$R^2=0.256$ p-value < 0,001	$R^2=0.526$ p-value < 0,001	$R^2=0.656$ p-value < 0,001	$R^2=0.409$ p-value < 0,001	$R^2=0.425$ p-value < 0,001	$R^2=0.383$ p-value < 0,001	$R^2=0.374$ p-value < 0,001
<u>Reservoir</u>	Santana	4.24		5.22	1.66	0.94	0.76	5.71	1.40	2.29	2.09		
	Vigário	0.29	0.06	6.66	1.55	4.66	4.36			4.08		11.48	
	Ponte Coberta			7.25				5.76					
	Lajes	0.73	1.79	8.88	6.71	6.76	6.63	7.88	5.48	2.29	3.20	4.68	2.08
<u>Rainfall</u> (mm)	Santana							0.18	-0.97	-3.31			
	Vigário							-4.11	-4.22	-2.15		-3.36	
	Ponte Coberta									-0.21		-4.39	
	Lajes			-1.72	-2.00			2.07	3.17	5.84			
<u>Chlorophyll-a</u> log( $\mu\text{g/L}+1$ )	Santana							-5.14					-4.88
	Vigário					-8.36	-7.70						
	Ponte Coberta												
	Lajes												

**Table 4:** Multiple linear regressions (MLR) coefficients of density and biomass of the functional groups from environmental variables (showed only coefficients with p-value < 0.05) and its R2 and p-values.



**Figure 6:** Heatmap showing ZFG dominance by reservoir. Trophic state index (TSI) showed by reservoir, year and season.

## Discussion

Our results show that habitat and feeding mode are the main traits for defining functional groups in tropical reservoirs with different trophic conditions. We found importance of body size to characterize the zooplankton community, but this trait was not considered important to the functional grouping, and the same was shown for life span and mode of reproduction.

Delineating trophic dynamics in zooplankton is a challenge, but the synthesis through the construction of functional groups can somewhat facilitated the understanding of its dynamics in the water column. Zooplankton species have been grouped together according to similarities in trophic features or in response to abiotic conditions (Czerniawski & Sługocki, 2018; Kosiba, Krztoń & Wilk-Woźniak, 2018), but richness of species and abundances are consistently poor at predicting ecosystem functioning as in other natural animal communities

(Gagic et al., 2015). Otherwise, the use of functional traits in aquatic ecosystems has recently expanded and the functional diversity has been considered one of the best predictors of ecosystem function, helping to provide insights into many ecological processes in freshwater (Allesina & Pascual, 2009; Griffin et al., 2009; Rizo et al., 2017).

According to Hébert et al. (2017), select ecologically meaningful traits that mechanistically link levels of biological organization remains a challenge in aquatic ecology. The wide variety of zooplankton traits studied and proposed in recent times (Litchman et al., 2013; Hébert et al., 2017; Lokko et al., 2017; Rizo et al., 2017; Braghin et al., 2018) highlighted the critical point of choosing traits.

In our search for the most relevant functional traits considering all zooplankton community, we verified some important aspects regarding the body size of the zooplankters. In the majority of zooplankton communities studies from temperate and subtropical environments, body size is pointed out as a far-reaching factor in ecology approach (Peters, 1983). When evaluated competition and predation interactions influencing the structure of zooplankton in lakes in the USA, Brooks & Dodson (1965) proposed "size-efficiency hypothesis", which states that zooplankton compete for similar resources and that larger size ranges allow greater competitive efficiency. In warm weathers, Bonecker (2011) investigated the relationship of body size structuring in tropical floodplain lakes and suggested that, in addition to competition for resources, different mechanisms acted in zooplankton size. Given the lack of studies in the tropics focusing this issue, particularly in reservoirs, we sought to investigate the size patterns in zooplankton in the present study. We expected to find dependent value for length and width in rotifers, since part of the geometric formulas for volume given by Ruttner-Kolisko (1977) determines width as a function of length. In cladocerans and copepods, this pattern was also expected, although the literature record is restricted to temperate environments. Bird & Prairie (1985) reported the collinearity between length and width values of aquatic microcrustaceans. Nevertheless, here we found an interesting difference within microcrustaceans. Cladocerans presented a smaller increment of width in relation to the increase in size what can favour a less conspicuousness when compared to copepods. The greater escape potential of the latter may explain this difference.

Another aspect observed related with body size was regarding to taxonomic group, habitat, mode of feeding and escape to predators (Figure 4). The larger zooplankters in the reservoirs were pelagic copepods and cladocerans, mostly feeding by filtration or raptorial, and the larger are the ones with rapid swimming capacity. Taxa with larger body sizes usually dominate in pelagic environments, since they exhibit a greater competitive capacity by having better predation escape response of planktivorous fish and predating smaller species in zooplankton (Dodson, 1974). Small taxa, in order to avoid predation, find better refuges against predation in littoral areas or among macrophytes, where predators are less efficient (Estlander et al., 2009).

Conversely, while in temperate region aquatic macrophytes or filamentous algae in littoral areas can serve as refuge for large-bodied zooplankton, in warm lakes small omnivorous fish in high abundance tended to aggregate in those areas that are not a suitable refuge for zooplankton (Jeppesen et al., 2007). Despite this difference between habitats in warm waters this criteria was not widely observed in the choosing of functional traits. Aranguren-Riaño et al. (2018), for instance, evaluated functional diversity in 14 tropical lakes without establishing habitat as a trait, even with a gradient of habitats. In our study, it was possible to observe a large decrease of body size from pelagic to littoral-related organisms, showing that the latter is not suitable habitat or refuge for larger zooplankters and pointing habitat as an important as a functional feature. Although our samplings were always carried out in the limnetic zone of the reservoirs, the presence of taxa associated to the littoral area was related to the presence of aquatic plants in reservoirs.

We could also foster size difference between pelagic and littoral organisms evaluating predatory escape response. We got taxa with high swimming efficiency with the largest size range, while taxa with slow swimming and passive defense are the smallest. Among the zooplankton taxonomic groups, we found the largest size range among copepods. This is because we considered juvenile and nauplii individuals in this group. In habitat, we found a larger size range for pelagic taxa.

In feeding, we observed the greater size range in filter feeders and raptors. Among filter feeders, this amplitude is due to Daphnidae cladocerans, which are the largest in this



zooplankton taxonomic groups. These also have their feeding efficiency related to the body size. Burns (1968) proposed a regression equation for filter-feeders cladocerans in relation to body size, where larger body sizes enable higher feeding efficiency by filter feeders. This is in line with Brooks & Dodson (1965) and shows that the "size efficiency hypothesis" is applicable to tropical zooplankton. Raptors had also a large size range. It covered few rotifers and Cyclopoida copepods that have different size ranges. This diversity of zooplankton taxonomic groups among the raptors allowed a greater size range. Scrapers and suckers do not have a wide size distribution. Taxa with this type of feeding found in our study do not have escape strategies to predation such as *Alona* and rotifer sucker *Trichocerca*, according to, respectively, Elmoor-Loureiro (1997) and Koste (1978). Being smaller species, they are less susceptible to predation by fish that generally feed on larger individuals in zooplankton (O'Brien, 1979), but they can be predated by other invertebrates. Given this, we expect to find these types of feeding in littoral environments, as discussed above.

Again, predation pressure on zooplankters seems to be important for explain features of the zooplankton community of the studied reservoirs, from the larger pelagic zooplankter with higher capacity of escape to the dominance of small size within littoral species. This statement is supported by some other studies in these reservoirs. Studying the natural diet of fish species from Lajes Reservoir (Dias, Branco & Lopes, 2005) found zooplankton in most diets being the most representative the cladocerans. The study of the diet of *Loricariichthys castaneus* a detritivorous-omnivorous fish in this same reservoir and in Santana and Vigário reservoirs revealed the presence of microcrustaceans in the diet of fish from the three reservoirs (Ferreira et al., 2013). The constant presence of the phantom midge *Chaoborus* in Lajes Reservoir (Macêdo et al., 2018) also can be a threat for the pelagic zooplankters, as reported for other tropical Brazilian reservoir (Arcifa, Gomes & Meschiatti, 1992).

The relationship between body size and biomass is also dependent. Uye (1982) described this relation in zooplankton as common. We even obtained regression equations with considerable coefficient ( $R^2$ ) as found by Uye ( $0,5 < R^2 < 1$ ). Despite the elimination of biomass as a trait, it was important to obtain the biomass of the ZFGs, since there were interactions between community and environment that were observable strictly in relation to

biomass. This fact had already been expressed in tropical reservoirs by Sendacz et al. (2006), where biomass variations between drought and rainfall differed from variations in abundance.

Despite the importance of body size for zooplankton habitat dynamics, this trait did not appear to be important in separating functional groups. In fact, by establishing ZFGs by cluster analysis from Gower's dissimilarity matrix, we observed poorly partitioned groups. We were able to diagnose ZFGs with similar functional approaches on different partitions. K-means confirmed the dendrogram, maintaining its classification. Xu & Tian (2015) reported that clustering and partitioning analyses are relatively sensitive to discrepant values, which becomes a problem when dealing with biological and environmental data. Lokko, Virro & Kotta (2017) opted, instead of clustering, to insert their Gower's dissimilarity matrix into boosted regression trees to assess relationships between environmental parameters and taxonomic and functional diversity of rotifer communities. Kruk & Segura (2012) also used regression trees to evaluate functional diversity, but in a way to validate groups. They tested the validity of groups using CARTs. We chose to apply Kruk & Segura methodology to our ZFGs to test the validity of the groups established by clustering and to make adjustments in the groups. As we had assumed, CART pointed to the presence of poorly classified taxa and redundant groups. When realizing the changes suggested by CART, we obtained ZFGs with taxa expressing the functional characteristic of the group, without the presence of exceptions, as previously observed in the cluster.

Among the other traits explored, we had considered to use life span and reproduction in the trait definition process, since these have already been pointed out as important in studies of zooplankton functional diversity (Benedetti, Gasparini & Ayata, 2015; Braghin et al., 2018). However, in our case these traits influenced the cluster phylogenetically. These traits only have variations when compared taxa from different phylogenetic groups. When using these traits in the cluster, we obtained more than one functional group with identical functional characteristics. This fact did not occur in the aforementioned studies because they presented different approaches and communities. Benedetti, Gasparini & Ayata (2015), besides working with only copepods, attributed growth values along life span / reproduction. Braghin et al.

(2018) worked with all zooplankton phylogenetic groups as in our study, but did not use traits for functional grouping.

According to our results, habitat and feeding were the main determinants of ZFG. The habitat first defined the position of the group of species considered in the trait analyses. This trait is determinant for other functional aspects of zooplankton, such as where and what they are going to feed and how is the escape response to predators (Meerhoff et al., 2007a). In addition, we expected that habitat was important since the studied reservoirs presented heterogeneous hydrology and colonization by aquatic macrophytes. Feeding mode has been the most used functional trait to characterize functional features in several groups of invertebrates and vertebrates (Gagic et al., 2015; Lamothe et al., 2018). Feeding has already been described as a functional aspect in zooplankton related to environmental trophic conditions (Bays & Crisman, 1983; Pejler, 1983). Given this fact, we understand that this trait was important in the process of composition of ZFG especially expecting influence of the trophic gradient (eutrophic to oligo-mesotrophic) of the reservoirs.

The six functional groups formed in the present study summarized functional niches occupied by zooplanktonic organisms in the four reservoirs. The habitat divided the groups into pelagic (Pms, Prs, Pfi, Pmi) and littoral (Lrs and Lmi). Microphages, filters and raptors are present in both habitats and in the pelagic environment defense strategy seemed to be important to functional separations. Something interesting came up in our results when we noticed that we had aggregates of taxa with different sizes and from different taxonomic group forming a same functional group. This shows evidence for resource partitioning within zooplankton community and reflected a functional redundancy among different taxonomic groups. Functional redundancy occurs when species share overlapping ecological functions and has been considered an important component of ecosystem resilience (Lamothe et al., 2018). However, this redundancy have to be more explored since different body size permits species to feed on different resources (Hutchinson, 1961). Further, overlapping niches indicate the possibility of coexistence and/or competition among zooplankters in a same habitat.

ZFG Prs (pelagic raptors and suckers) and Pmi (pelagic microphages with passive defense or rapid swimming) were dominant in most reservoirs except in the most eutrophic

SAN Reservoir where the ZFG Lmi (littoral microphages) prevailed. Despite the tendency of trophic conditions increase in rainy seasons, rainfall influenced the rise of turbidity decreasing water transparency and favouring the increase of microphagous (Pmi) organisms in detriment of raptors and suckers (Prs). Rainfall increases seemed to be more important for ZFGs than changes in trophic state conditions in most reservoirs.

Few studies have explored functional diversity in relation to abiotic factors, considering functional diversity as diversity of species' niches or functions (Cadotte, Carscadden & Mirotchnick, 2011). As a representation of niches or functions, functional diversity has been used to understand how species richness relates to local environment function spatially and temporally, and so can be used as a proxy for ecosystem functioning (Mouchet et al., 2010; Cadotte et al., 2011; Gagic et al., 2015). Composition shifts are expected to occur in functionally diverse communities due to nutrient input, since some traits can be favoured in the exploitation of the added resource (Wang, Xie & Geng, 2010) causing changes in dominance of ZFGs.

Since ZFGs have distinct abundances patterns in the reservoirs, the calculated dominance (%) of the ZFGs helped to understand their spatial and temporal distributions. Pelagic groups had a higher percentage of dominance in all reservoirs excepting SAN, where this dominance was attained mostly by the Lmi (littoral microphages). This reservoir presents high content of particulate matter in suspension, higher trophic state, low retention time, and is intensively colonized by floating and rooted aquatic macrophytes (Pitelli & Pitelli, 2008), which can impair pelagic zooplankters and favour littoral organisms or associated to aquatic plants. The presence of aquatic macrophytes likewise in VIG Reservoir, but in a smaller quantity, high trophic conditions, low water retention time and high flow also favoured the presence littoral groups that represented up to 20% of dominance in this reservoir. PCO Reservoir that receives waters from VIG and LAJ reservoirs has a low retention time, but is not colonized by aquatic macrophytes, showed dominance of pelagic ZFGs as LAJ Reservoir. This latter has the highest retention time and the lowest trophic state when comparing to the other reservoirs, and presented more than 95% of dominance of pelagic ZFGs. A high water residence time favours the development of organisms with long life cycles such as copepods and the

presence of pelagic organisms throughout the year in the reservoir water column (Lansac-Tôha, Bonecker & Velho, 2005).

Although we aimed to study the relationships between the trophic state and functional groups of zooplankton, we found that aquatic macrophytes colonize the most eutrophic reservoirs and influenced the zooplankton community features and trophic dynamics. Zooplankton species may be divided into littoral or limnetic specialists, but some can occur in both environments having a preference for either the littoral or limnetic zone and many can occur in the limnetic due to drifting from vegetated areas by currents (Šorf & Devetter, 2011; Branco et al., 2018). At the same time, plants influenced a greater contribution of littoral zooplankters in the limnetic area of SAN and VIG reservoirs and probably allowed the maintenance of an expressive zooplankton community even in an environment with a low retention time, where the loss by drifting can be expressive. Otherwise, as the ecological function of a zooplankton community is connected to secondary production as a primary grazer, prey item for predators, and nutrient recycling (Rizo et al., 2017) the role of zooplankters in reservoirs with macrophytes must be linked to them. Difference within trophic guilds of tropical microcrustaceans was associated with the macrophytes communities by Elmoor-Loureiro (2007) and by Stephan et al. (2017). High abundance of aquatic plants in a tropical reservoir with eutrophic conditions corresponds to higher rates of decomposition, a constant input of organic matter, and a probably productive periphyton community. This high heterogeneity of food sources can sustain several taxa included in the LMI that are feeding through microphagia such as *Lecane* spp. and bdelloideans. The organisms included in the LRS, in its turn, are living and feeding within macrophytes. Zooplanktonic species of small size, such as *Bosminopsis deitersi* and *Alona* spp. have advantages for catching food in these conditions because these taxa can swim and feed on phytoplankton in the middle of macrophytes as reported by Stephan et al. (2017).

Despite the observed differences among the dominances of the ZFGs, the six groups were found in all reservoirs. In LAJ Reservoir, a greater functional richness was found, since all the functional groups were found in most of the samplings. In this reservoir, differently from the others, the ZFG Pms (pelagic microphages with low swimming) and Pfi were always

present. This points to a slight differentiation of functionality of zooplankton in the oligotrophic ecosystem.

Because functional traits may interact and influence different aspects of ecosystem functioning (Hébert et al., 2017), identifying which traits are most relevant in the zooplankton community can give clues on aquatic ecosystem dynamics. The importance of the niche of microphages in both littoral and limnetic zooplankters in all reservoirs was highlighted by our study. This pointed to the existence of a myriad of food sources sustaining microphages zooplankters in these systems and help to explain the high richness of rotifers found in the reservoirs. Conversely, reveals the important role of zooplankton by conveying energy from detritus and primary producers to higher links in the food web through microphagia. The phytoplankton community of most studied reservoirs is dominated numerically by picocyanobacteria (Branco, 2015), which may be a food source for microphages zooplankters. In a study with modelling approach on the dominance of picocyanobacteria in LAJ Reservoir (Rocha et al., 2019) showed an inverse relation between rotifers and picocyanobacteria suggesting that those organisms may directly control picocyanobacterial populations in this reservoir. A broad niche for microphages may also help to explain the success of the invasive rotifer species *Kellicottia bostoniensis* that was found in all studied reservoirs and included in PMI. *K. bostoniensis* is considered a microphagous species, consuming detritus, small algae and bacteria (Pourriot, Horeau & Rougier, 1997).

The wide variety of organisms and the taxonomic diversity of the microphages probably causes redundancy in some of these groups (PMI and LMI), which may explain the low influence of trophic state change on them. There is always one or several organisms favoured by the increase or decrease of trophic conditions. This redundancy seems to be smaller among the filters, included in the PFI and LRS. Among the components of those last groups are cladocerans, considered the main secondary consumers in their aquatic habitats, as they show the highest rate of filtration among freshwater zooplankton (Dumont & Negrea, 2002). Analysis of functional traits revealed that tropical and subtropical cladocerans have traits that are specialized in surviving high food/resource availability as well as high predation pressure in their habitats (Rizo et al., 2017).

Other important niche also dominant in most reservoirs was the raptorial, including in Prs and Lrs. Prs were always present in all reservoirs, despite presenting a lower number of species, and seemed a group with less redundancy. The partitioning and selection of resources by raptorial feeding through discrimination between individual food items, and a change in diet from juveniles to adults as in cyclopoid copepods (Gliwicz, 2003) may explain this.

Although the redundancy of niche occupation has been suggested to explain the low influence of trophic state variation on the dominance of functional groups, a closer look at their relationship with environmental variables can elucidate some important issues of the zooplankton dynamics. We found significant relationship between ZFGs and chlorophyll-a and rainfall. Chlorophyll-a is a proxy of the biomass of phytoplankton and was associated to ZFG C in VIG reservoir and to ZFG D in SAN reservoir. Despite the low values of chlorophyll-a found in all reservoirs, an association between filter and microphages zooplankters and phytoplankton was shown. Rainfall was the main environmental factor influencing the dominance of ZFGs. Water residence time is well known as a driving force of zooplankton structure and succession in lakes (Obertegger et al., 2007) and reservoirs (Sartori et al., 2009), but there are few records in the literature about the direct influence of rainfall on zooplankton communities in reservoirs. Rainfall promoting alterations in zooplankton community structure through a strong densities reduction (Pinto-Coelho, 1987; Panarelli, Nogueira & Henry, 2001) or increase (Lansac-Tôha et al., 2005) was reported for tropical reservoirs as well for a downstream river influenced by these systems (Perbiche-Neves et al., 2012).

Rainfall events can change environmental patterns in the water column of reservoirs (Tundisi, 1997; Sadras & Baldock, 2003; Branco et al., 2009; Li, Yin & Leo, 2010). Increase of pluviosity is an important driver for carrying particulate matter and nutrients to the water column in the studied reservoirs (Guarino et al., 2005) and influenced density and biomass of most ZFGs. As showed by the MLR results, rainfall affected differently the functional groups. Increase of rainfall in LAJ Reservoir was associated negatively to Prs and positively to ZFGs Pmi and Lrs. In the other reservoirs, this increase affected negatively ZFGs, such as Pmi in SAN and VIG reservoirs, and Lrs in SAN, VIG and PCO reservoirs. During the first years of study, the group of pelagic raptors (Prs) dominated in LAJ and in PCO reservoirs. In the rainy

period of 2013, rainfall reached values close to 250mm in these reservoirs, higher than other months, when the maximum rainfall value did not exceed 170mm. Differently from other studies, rainfall caused no significant reduction in density in zooplankton in the reservoirs but influenced ZFGs dominance increasing microphages populations and decreasing raptors.

Therefore, the increase of water turbidity caused by rainfall constitutes an important environmental filter for most functional groups, acting on the trophic dynamics of zooplankton in the reservoirs. Apparently, the intensity of this filter is related to the intensity of the rainfall. Turbidity was not inserted in the MLR because the VIF test showed it colinear with rainfall. That both have the same effect on the ZFGs.

Food webs have been considered complex adaptive systems in which changes in external drivers and changes in species composition or density within a functional group can reveal stability, resilience or transition within communities affecting or not ecosystem functioning (Lamothe et al., 2018). Functional grouping can simplify the overview of the role of a community in the ecosystem and facilitate the synthesis of the dynamics of this community facing ecological gradients and when subjected to strong environmental filters. The knowledge of how systems respond to variation sheds light on ecosystem adaptive capacity and provide insights into the possible consequences of human activities through eutrophication or global changes causing extremes events of rainfall or drought (Mcmeans et al., 2011).

Our study thus provides new insights into functional mechanisms within zooplankton communities of tropical reservoirs. Warm waters are known to have higher rates of omnivory than temperate systems and are more strongly influenced by fish predation (Lazzaro, 1987; Meerhoff et al., 2007b). Here we showed a functional organization in which microphagia, raptorial and filtering feeding revealed part of the microscopic tropical omnivory. Fish and predation by invertebrates seemed to be an important driving force on zooplankton features of most reservoirs.

This study further revealed that zooplankton traits and groups assessment help to understand community changes and environment interactions. The set of functional groups produced by our study revealed the resilience of the zooplankton community to changes



occurring in the water column. Due to this, we encourage monitoring functional aspects of zooplankton communities since the information contained in groups of species with different functionalities brought a greater understanding of the dynamics occurring in the water column. The features and changes in dominance of the ZFGs gave clues on the ecological status of the reservoirs as aquatic ecosystems. For instance, the Pms (pelagic microphages with low swimming) and Pfi were mostly associated to lower trophic conditions of the reservoirs and the Lmi to more eutrophic conditions due their connection with aquatic macrophytes. The extreme events of pluviosity expected for the region of the reservoirs (Marengo, 2018) can also be a threat to the dynamics of the aquatic ecosystem since can deeply change dominance of functional groups in zooplankton.

Successful conservation and restoration strategies that explicitly account for community diversity are the ones that prioritize ecosystem function or stability (Cadotte et al., 2011). There is little doubt that ecosystem functions are a top conservation priority especially in tropical regions where biodiversity is still underestimated including the ecosystem services species provide (Millenium Ecosystem Assessment, 2005). Considering zooplankton communities, the multiple resources for microphagia, filtering and raptorial feeding and the multiple processes of resources partitioning, competition, predation pressure by other invertebrates and fish, favourable chemical or physical conditions should promote the tropical zooplankton diversity. The application of zooplankton functional grouping in monitoring studies in tropical reservoirs can be of high interest, since they can synthetize functional responses to conditions in environments with different hydrological and trophic aspects, and may reveal part of the plankton dynamics in the aquatic ecosystem.

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## APÊNDICES DO CAPÍTULO 1

### 1. Seção de material suplementar

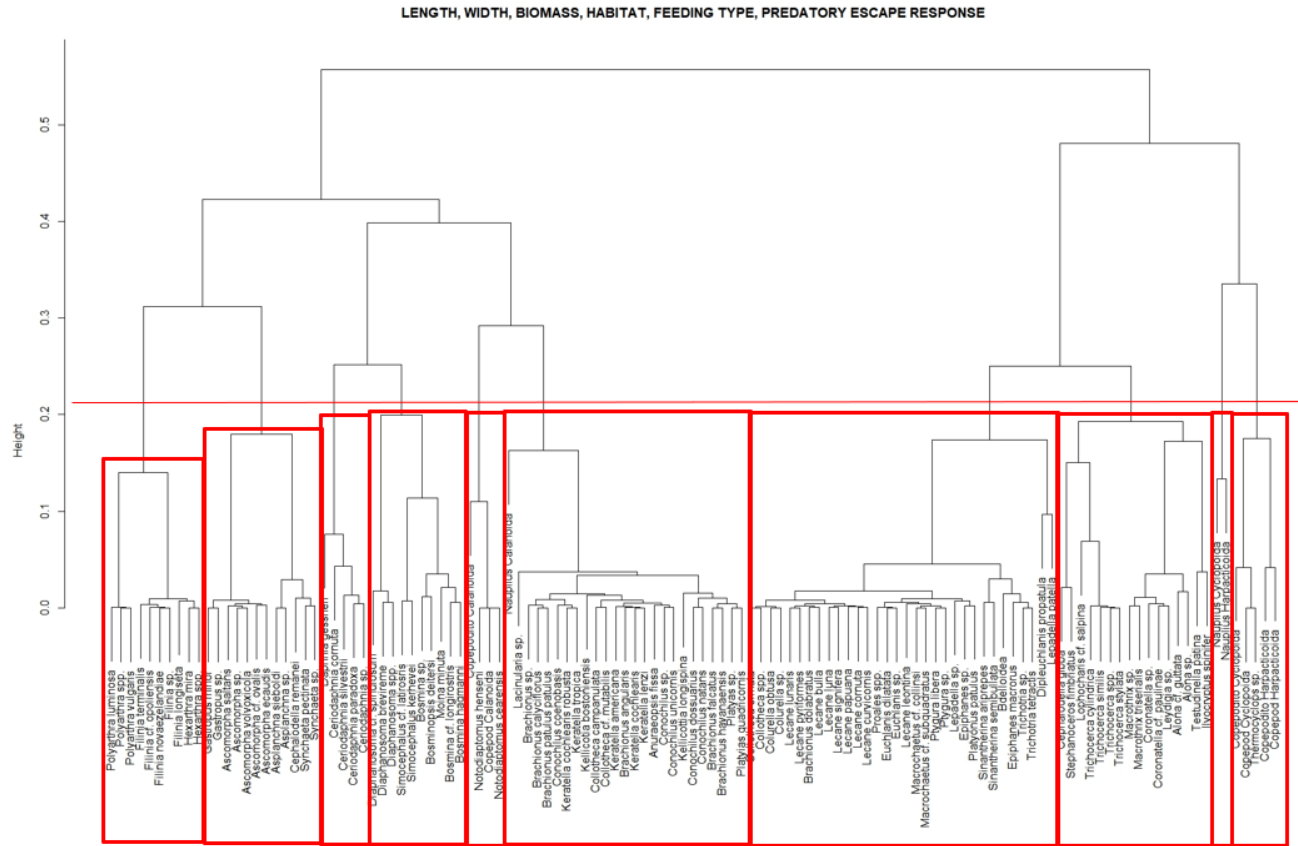
**Tabela 1 suplementar:** Matriz de atributos funcionais utilizados e classificação taxonômica por espécie. Length e width ( $\mu\text{m}$ ) e Biomass ( $\mu\text{gC.m}^{-3}$ )

PHYLOGENY					FUNCTIONAL							
TAXA / GROUP	GROUP	PHYLUM	CLASS	ORDER	LENGTH	WIDTH	BIOMASS	HABITAT	FEEDING TYPE	LIFE SPAN	PREDATORY ESCAPE RESPONSE	REPRODUCTION
<b>ROTIFERA</b>												
<i>Anuraeopsis fissa</i>	Rotifera	Rotifera	Monogononta	Ploima	121	58	0.097334	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Ascomorpha cf. ovalis</i>	Rotifera	Rotifera	Monogononta	Ploima	150	60	0.02025	Pelagic	Sucker	Short	Passive	Assexual / Sexual
<i>Ascomorpha ecaudis</i>	Rotifera	Rotifera	Monogononta	Ploima	165	80	0.026953	Pelagic	Sucker	Short	Passive	Assexual / Sexual
<i>Ascomorpha saltans</i>	Rotifera	Rotifera	Monogononta	Ploima	132.5	100	0.013957	Pelagic	Sucker	Short	Passive	Assexual / Sexual
<i>Ascomorpha sp.</i>	Rotifera	Rotifera	Monogononta	Ploima	165	100	0.013957	Pelagic	Sucker	Short	Passive	Assexual / Sexual
<i>Ascomorpha volvoxicola</i>	Rotifera	Rotifera	Monogononta	Ploima	165	100	0.013957	Pelagic	Sucker	Short	Passive	Assexual / Sexual
<i>Asplanchna sieboldi</i>	Rotifera	Rotifera	Monogononta	Ploima	700	200	0.104	Pelagic	Raptorial	Short	Passive	Assexual / Sexual
<i>Asplanchna sp.</i>	Rotifera	Rotifera	Monogononta	Ploima	700	200	0.104	Pelagic	Raptorial	Short	Passive	Assexual / Sexual
Bdelloidea	Rotifera	Rotifera	Bdelloidea		425	185	0.004224	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Brachionus angularis</i>	Rotifera	Rotifera	Monogononta	Ploima	150	50	0.011719	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Brachionus calyciflorus</i>	Rotifera	Rotifera	Monogononta	Ploima	156	100	0.183105	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Brachionus dolabratus</i>	Rotifera	Rotifera	Monogononta	Ploima	125	60	0.011719	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Brachionus falcatus</i>	Rotifera	Rotifera	Monogononta	Ploima	312.5	120	0.183105	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Brachionus havanaensis</i>	Rotifera	Rotifera	Monogononta	Ploima	312.5	120	0.183105	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Brachionus patulus patulus</i>	Rotifera	Rotifera	Monogononta	Ploima	156	100	0.183105	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Brachionus sp.</i>	Rotifera	Rotifera	Monogononta	Ploima	156	100	0.011719	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Cephalodella gibba</i>	Rotifera	Rotifera	Monogononta	Ploima	350	106	0.102248	Littoral	Raptorial	Short	Passive	Assexual / Sexual
<i>Cephalodella remanei</i>	Rotifera	Rotifera	Monogononta	Ploima	350	106	0.102248	Pelagic	Raptorial	Short	Passive	Assexual / Sexual

<i>Collotheca campanulata</i>	Rotifera	Rotifera	Monogononta	Collothecaceae	600	90	0.013023	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Collotheca cf. mutabilis</i>	Rotifera	Rotifera	Monogononta	Collothecaceae	150	40	0.06561	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Collotheca ormata</i>	Rotifera	Rotifera	Monogononta	Collothecaceae	250	90	0.013023	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Collotheca</i> spp.	Rotifera	Rotifera	Monogononta	Collothecaceae	250	53	0.013023	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Colurella obtusa</i>	Rotifera	Rotifera	Monogononta	Ploima	70	35	0.06561	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Colurella</i> sp.	Rotifera	Rotifera	Monogononta	Ploima	70	35	0.06561	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Conochilus coenobasis</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	200	60	0.004636	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Conochilus dossuarius</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	390	188	0.179194	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Conochilus natans</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	395	190	0.185374	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Conochilus</i> sp.	Rotifera	Rotifera	Monogononta	Flosculariaceae	115.5	55.5	0.004636	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Conochilus unicornis</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	110	51	0.003719	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Dipleuchlanis propatula</i>	Rotifera	Rotifera	Monogononta	Ploima	423	190	0.567652	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Epiphanes macrorus</i>	Rotifera	Rotifera	Monogononta	Ploima	325	160	0.10816	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Epiphanes</i> sp.	Rotifera	Rotifera	Monogononta	Ploima	235	114	0.10816	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Euchlanis dilatata</i>	Rotifera	Rotifera	Monogononta	Ploima	177	45	0.097334	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Euchlanis</i> sp.	Rotifera	Rotifera	Monogononta	Ploima	177	45	0.097334	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Filinia cf. opoliensis</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	177	45	0.008951	Pelagic	Microphagous	Short	Low Swim.	Assexual / Sexual
<i>Filinia longiseta</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	240	80	0.008951	Pelagic	Microphagous	Short	Low Swim.	Assexual / Sexual
<i>Filinia novaezelandiae</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	170	45	0.009319	Pelagic	Microphagous	Short	Low Swim.	Assexual / Sexual
<i>Filinia</i> sp.	Rotifera	Rotifera	Monogononta	Flosculariaceae	170	45	0.008951	Pelagic	Microphagous	Short	Low Swim.	Assexual / Sexual
<i>Filinia terminalis</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	125	40	0.0052	Pelagic	Microphagous	Short	Low Swim.	Assexual / Sexual
<i>Gastropus minor</i>	Rotifera	Rotifera	Monogononta	Ploima	80	60	0.008951	Pelagic	Sucker	Short	Passive	Assexual / Sexual
<i>Gastropus</i> sp.	Rotifera	Rotifera	Monogononta	Ploima	80	60	0.0052	Pelagic	Sucker	Short	Passive	Assexual / Sexual
<i>Hexarthra mira</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	150	110	0.015379	Pelagic	Microphagous	Short	Low Swim.	Assexual / Sexual
<i>Hexarthra</i> spp.	Rotifera	Rotifera	Monogononta	Flosculariaceae	150	110	0.015379	Pelagic	Microphagous	Short	Low Swim.	Assexual / Sexual
<i>Kellicotia bostoniensis</i>	Rotifera	Rotifera	Monogononta	Ploima	294.2	37.8	0.03823	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Kellicotia longispina</i>	Rotifera	Rotifera	Monogononta	Ploima	520	140	0.03823	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Keratella americana</i>	Rotifera	Rotifera	Monogononta	Ploima	174.7	51.3	0.00299	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Keratella cochlearis</i>	Rotifera	Rotifera	Monogononta	Ploima	153	52.3	0.002722	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Keratella cochlearis robusta</i>	Rotifera	Rotifera	Monogononta	Ploima	200	90	0.002722	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Keratella lenzi</i>	Rotifera	Rotifera	Monogononta	Ploima	153	52	0.002722	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Keratella tropica</i>	Rotifera	Rotifera	Monogononta	Ploima	200	90	0.002722	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Laciniularia</i> sp.	Rotifera	Rotifera	Monogononta	Flosculariaceae	700	32	0.009318	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Lecane bulla</i>	Rotifera	Rotifera	Monogononta	Ploima	120	60	0.01296	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lecane cornuta</i>	Rotifera	Rotifera	Monogononta	Ploima	120	40	0.011407	Littoral	Microphagous	Short	Passive	Assexual / Sexual

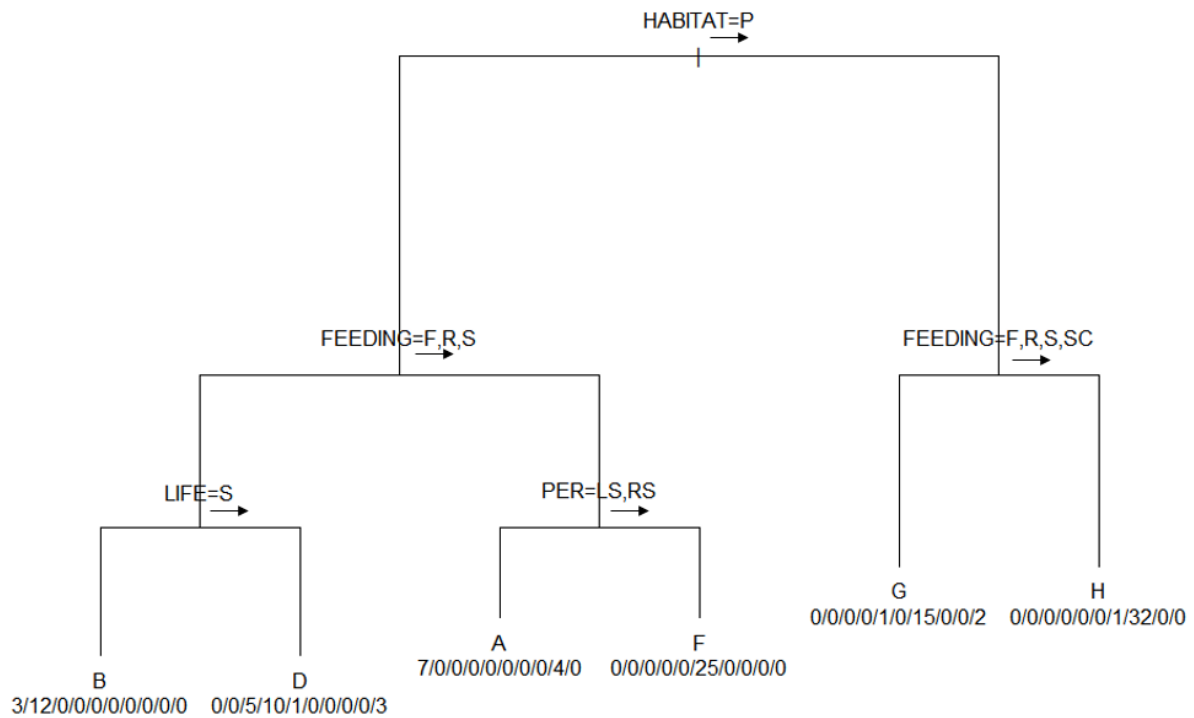
<i>Lecane curvicornis</i>	Rotifera	Rotifera	Monogononta	Ploima	115	38	0.011407	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lecane leontina</i>	Rotifera	Rotifera	Monogononta	Ploima	175	90	0.040195	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lecane luna</i>	Rotifera	Rotifera	Monogononta	Ploima	142	47	0.021475	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lecane lunaris</i>	Rotifera	Rotifera	Monogononta	Ploima	130	80	0.016478	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lecane papuana</i>	Rotifera	Rotifera	Monogononta	Ploima	106	50	0.008933	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lecane pyriformes</i>	Rotifera	Rotifera	Monogononta	Ploima	130	80	0.008933	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lecane signifera</i>	Rotifera	Rotifera	Monogononta	Ploima	129.5	45	0.016288	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lepadella patella</i>	Rotifera	Rotifera	Monogononta	Ploima	132.5	110	0.017447	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lepadella</i> sp.	Rotifera	Rotifera	Monogononta	Ploima	132.5	110	0.017447	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Lophocharis</i> cf. <i>salpina</i>	Rotifera	Rotifera	Monogononta	Ploima	140	56	0.102248	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Macrochaetus</i> cf. <i>collinsi</i>	Rotifera	Rotifera	Monogononta	Ploima	223	74	0.044358	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Macrochaetus</i> cf. <i>subquadratus</i>	Rotifera	Rotifera	Monogononta	Ploima	223	74	0.044358	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Platyias</i> sp.	Rotifera	Rotifera	Monogononta	Ploima	300	160	0.162	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Platyias quadricornis</i>	Rotifera	Rotifera	Monogononta	Ploima	300	160	0.162	Pelagic	Microphagous	Short	Passive	Assexual / Sexual
<i>Platyonus patulus</i>	Rotifera	Rotifera	Monogononta	Ploima	213	113	0.183105	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Polyarthra luminosa</i>	Rotifera	Rotifera	Monogononta	Ploima	140	70	0.024192	Pelagic	Raptorial	Short	Low Swim.	Assexual / Sexual
<i>Polyarthra</i> spp.	Rotifera	Rotifera	Monogononta	Ploima	135	70	0.024192	Pelagic	Raptorial	Short	Low Swim.	Assexual / Sexual
<i>Polyarthra vulgaris</i>	Rotifera	Rotifera	Monogononta	Ploima	135	70	0.024192	Pelagic	Raptorial	Short	Low Swim.	Assexual / Sexual
<i>Proales</i> spp.	Rotifera	Rotifera	Monogononta	Ploima	178	53	0.102248	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Ptygura libera</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	200	70	0.0070	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Ptygura</i> sp.	Rotifera	Rotifera	Monogononta	Flosculariaceae	200	70	0.0070	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Sinanotherina ariprepes</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	800	100	0.104	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Sinanotherina semibullata</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	700	100	0.091	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Stephanoceros fimbriatus</i>	Rotifera	Rotifera	Monogononta	Collotheceae	250	90	0.091	Littoral	Raptorial	Short	Passive	Assexual / Sexual
<i>Synchaeta pectinata</i>	Rotifera	Rotifera	Monogononta	Ploima	256.5	159	0.079872	Pelagic	Raptorial	Short	Passive	Assexual / Sexual
<i>Synchaeta</i> sp.	Rotifera	Rotifera	Monogononta	Ploima	237	146	0.079872	Pelagic	Raptorial	Short	Passive	Assexual / Sexual
<i>Testudinella patina</i>	Rotifera	Rotifera	Monogononta	Flosculariaceae	235	170	0.077867	Littoral	Filtration	Short	Passive	Assexual / Sexual
<i>Trichocerca cylindrica</i>	Rotifera	Rotifera	Monogononta	Ploima	140	56	0.095576	Littoral	Sucker	Short	Passive	Assexual / Sexual
<i>Trichocerca similis</i>	Rotifera	Rotifera	Monogononta	Ploima	140	56	0.011415	Littoral	Sucker	Short	Passive	Assexual / Sexual
<i>Trichocerca</i> spp.	Rotifera	Rotifera	Monogononta	Ploima	135	54	0.010235	Littoral	Sucker	Short	Passive	Assexual / Sexual
<i>Trichocerca stylata</i>	Rotifera	Rotifera	Monogononta	Ploima	135	54	0.010235	Littoral	Sucker	Short	Passive	Assexual / Sexual
<i>Trichotria</i> sp.	Rotifera	Rotifera	Monogononta	Ploima	275.5	128	0.117359	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<i>Trichotria tetractis</i>	Rotifera	Rotifera	Monogononta	Ploima	275.5	128	0.117359	Littoral	Microphagous	Short	Passive	Assexual / Sexual
<b>CLADOCERA</b>												
<i>Alona</i> cf. <i>guttata</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	400	350	0.319	Littoral	Scraper	Long	Passive	Assexual / Sexual

<i>Alona</i> sp.	Cladocera	Arthropoda	Branchiopoda	Cladocera	610	386	0.127225	Littoral	Scraper	Long	Passive	Assexual / Sexual
<i>Bosmina</i> cf. <i>longirostris</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	415	330	0.565	Pelagic	Filtration	Long	Passive	Assexual / Sexual
<i>Bosmina</i> <i>hagmanni</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	450	350	0.701811	Pelagic	Filtration	Long	Passive	Assexual / Sexual
<i>Bosmina</i> sp.	Cladocera	Arthropoda	Branchiopoda	Cladocera	350	300	0.35786	Pelagic	Filtration	Long	Passive	Assexual / Sexual
<i>Bosminopsis</i> <i>deitersi</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	298	200	0.35786	Pelagic	Filtration	Long	Passive	Assexual / Sexual
<i>Ceriodaphnia</i> <i>cornuta</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	197	160	0.637434	Pelagic	Filtration	Long	Med. Swim.	Assexual / Sexual
<i>Ceriodaphnia</i> <i>paradoxa</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	530	280	0.80566	Pelagic	Filtration	Long	Med. Swim.	Assexual / Sexual
<i>Ceriodaphnia</i> <i>silvestrii</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	600	352	1	Pelagic	Filtration	Long	Med. Swim.	Assexual / Sexual
<i>Ceriodaphnia</i> sp.	Cladocera	Arthropoda	Branchiopoda	Cladocera	538	320	0.80566	Pelagic	Filtration	Long	Med. Swim.	Assexual / Sexual
<i>Coronatella</i> cf. <i>paulinae</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	380	250	0.3185	Littoral	Scraper	Long	Passive	Assexual / Sexual
<i>Coronatella</i> sp.	Cladocera	Arthropoda	Branchiopoda	Cladocera	380	250	0.154375	Littoral	Scraper	Long	Passive	Assexual / Sexual
<i>Daphnia</i> <i>gessneri</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	737	565	1.5	Pelagic	Filtration	Long	Med. Swim.	Assexual / Sexual
<i>Diaphanosoma</i> <i>brevireme</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	800	280	1.771647	Pelagic	Filtration	Long	Pause/Jump	Assexual / Sexual
<i>Diaphanosoma</i> cf. <i>spinulosum</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	860	338.2	2.008932	Pelagic	Filtration	Long	Pause/Jump	Assexual / Sexual
<i>Diaphanosoma</i> spp.	Cladocera	Arthropoda	Branchiopoda	Cladocera	759.4	265.8	1.618321	Pelagic	Filtration	Long	Pause/Jump	Assexual / Sexual
<i>Ilyocryptus</i> <i>spinifer</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	550	350	0.437938	Littoral	Filtration	Long	Passive	Assexual / Sexual
<i>Leydigia</i> sp.	Cladocera	Arthropoda	Branchiopoda	Cladocera	380	250	0.437938	Littoral	Scraper	Long	Passive	Assexual / Sexual
<i>Macrothrix</i> sp.	Cladocera	Arthropoda	Branchiopoda	Cladocera	280	230	0.285738	Littoral	Scraper	Long	Passive	Assexual / Sexual
<i>Macrothrix</i> <i>triserialis</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	280	230	0.437938	Littoral	Scraper	Long	Passive	Assexual / Sexual
<i>Moina</i> <i>minuta</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	600	410	0.263123	Pelagic	Filtration	Long	Passive	Assexual / Sexual
<i>Simocephalus</i> cf. <i>latirostris</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	1000	810	2.008932	Pelagic	Filtration	Long	Passive	Assexual / Sexual
<i>Simocephalus</i> <i>kervevei</i>	Cladocera	Arthropoda	Branchiopoda	Cladocera	950	755	2.008932	Pelagic	Filtration	Long	Passive	Assexual / Sexual
<b>COPEPODA</b>												
Copepodito Calanoida	Copepoda	Arthropoda	Maxillopoda	Calanoida	731	186	0.054312	Pelagic	Microphagous	Long	Rapid Swim.	Sexual
Copepodito Cyclopoida	Copepoda	Arthropoda	Maxillopoda	Cyclopoida	600	151	0.029335	Pelagic	Raptorial	Long	Rapid Swim.	Sexual
Copepodito Harpacticoida	Copepoda	Arthropoda	Maxillopoda	Harpacticoida	600	151	0.029335	Littoral	Raptorial	Long	Rapid Swim.	Sexual
Copépole Calanoida	Copepoda	Arthropoda	Maxillopoda	Calanoida	1340	327	4.5	Pelagic	Microphagous	Long	Rapid Swim.	Sexual
Copépole Cyclopoida	Copepoda	Arthropoda	Maxillopoda	Cyclopoida	800	287	1.367383	Pelagic	Raptorial	Long	Rapid Swim.	Sexual
Copépole Harpacticoida	Copepoda	Arthropoda	Maxillopoda	Harpacticoida	800	287	1.367383	Littoral	Raptorial	Long	Rapid Swim.	Sexual
Náuplio Calanoida	Copepoda	Arthropoda	Maxillopoda	Calanoida	285.6	110.3	0.054312	Pelagic	Microphagous	Long	Med. Swim.	Sexual
Náuplio Cyclopoida	Copepoda	Arthropoda	Maxillopoda	Cyclopoida	174.9	99.8	0.029335	Pelagic	Raptorial	Long	Med. Swim.	Sexual
Náuplio Harpacticoida	Copepoda	Arthropoda	Maxillopoda	Harpacticoida	174.9	99.8	0.029335	Littoral	Raptorial	Long	Med. Swim.	Sexual
<i>Notodiptomus</i> <i>cearensis</i>	Copepoda	Arthropoda	Maxillopoda	Calanoida	1340	327	4.5	Pelagic	Microphagous	Long	Rapid Swim.	Sexual
<i>Notodiptomus</i> <i>henseni</i>	Copepoda	Arthropoda	Maxillopoda	Calanoida	1340	327	4.5	Pelagic	Microphagous	Long	Rapid Swim.	Sexual



**Figura suplementar 1:** Dendrograma obtido a partir de matriz de distâncias euclidianas completas abrangendo os atributos comprimento, largura, biomassa, habitat, tipo de alimentação e estratégia de escape a predação.





Taxon of each group(A,B,C,D,E,F,G,H,I,J) well classified.

**Figura suplementar 2:** Árvore de classificação e regressão (CART) dos grupos funcionais obtidos na figura suplementar 1, onde (LIFE; S=short), (HABITAT; P=Pelágico), (FEEDING; F=filtration, R=raptorial, S=sucker, SC=scrapper), (PER=predatory escape response; LS=slow swimming, RS=rapid swimming).

**Tabela suplementar 2:** grupos funcionais obtidos na figura suplementar 1 e os erros de classificação apontados pelo CART (figura suplementar 2).

Zooplankton functional groups obtained by clustering	Code	Error (%)
Pelagic microphagous with low swimming	A	42,85
Pelagic sucker with passive defense	B	0
Pelagic filtration with medium swimming	C	100
Pelagic filtration with passive or pause and jump defense	D	0
Raptorial with medium swimming	E	100
Pelagic microhagous with passive defense	F	0
Littoral with passive defense	G	6,66
Littoral microphagous	H	0
Pelagic microphagous with rapid swimming	I	100
Pelagic raptorial	J	100

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## CONCLUSÃO GERAL

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O presente estudo corrobora a detecção de diferenças na abundância e distribuição dos grupos funcionais do zooplâncton em relação às variáveis ambientais. Foi fundamental a revisão dos atributos para o estabelecimento de grupos funcionais do zooplâncton em reservatórios tropicais, já que a bibliografia adotada para este tipo de estudo compreende, em sua maioria, ambientes localizados em altas latitudes.

Foi importante entender o padrão de distribuição dos atributos quantitativos e qualitativos para adequar os grupos funcionais. Entendemos que o tamanho corporal do zooplâncton em reservatórios tropicais não é um fator decisivo para o agrupamento, mas é uma variável que explica a distribuição das categorias dos atributos, bem como a associação com abundância e biomassa.

Ao associar os grupos obtidos com as variáveis ambientais, foi observada a grande influência da chuva sobre os grupos funcionais. Porém, na tentativa de incluir variáveis associadas a chuva, como turbidez e condutividade elétrica, foi detectada alta colinearidade entre as variáveis. O fato nos permitiu entender que a chuva exerce forte influência na turbidez e condutividade. E estas últimas representam variáveis importantes para o condicionamento do estado trófico dos reservatórios. Por estes motivos, entendemos que a chuva exerce influência no estado trófico dos reservatórios e, por consequência, afeta os grupos funcionais.

Apesar dos grupos serem suscetíveis às alterações do estado trófico, notou-se que, apesar das grandes variações de abundância, os grupos são resilientes na ampla maioria dos casos e não apresentaram densidade zero durante o período estudado.

Os dados a serem publicados neste trabalho serão úteis em novos estudos, onde será possível avaliar a dinâmica funcional das comunidades zooplanctônicas em reservatórios tropicais, como avaliar a dispersão e diversidade funcional local e regional.